Arbuscular Mycorrhizal Fungal Dynamics in Wetland Habitats: An Assessment of Seasonal and Soil Gradient Effects

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ABSTRACT

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Arbuscular mycorrhizal (AM) fungi are important soil microbes that influence plant nutrition, community composition, and species diversity. Recent research has indicated that AM fungi are abundant in wetland soils; however, the ecosystem dynamics of AM fungal colonization in wetlands is still not fully understood. This study set out to assess the soil factors affecting mycorrhizae in differing wetland habitats and to describe the seasonal and moisture gradient dynamics of the AM fungal colonization levels. The effect of season, gradient, and edaphic factors on colonization levels was investigated by sampling both soils and specific plant species in fen and marsh habitats. It was found that mycorrhizae were present in both habitats and that the colonization levels of AM fungi varied with gradient position and with month. Principle components analysis of edaphic factors revealed differences among the wetland sites and separated fen habitat from marsh habitat based on these factors. Further analysis indicated that site had a significant effect on all edaphic variables ($p<0.001$). Site did have an effect on %AM colonization; however, this was not significantly related to specific edaphic factors of the two wetland habitat types. Spatial analysis of AM fungi indicated that moisture gradient position did not have a strong effect on %AM colonization; however, the inundated areas had significantly less colonization levels ($p<0.05$) than other areas of the wetlands. Month did have a significant effect on %AM colonization at all sites with colonization

levels significantly higher at the beginning of the growing season (March/April) than at the end (September) ($p<0.05$). The seasonal trend found for colonization levels was not correlated to phosphorus or soil moisture, both of which are commonly found to regulate mycorrhizae in terrestrial ecosystems. Rather, it is speculated that the seasonal trend is largely controlled by phenology of wetland plants. These temporal results indicate the need for mycorrhizal investigations that are more thorough than the typical one time sampling approach. In summary, the variation in edaphic factors of the four wetlands were primarily controlled by site while variation in %AM colonization was mostly controlled by month and inundated soils and slightly controlled by plant species. AM fungi were found in all four wetlands and 100% of the plants species sampled were mycorrhizal to some extent (38% of the species had arbuscules). This suggests that AM fungi do have a functional role in wetlands and that their presence is not completely dependent on soil edaphic features of a specific wetland habitat. This study indicates the importance of both the time of the growing season and plant phenology for assessing the distribution and functional roles of mycorrhizal fungi in wetlands. Furthermore, this study not only provides insight into the dynamics of mycorrhizae in these ecosystems, but also has implications for wetland restoration and preservation.

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Chapter 1

Introduction

Wetlands are unique and complex ecosystems that provide numerous benefits for society and for nature. Wetlands play a key role in geochemical cycling, groundwater aquifer recharge, flood mitigation, and water quality improvement. Furthermore, they support highly diverse communities of plants and animals (Mitsch and Gosselink 1993, Kent 1994, Kadlec and Bevis 1990). The uniqueness and complexity of these ecosystems is due to their hydrology, soils, and vegetation. Typical characteristics of these three components in a wetland include the presence of water at the soil surface or within the root zone of plants, the presence of soils which either accumulate organic plant material or are high in clay (good water holding capacity), and the presence of hydrophytic vegetation. The differences in hydrology, soils, and vegetation (All influencing each other) determines the type of wetland found in a particular area. For instance, based on these three components, wetlands can range from freshwater to saltwater ecosystems and from having a canopy of trees to having a vegetative cover of sedges and grasses (Mitsch and Gosselink 1993). It is important to understand how the three above named components of a wetland influence each other in maintaining a healthy wetland ecosystem. In addition, it is important to understand the general functions of a wetland and the community of organisms that might be influencing these functions.

The complexity of wetlands is amplified by the numerous stresses induced in wetland ecosystems. In particular, plants in wetlands are subjected to stresses such as flooding, anoxia, reducing conditions, and great fluctuations in nutrient loading. Because of these stresses, hydrophytes are forced to develop adaptations to their environment.

Those that do not adapt well occur less frequently in wetland ecosystems. Based on the plants' probability of occurrence in a wetland, scientists have designed a classification system which categorizes plants into wetland indicator categories. These categories range from "upland" plants (rarely found in wetlands) to "obligate" (probability of occurrence in wetlands is 99% or more) (Resource Management Group, Inc. 1992). Those that occur more often than not in wetlands, the obligates, typically will have adaptations to the anoxic environment. These adaptations include pneumatophores, hypertrophied lenticels, buttressed trunks, and aerenchymatous tissue (Mitsch and Gosselink 1993, Hammer 1992).

Other factors, outside of plant structures, may enhance plant survival in these stressful environments. One possibility is arbuscular mycorrhizae (AM), which are now well known to enhance survival in stressful terrestrial environments (Allen 1991, Smith and Read 1997). Mycorrhizae are symbiotic relationships between a fungus and a plant in which the fungus actually penetrates the tissue of the root. They occur in 85% - 90% of all terrestrial plants (Jurgensen et al. 1997) and, of all mycorrhizae, arbuscular mycorrhizae (AM) are the most common type. These fungi are so named because of the arbuscules they form in the cortical cells of the plant root. Arbuscules are the site of nutrient exchange between the fungus and the plant in which the fungus gives the plant phosphorous (Smith and Read 1997). Mycorrhizae can enhance plant survival in terrestrial ecosystems by increasing photosynthetic rates and biomass production, increasing nutrient uptake, enhancing resistance to pathogens, alleviating drought stress, and stabilizing soil particle aggregates (Smith and Read 1997, Brown and Bledsoe 1996, Miller and Jastrow 1992, Pfleger and Linderman 1994, Brundrett 1991).

Historically, research on mycorrhizae in wetlands has been limited. Thirty years ago scientists assumed that mycorrhizal fungi did not colonize hydrophytic vegetation (Ragupathy and Mahadevan 1990). Now, not only is it well known that these AM fungi do colonize hydrophytic vegetation, but it also has been found that AM fungi are a significant component of wetland ecosystems (Ragupathy and Mahadevan 1990, Stenlund and Charvat 1994, Turner et al. 2000). The distribution and ecological role of mycorrhizae in these wetland ecosystems is, at this time, poorly understood. In recent studies, researchers have considered either the role of phosphorous levels or soil moisture to explain the regulation of mycorrhizal fungal colonization levels in wetlands (Wigand and Stevenson 1997, Cantelmo and Ehrenfeld 1999, Miller and Bever 1999, Thormann et al. 1999, Stevens and Peterson 1996). A more comprehensive and possibly enlightening study would consider both the phosphorous and the soil saturation levels along with other environmental factors as regulators of mycorrhizae in wetlands.

Certain environmental factors may be important regulators of mycorrhizae in only one type of wetland or in a particular season of the year; therefore, it is important to compare and contrast mycorrhizal associations in different wetlands and in different seasons. Although research on mycorrhizae has been conducted in several different types of wetland ranging from the Carolina bays (Miller 2000) to the prairie potholes in North Dakota (Wetzel and van der Valk 1996), these studies have not compared the occurrence of mycorrhizae in contrasting types of wetlands. Such a comparison would provide insight into how similar variables might regulate the mycorrhizal symbiosis in different habitats. Another important aspect of wetlands is the seasonal variations in soil moisture and nutrient levels. Wetzel and van der Valk (1996) have suggested that these seasonal

variations could have a substantial influence on the extent of the mycorrhizal fungal colonization in wetland plants; therefore, they advise the assessment of seasonal variations in AM fungal colonization levels.

Research Objectives

More often than not, the status of a wetland is determined by the health and biological diversity of the plant community present as well as the physical and chemical factors that affect this community. Unfortunately, little attention is given to the other organisms and their functional roles in the wetlands, especially the microorganisms and their important roles in soil processes and nutrient cycling (Cooke and Lefor 1998; Schneble 1997). The health and stability of the plant soil system in habitats largely depends on the microorganisms in the rhizosphere, which includes the roles of mycorrhizae (Bethlenfalvay and Linderman 1992). AM fungal colonization levels are known to vary temporally and spatially in wetlands, yet little is understood about which biotic or abiotic factors are the main controls for this variation. Understanding the relationships between mycorrhizal fungal colonization and the environmental gradients within a wetland will only help the success of restoration projects throughout Ohio.

In this study, I conducted a seasonal study on the arbuscular mycorrhizal (AM) dynamics in two types of wetland habitats, fen and marsh, found in Greene County, Ohio. Characteristics of the soil, plant community, and mycorrhizae found in these two habitats were analyzed. The overall objective of this research was to study the effects of spatial and temporal variation on mycorrhizal colonization levels in two wetland ecosystems in order to thoroughly assess the significance and distribution of AM fungi in wetlands.

The temporal variation was assessed by surveying mycorrhizal colonization levels throughout the entire growing season, while the spatial variation was assessed by sampling along a moisture gradient in each wetland site. Information from this research provided further understanding of the role of mycorrhizal fungi in wetlands in addition to broadening our understanding of the basic ecology of mycorrhizae. This research revealed important data that can be applied towards developing better restoration techniques to reestablish fully functional wetland ecosystems.

The following objectives and hypotheses are addressed in this thesis:

Objective 1: To determine the AM status of wetland plants and to determine how AM colonization levels vary in response to spatial and temporal dynamics within fen and marsh habitats. These dynamics include both abiotic factors (edaphic characteristics) and biotic factors (plant community).

Hypothesis 1: Marsh habitats will have lower colonization levels compared to fen habitats.

Hypothesis 1A: Marsh habitats will have lower colonization levels since these wetland habitats have higher soil moisture.

Hypothesis 1B: Marsh habitats will have lower colonization levels since these wetland habitats have higher available P.

Hypothesis 1C: Marsh habitats will have lower colonization levels since these wetland habitats have completely inundated soils.

Hypothesis 2: Colonization levels of AM fungi in marsh habitats will vary seasonally while the colonization levels in fen habitats will remain constant.

Hypothesis 2A: Habitats with periodic drawdowns, as in marsh habitats, will show periodic change in colonization levels.

Hypothesis 2B: Habitats with soils that remain saturated year round, as in fen habitats, will show consistent colonization levels.

Hypothesis 3: AM colonization levels will be related to changes in soil nutrient and moisture availability across a spatial gradient.

Hypothesis 3A: AM colonization will be higher where availability of phosphorus is lower.

Hypothesis 3B: AM colonization will be lower where soil moisture is higher.

Hypothesis 3C: AM colonization will be lower where water levels are higher.

Hypothesis 4: Changes in AM colonization levels will be related to changes in the wetland temporal gradients.

Hypothesis 4A: AM colonization will be higher at times that the wetlands are drier.

Hypothesis 4B: AM colonization by arbuscules will decrease throughout the growing season.

Hypothesis 5: Plants found in the wetter parts of the wetlands will have lower colonization levels than plants in the drier soils.

Hypothesis 5A: Facultative obligate and obligate plants and members of Cyperaceae and Juncaceae will have lower colonization levels.

Objective 2: To determine the relative importance of different environmental factors in distinguishing marsh habitats from fen habitats in Ohio.

Hypothesis 1: Fens will be distinguished by their low nutrient availability and their high organic matter content.

Hypothesis 2: Marshes will be distinguished by their high nutrient availability and their inundated soils.

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Chapter 2

Literature Review

Introduction

Wetland ecosystems are unique habitats that support highly diverse communities of plants and offer numerous functional roles for the environment. Wetlands act as sources, sinks, and transformers of nutrients, and therefore play a large role in ecosystem nutrient cycling. Other functions of wetlands include providing water purification, groundwater recharge, valuable wildlife habitat, and floodwater control. Unfortunately, over 50% of the United States' wetlands and 90% of wetlands in Ohio have been destroyed and lost; thus, it is of utmost importance that the remaining wetlands are well described and understood (Mitsch and Gosselink 1993, Tiner 1998). Restoration efforts are currently taking place that need more background studies on the driving forces of wetland ecosystems and the characteristics of a healthy wetland habitat. For example, restoration success could increase with knowledge of how the biotic and abiotic factors of a wetland interact and influence each other in maintaining a fully functional and natural wetland.

More often than not, the status of a wetland is determined by the health and biological diversity of the plant community present as well as the physical and chemical factors that affect this community. Unfortunately, little attention is given to the other organisms and their functional roles in the wetlands, especially the microorganisms and their important roles in soil processes and nutrient cycling (Cooke and Lefor 1998, Schneble 1997). The health and stability of any plant-soil ecosystem largely depends on a wide diversity of soil microbes including mycorrhizae (Bethlenfalvay and Lindermann

1992). This chapter will examine the characteristics of wetlands, will describe the differences between fens and marshes (the most common wetland habitats in the Midwest), will examine the role of mycorrhizae in wetlands, and will examine current wetland restoration practices.

Characterizing Wetlands

Over the years, many different definitions for describing a wetland have been developed, none of which has fully suited researchers, managers, and delineators. The reason for the complexity in developing an agreed upon wetland definition is due to the ambiguity of the parameters designated as important in defining a wetland. These parameters include the presence of water at or near the soil surface, the presence of hydrophytic vegetation, and the presence of hydric soils which either accumulate organic plant material or are high in clay (good water holding capacity) (Mitsch and Gosselink 1993, Brady and Weil 2000). Compounding the situation is the issue of individual organizations having different perspectives on how important each of these parameters are and the usefulness of a wetland to their organization (Kent 1994). Furthermore, because these ecosystems are extremely diverse and are typically found as a "boundary" between aquatic ecosystems and terrestrial ecosystems, there is a lot of confusion as to where a wetland begins and where it ends.

The current definition used for delineating wetlands in the United States was established in 1987 by the U.S. Army Corps of Engineers and the Environmental Protection Agency and is as follows:

> The term wetland means those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under

> normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions.

This definition is used to enforce the Clean Water Act of 1977 and currently regulates the dredging and filling of wetlands (Brady and Weil 2000). With the Clean Water Act and the wetland definition in place, preservation of wetlands has become a major issue and the destruction of wetland habitats has, at least, been slowed. What this definition lacks is answers to questions regarding the exact locations of the wetland boundaries. The wetter end of a wetland is easily definable and recognized as where the water is too deep to support rooted, emergent vegetation. What is not so clear is the drier end beyond which upland species thrive and the biotic communities are no longer driven by the presence of saturated soils. Straightening out this vagueness can be accomplished by wetland delineations which are necessary for wetland regulation and preservation by the government. In the delineation manual put out by the U.S. Corps of Engineer (1987), a wetland delineator identifies wetland boundaries based on three primary wetland components: wetland hydrology, hydric soils, and hydrophytic vegetation.

Most essential to the maintenance of wetland structure and function is the hydrologic regime of the wetland. The hydrology of wetlands is balanced by the inflows (groundwater, surface run-off, tides, and/or precipitation) and the outflows (surface and subsurface flows and evapotranspiration). Based on the balance of these, the hydrology can range from the wetland being permanently to periodically flooded or having saturated soils within the root zone. Wetlands can be flooded on a daily basis, seasonal basis, or randomly fluctuating basis. Some wetlands never flood but remain saturated for the entire year. What is most important is not if the site is flooded or saturated, but for how long the site has anaerobic conditions due to the water levels, especially during the

growing season (Brady and Weil 2000, Mitsch and Gosselink 1993, and Tammi 1994). It has been determined that the development of anaerobic, reduced conditions could take at least 14 to 28 days of inundation or saturation of the wetland soils (Megonigal et al. 1993). Using hydrology parameters to delineate wetlands becomes complex not only because of the need for a time period of inundation, but also because hydrology often varies annually and seasonally. Therefore, a one time glance at hydrology can give spurious results (Richardson and Vepraskas 2001).

The specific hydrology of a wetland greatly influences both biotic and abiotic factors in that wetland. Soil formation, decomposition, nutrient cycling, plant composition, and soil microbial communities are all affected by the hydrologic regime (Anderson and Perry 1996, Mitsch and Gosselink 1993). The physical and chemical nature of soils and water in wetlands, along with the boundaries of the wetland habitat, are affected by hydrology. For example, Miller (2000) found pH to be significantly correlated with water depth in Carolina Bay wetlands with higher water levels leading to higher pH levels. Such changes in pH due to hydrology can influence soil and water nutrient availability, plant community composition, and the solubility of toxic substances (Richardson and Vepraskas 2001, Brady and Weil 2000). Furthermore, plant species distribution, productivity, and biomass are controlled by the physiological tolerance of plants to different water levels (Bridgham et al. 1996). These plant community changes then will influence the fauna that utilize the wetland for various activities. Therefore, hydrology can affect all parameters and food web levels within a functional wetland ecosystem.

Due to the large variation in the hydrology of different wetlands, the presence of

hydric soils is probably the better indicator for delineating wetlands. Wetland soils are classified as hydric soils. A hydric soil is defined by the *Federal Register* as: "A soil that formed under conditions of saturation, flooding, or ponding long enough during the growing season to develop anaerobic conditions in the upper part." These soils are also developed by undergoing reduced conditions for a large period of time. The amount of time needed to develop hydric soils is highly dependent on other factors such as the amount and the frequency of flooding in the wetland. All of this must occur during the growing season, which is defined as the part of the year during which the moisture conditions and temperature of the soil permit microbial activity (Keddy 2000, Richardson and Vepraskas 2001).

Wetland soils are altered in very distinct ways by the chemical reactions that occur when water moves into, through, and from the soil. These alterations are often visible and are used as hydric soil indicators that help a wetland delineator appropriately identify hydric soils. These indicators are often formed due to reduced and anoxic conditions of flooded soils and include mottling, gleying, oxidized root zones, redox depletions, and organic matter buildup (Brady and Weil 2000, Mitsch and Gosselink 1993). The extent to which the indicators are developed depend on the frequency, duration, and intensity of flood events in which the soil at the root zone is saturated or inundated. With extensive flooding, oxygen is severely depleted and can be completely unavailable to the belowground soil organisms as well as to the plants, thus having significant effects on the structure and function of wetlands (Tammi 1994).

There are two main types of hydric soils: mineral and organic (U.S. Department of Agriculture Soil Conservation 1991). Compared to organic soils, mineral soils contain

lower organic matter (only 20-35%) and are formed where the soil is poorly drained. Organic soils have at least 46cm of organic matter made up of plant fibers and other decomposed material in the upper portion of the soil profile. Which soil is most dominant in one particular area is first a function of parent material and the change in this material over time due to biotic and abiotic factors (Keddy 2000). Second, it is a function of the chemical and physical changes due to the hydrology of the area. In anoxic environments, where decomposition is greatly reduced, organic matter can build up enough to form very thick layers of organic soil, especially if the wetlands are very productive. These soils are often termed peat, peaty-muck, mucky-peat, and muck based on the amount of decomposition that has taken place (Tammi 1994, Mitsch and Gosselink 1993). These organic soils have very low bulk density, high water holding capacity, high nutrient content (although largely unavailable), high cation exchange capacity (CEC), and high organic matter content. The temperature and the moisture levels of wetland soils affect accumulation and decomposition of organic matter - the colder and moister soils typically having lower rates of decomposition, thus organic matter accumulation is enhanced. Organic matter accumulation can further be influenced by nutrients and toxins that affect the ability of organisms to survive and grow in and upon the soils (Mitsch and Gosselink 1993, Brady and Weil 2000, Richardson and Vepraskas 2001). On the other hand, mineral soils are soils high in cations such as Mg, Ca, Fe, and Al and are often supplied with excess cations from groundwater discharges into wetlands. Due to the large cation content, pH levels are usually above neutral and cation exchange capacity is high (Richardson and Vepraskas 2001). Wetlands with these soils are usually nitrogen limited while wetlands with organic soils are mainly phosphorus limited (although they

could also be nitrogen limited) (Bedford et al. 1999).

Wetlands are not restricted to one of these two types of soils. In fact, it is possible to find soils that contain both mineral and organic soils. Often times, a wetland can have a mineral base and, due to flooded conditions, an organic layer of muck or peat. The ramification of such situations is that the soil characteristics will be very heterogeneous and will influence wetland processes in a variety of ways. The amount of organic matter and/or mineral that does accumulate will have large influences on plant productivity, fauna habitat quality, and nutrient availability (Mitsch and Gosselink 1993, Richardson and Vepraskas 2001).

One very important plant nutrient, phosphorus, can be expected to vary greatly according to the conditions of the soil since the cycling of this nutrient remains largely within sediment and living organisms. Phosphorus (P) is important to plants for energy storage and structural integrity and is mostly found in nucleic acids and phospholipids. Soil P can be found as organic P, fixed mineral P, and/or orthophosphate P (Brady and Weil 2000). In wetlands rich in cations, such as Ca and Mg, ortho-P becomes fixed mineral P (unavailable) as it binds to these cations to form phosphate complexes (Bridgham et al 1996, Richardson and Marshall 1986). Organic P is also unavailable when bound to organic compounds found in partially decomposed plant tissue. This fixed mineral P and organic P make up 80-90% of P in wetlands. The rest of the P in wetlands is tied up in living biomass (Richardson and Vepraskas 2001, Brady and Weil 2000).

Long term storage of P in wetlands is dependent on slow decomposition, low mineralization rates, and inorganic P removal from the water by soil adsorption (Patrick

and Khalid 1974). Wetlands can actually be a huge source of P; however, most of this P is relatively unavailable to plants due to processes stated above. The concentration of P in the wetland soil solution and the sorption power of the soils play a huge role in the availability of P to the plants and the amount of P stored in the wetland. For example, Patrick and Khalid (1974) found that anaerobic soils (typical in wetlands) can release additional phosphate to the soil solution having low levels of available P and, when the soil solution has high levels of available P, wetland soils can sorb more phosphate from it. The transformation of fixed mineral P to available, soluble P is largely controlled by waterlogging, soil and water pH, organic matter content, and clay content. When soils become greatly waterlogged and reduced, P becomes substantially more soluble and available to plants due to both the solubilization of iron phosphates and release from soil microbes killed under anaerobic conditions (Richardson and Vepraskas 2001, Willet 1989, Brady and Weil 2000, Shahandeh et al. 1994). The level of P in hydric soils, along with other nutrients, has great effects on many wetland ecosystem processes and is, therefore, important to consider and understand in each wetland habitat studied.

Together, the hydric soil composition and hydrologic regime of a wetland influences plant community dynamics - the third parameter for wetland delineations. Wetland plants are called hydrophytes and are plants that grow in water or on a substrate that is deficient of oxygen due to excessive flooding or saturation. They are not restricted to areas that are constantly devoid of oxygen, but can also be found in and adapted to wetlands where there is annual or seasonal variation in hydrology (Tiner 1998). The lack of oxygen in wetland soils is the factor that limits the survival of most plants in wetlands. The plants that are able to survive and thrive in waterlogged soils posses anatomical and

physiological adaptations to the limited oxygen availability (Tammi 1994). In general, plants require the presence of oxygen around their roots for the uptake of nutrients and water and for use in respiration. Without this oxygen, necessary cellular processes cannot occur and the plant will eventually die. Anoxia of soils is also associated with the accumulation of potential phytotoxins produced by anaerobic microorganisms in soil and can be associated with the deficiency of essential nutrients such as nitrate (Crawford 1989, Armstrong 1978). Those plants that do not adapt well occur less frequently in wetland ecosystems. Based on the plant's probability of occurrence in a wetland, scientists have designed a classification system which categorizes plants into wetland indicator categories. These categories range from "upland" plants (rarely found in wetlands) to "obligate" plants (probability of occurrence in wetlands is 99% or more) (Resource Management Group, Inc. 1992).

Hydrophytic plants find ways to tolerate or to avoid the stresses of anaerobic and reduced substrates. Tolerators withstand low oxygen concentrations typically by modifying their metabolism. These plants often cannot withstand waterlogged conditions for excessive periods of time. On the other hand, the avoiders have actually developed an anatomical or physiological adaptation to the environment in which oxygen is made available to the roots in some way. Some of these adaptations include pnuematophores, hypertrophied lenticels, and buttressed trunks. The main plant adaptation used to avoid the stress of flooded soils is to develop air spaces within the root that allows the transport of oxygen from the leaves, through the stem, to the roots. These air spaces are called lacunae and the system of the spaces are referred to as aerenchyma (Hammer 1992, Mitsch and Gosselink 1993, Keddy 2000).

Aerenchymatous tissue allows the passive diffusion of oxygen from leaves and stems to roots and rhizomes and can also allow bulk flow of air if an internal pressure gradient exists. The air cells of aerenchyma that allow gaseous diffusion are formed by either cell breakdown or by cell separation during maturation, and this change is initiated by the concentration of ethylene in hypoxic tissues. These cellular changes in the plant lead to a honeycomb structure of air spaces through which oxygen can easily diffuse (Keddy 2000, Crawford 1989). The amount of aerenchyma developed in flood tolerant plants will increase with increased flooding and decreased availability of oxygen (Brix 1989). The amount of pore space in flood tolerant species can exceed 60% of the plant body while porosity of normal upland plants is usually only 2-7% (Mitsch and Gosselink 1993). It is this large amount of root porosity in hydrophytic plants that maintains adequate oxygen levels to prevent mitochondrial degradation should oxygen be completely unavailable (Levitt 1980).

Aerenchyma development and oxygen diffusion to roots has ramifications beyond helping wetland plants tolerate stress. It has been shown in numerous cases that when oxygen arrives in the root, some of it can leak out into the anaerobic soils and can oxygenate the rhizosphere (area extending out to 2mm from the root) of wetland plants. This diffusion of oxygen leads to oxidation of the soil immediately surrounding the root and is visually evident by an orange halo of oxidized iron around the roots (Moore et al 1994, Wigand and Stevenson 1997, Tiner 1998). This oxidation of the rhizosphere is actually essential for the plant to avoid the uptake of toxic soil chemicals (Mitsch and Gosselink 1993). Gries et al. (1990) found that a well developed reed stand released oxygen from their roots at a rate of up to 65-129mg O_2 m^{-2} h^{-1}. Iron precipitation of the

rhizosphere (expected when soil is oxidized) of these roots in the spring was very low when little oxygen was being transported to the anoxic roots, but increased to the above stated level when above ground biomass developed. In addition to this seasonal effect on oxygen diffusion from the roots, there is also a plant species effect in the amount of oxygen released into the rhizosphere. Steinberg and Coonrod (1994) found cattails and alpine rush to have a well developed aerobic root zone while canary grass showed less of an aerobic root zone. Furthermore, there is a plant anatomical effect in that proximal roots are better supplied by oxygen, and therefore can release more oxygen, then distal roots of a hydrophytic plant (Keeley 1980).

Many researchers believe this loss of oxygen to the rhizosphere is significant in that it has large effects on the microbes, on interactions between wetland plants, and on soil chemistry in the area. Callaway and King (1996), in studying the effects of temperature on oxygen release from *Typha* roots, found that *Typha* plants can help the growth of other wetland plants by oxygenating the immediate soil environment. This finding has also been supported by research done by Bertness and Hacker (1994) who suggest that positive associations, such as enhancing oxygen conditions through an oxidized rhizosphere, is very common among marsh plants in times of physical stress. As for the effect of rhizosphere oxygenation on soil chemistry, the most well understood effect is on phosphorus availability. Oxygen release into the rhizosphere can contribute to phosphate limitation and potentially can be a mechanism for sequestering P in wetlands (Moore et al 1994, Wigand and Stevenson 1997). On the other hand, other researchers believe that the radial loss of oxygen by the roots is so little that it is virtually unimportant to soil processes (Bedford et al. 1991, Howes and Teal 1994). Bedford et al.

(1991) found that little oxygen from the root was leftover after taking into account root respiration, oxidation of soil minerals, and microbial decomposition of plant materials. Whether a lot or a little oxygen is released into the soil, the oxidation of the rhizosphere, especially to decrease the amount of reduced phytotoxins, appears to be at least a secondary benefit to plant adaptations in anaerobic soils.

Fen vs. Marsh Wetland Habitats

Wetlands can be and have been classified based on soil type, geographical location, hydrology, organic matter accumulation, and nutrient content (Keddy 2000, Mitsch and Gosselink 1993, Brady and Weil 2000). The differences in hydrology, soils, and vegetation can determine the type of wetland found in a particular area. For instance, based on these three components, wetlands can range from freshwater to saltwater ecosystems and from having a canopy of trees to having a vegetative cover of sedges and grasses (Mitsch and Gosselink 1993). Two of the most common wetlands in Ohio are fens and marshes. These two areas can have anywhere from subtle to stark differences in soil types and vegetative communities based largely on the substrate and the source of water to the wetland. These two wetland habitats were chosen for this research to encompass all of the variables in question (and explained later) such as differences in phosphorus levels, soil organic content, seasonality, and moisture levels.

The general characteristics of fens include low available nutrient levels, a water table near the soil surface, and high organic matter accumulation. Fens are groundwater fed and, therefore, the soils can be very rich in minerals (Mitsch and Gosselink 1993). In Ohio, where the parent rock is limestone, the calcium content of the groundwater is high

producing alkaline conditions in the fens (Dykyjova and Ulehlova 1998). Furthermore, because the fens of Ohio are mineral rich, phosphorus is largely unavailable to plants as it is tied up in calcium and magnesium phosphate complexes (Richardson and Vepraskas 2001). The soils of a fen are saturated for much of the year and the saturation never sinks below the plant roots. This year-round soil saturation is largely due to the groundwater supply and to the water table near the soil surface. Fens are peatlands and accumulate organic matter in the forms of peat and muck due to the low rate of decomposition as a result of these saturated soils (Keddy 2000). As peat accumulates, the soil saturation will be further enhanced by the high organic matter content which increases infiltration rate and water holding capacity of the soils (Richardson and Vepraskas 2001, Brady and Weil 2000). Furthermore, as the peat accumulates, soil available P will decline further as phosphorus is tied up by the organic matter - making the fen habitat largely P limited (Bedford et al. 1999).

The vegetation in fens is highly diverse and, in the Midwest, is typically dominated by grasses and sedges (Mitsch and Gosselink 1993, Richardson and Marshall 1986). Species distribution, productivity, and live biomass in fens are controlled by the tolerance of plants to a range of soil saturation conditions (Bridgham et al. 1996, Slock et al. 1980). Primary productivity of fens is generally low, especially when compared to marshes (Maltby 1990) because they are nutrient limited. The plant community dynamics of fens can be greatly influenced by large deposits of marl (CaCO3) on the soil surface which will select for plants that can tolerate these conditions. The marl deposit areas are commonly referred to as marl flats and support a plant community of specialists (and rare species) which can outcompete the generalists in these areas (Mitsch and

Gosselink 1993, Bridgham et al. 1996). Another important physical characteristic of fens affecting plant comminutes is the formation of hummocks. Hummocks promote the cohabitation of highly flood tolerant plant species living in the hollows with less flood tolerant species living on the hummocks (Cornwell et al. in review). Since fens have so many unique physical characteristics, the plant communities make up a mosaic of irregularities and are highly diverse due to the special conditions of the soil, the low productivity of the habitat (which has been found in studies to promote higher species richness (Bridgham et al. 1996)), the geomorphology of the area, and the consistency in moisture conditions and in soil/water temperatures (Walbridge 1994, Slack et al. 1980, Bedford et al. 1999).

Fens are classified as either mound or hillslope fens. Mound fens are made when groundwater upwells at a break in the low permeable substrate covering the aquifer. An actual mound or several mounds will form in this area with the wetter regions of the fen being at the top of the mound (Amon et al., in review). A hillslope fen forms when the break in the low permeable substrate occurs along a slope so that ground water is forced to discharge on the slope. The resulting point of discharge on the slope results in a calcerous fen. Typically there are several springheads coming out all along this slope with no one main discharge area. Above where the groundwater is forced out into the top soil layer the soil is much drier and supports upland vegetation. Often times, but not always, the groundwater will end up flooding the bottom of the slope, especially if there is a barrier helping it to pool. At this point in the wetland muck generally forms instead of the peat which forms thick layers below the points of groundwater discharge on the slope (Richardson and Vepraskas 2001).

While fens are typically oligotrophic, biologically diverse, and have saturated soils, marshes can range from oligotrophic to eutrophic, from continually flooded conditions to infrequently flooded conditions, and from highly biologically diverse to a monoculture (Dykyjova and Ulehlova 1998). There are numerous kinds of marshes ranging from saltwater to freshwater. In the Midwest, marshes are typically in river flood zones or in depressions and can be fed by groundwater, precipitation, and/or run-off. The characteristics of a freshwater depressional marsh include high nutrient content, inundation of the soils, and seasonal fluctuations of nutrients and water levels. Marshes are typically rich in nutrients from runoff and flooding which causes release of P from the soil into the soil solution and standing water (Mitsch and Gosselink 1993). The soils in a marsh are hard to classify as one specific type since they can range from being mineral enriched clay soils to peat soils saturated with both minerals and nutrients (Keddy 2000). Equally as hard to define is the hydrology of marshes. Marshes portray a large spectrum of hydrological regime possibilities. The marshes typical in Ohio show seasonal fluctuations of water which includes a springtime flooding and a late summer drawdown. There are also seasonal effects on available phosphorous levels which depends upon the productivity of the wetland and the flooding frequency and intensity (Mitsch and Gosselink 1993).

Ohio marshes are not as diverse in their vegetation as fens and contain more tall reeds and broad leafed monocots. The dominant vegetation is herbaceous plants that are very well adapted to inundation (most common adaptation is aerenchymatous tissue). The plant community compositional changes are determined by the soil moisture gradient, topography, and extent of inundated soils in the wetland. For example, Nelsen

and Anderson (1983) studied the plant compositional changes along a moisture gradient starting in an upland prairie habitat and ending in an inundated marsh habitat. Along this gradient, certain species were more well distributed than others based on their response to topography and soil moisture. They found grass leaved goldenrod, a generalist in these habitats, to be abundant throughout the gradient while, on the other hand, *Carex stricta* had a very discontinuous distribution indicating it to be more of a specialist to topographical changes. The discontinuous distributions could be due to plant competition and can be, in turn, creating plant competition. A large amount of this competition occurs among marsh plants due to the cycles of flooding and drawdown. Furthermore, herbaceous plants that have large shoots and deep rhizomes (cattails and reeds) create intense competition with their neighbors that do not possess this large amount of biomass in their underground structures (Keddy 2000). In summary, the plant community existing in a marsh largely reflects the costs imposed by living in an extreme environment of periodic flooding, drought, disturbance, and competition.

The main differences that stand out between fens and marshes are their hydrology (including both amount of water present and frequency of excessive water conditions), their plant diversity levels, and their nutrient levels. Marshes, with a higher available P content, can be expected to have greater productivity and thus, potentially lower species richness (Zedler 2000). Furthermore, the plant diversity of marshes may be kept lower than fens because of the extreme conditions of flooding with intermittent periods of drought (Bedford et al. 1999, Mitsch and Gosselink 1993). Fens, on the other hand, have a very consistent hydrology, are typically never flooded (except possibly at the end of a sloped fen where water can accumulate), and maintain a constant soil temperature due to

the groundwater. Besides these consistent conditions promoting plant diversity, unique conditions of fen soils will also promote diversity by providing many micro-habitats (Keddy 2000, Mitsch and Gosselink 1993).

It is possible for the hydrology of both types of wetland habitats to be driven by groundwater, thus both habitats could have similar amounts of mineral deposition into their soils. This deposition will affect plant species presence and availability of nutrients for both types of wetlands (Richardson and Vepraskas 2001). However, because the hydrology of marshes typically includes flooding and of fens includes soil saturation, the two habitats will differ greatly and support different plant species and fauna. Therefore, these two wetland habitats are best compared and assessed by examining the effects of all three basic wetland components – hydrology, hydric soils, and wetland plant species.

Mycorrhizae in Wetlands

Wetlands ecosystems are driven by both soil biotic and soil abiotic factors. One very important biotic factor, and the one dominating the biomass and metabolic activity of many soils, is fungi. Currently, it is estimated that there are as many as 2500 species of fungi occupying a given soil volume and potentially more than one million different fungal species in soil yet to be discovered (Brady and Weil 2000). One very important group of fungi in almost all ecosystems is the mycorrhizal fungi. Mycorrhizal fungi have actually been around for a very long period of the Earth's history – ever since the terrestrial environments of the Earth were colonized by vascular plants at the Silurian-Devonian boundary (395mya) (Miller et al. 1999). Mycotrophy is considered the ancestral condition in vascular plants making it the rule, not the exception, in many

ecosystems (Taylor et al. 1995).

Mycorrhizae are symbiotic relationships between a fungus and a plant in which the fungus penetrates the tissue of the root and enhances plant nutrition and growth while the plant supplies carbon to the fungus (Allen 1991). They occur in 85% - 90% of all terrestrial plants (Jurgensen et al. 1997) and, of all types of mycorrhizae, arbuscular mycorrhizae (AM) are the most common. AM fungi are classified as Zygomycetes and are further classified according to the plant-fungal association. Often AM species are identified and classified based on the species spore morphology. So far 150 different species of AM fungi have been identified (Morton 1988). The AM fungus is the initiator of the association with a plant as it penetrates the host root and establishes a network of hyphae within the root and externally throughout the soil system (Allen 1991, Brundrett 1991, Chanway et al. 1991, Friese and Allen 1991; Friese et al. 1997).

The AM fungi are so named because of the arbuscules they form in the cortical cells of the plant root. Arbuscules are the site of nutrient exchange between the fungus and the plant in which the fungus gives the plant phosphorous. Therefore, the arbuscules are considered the functional structures of arbuscular mycorrhizae. When arbuscules are absent from the colonized root system, scientists question the functional nature of the mycorrhizal relationship. It has been suggested that without the arbuscules, the AM fungi may actually be parasitic (they can still receive photosynthates from the plant via internal hyphae) (Smith and Read 1997; Allen, Allen, and Friese 1989; Anderson et al. 1984).

Important considerations in the formation of mycorrhizal colonization is the availability of fungal propagules in soil. Formation of AM fungi is dependent upon the

availability of inoculum which can be spores, colonized root fragments, and/or hyphae. Spores have relatively thick walls that are resistant to many environmental factors and could be the main mechanism in which mycorrhizal fungi disperse, although the extent of this has yet to be realized. The distribution of spores is affected by animal activity, water and wind dispersal, and microbial activity. The germination of spores is dependent on several environmental factors which can cause rather slow and variable germination rates. Therefore, spores may not be important in initial colonization of plants since they cannot be depended upon by the fungus or by the plant (Smith and Read 1997). Furthermore, spore productivity has been found to have no correlation with root colonization in certain habitats (Hetrick and Bloom 1983). The most probable means in which plants become newly colonized is through the mycelial network in the soil and extension of hyphae from colonized root fragments. These too, however, are affected by many factors especially including soil disturbance (Friese et al. 1997). Practices such as tilling and mining are very disruptive for the AM fungal hyphal network and could greatly lower the inoculation capabilities of AM fungi in any ecosystem (Smith and Read 1997, Jurgensen et al. 1997).

The significance of arbuscular mycorrhizae in terrestrial habitats has been well documented and studied. It has been found that mycorrhizal fungal colonization levels are negatively correlated with plant available phosphorous; therefore, it has been concluded that these fungi are most important to the plant when available phosphorous levels are limiting to the plant (Fitter 1988, Slankis 1974, Amigee et al. 1993, Hayman 1983, Koide 1993). When this occurs, the fungi help the plants to obtain more phosphorous than they could on their own by acting as extensions of the plant root

systems. These extensions (external hyphae) increase plant nutrient absorbance efficiency by providing up to 10X as much absorptive surface area as the plant root systems could alone and delivering up to 80% of the plants' P requirement and 25% of the plants' N requirement (Brady and Weil 2000, Marshner and Dell 1994). This assistance by the fungi not only affects plant nutrition and growth, but will also enhance survival by increasing photosynthetic rates and biomass production, enhancing resistance to pathogens, enhancing nodulation and N fixation by legumes, alleviating drought stress, and stabilizing soil particle aggregates (Smith and Read 1997; Brown and Bledsoe 1996; Miller and Jastrow 1992; Pfleger and Linderman 1994). Furthermore, the association has been known to have effects on plant competition within a habitat and ultimately on biological diversity of a habitat (Virant-Kim 1995; Hartnett and Wilson 1999, Allen 1991).

The AM fungal association has been known to be more important for plants (and perhaps more mutualistic) at different times of the year. The seasonal variations of the association has been noted by many researchers and has been designated as dependent on temporal variations of abiotic factors, on phenological characteristics of the roots, and/or on phenological turnover in plants (Abbott and Robson 1991, Dhillion et al. 1988). The abiotic factors most well known to negatively affect colonization levels include high soil moisture, low temperatures, and high available phosphorus; thus in spring, when these conditions are dominant, colonization levels can be very low (Demars and Boerner 1995, Smith and Bowen 1979, Anderson et al. 1984). Within a grassland ecosystem, Bentivenga and Hetrick (1992) found peaks in colonization levels of warm and cool season grasses highly correlated with temperatures favoring growth of the two types of

grasses. In this case, the changes in colonization levels were closely tied to metabolism of the plant regardless of plant phenology. Sporulation rates of AM fungi associated with these two types of grasses also changed in time with highest sporulation around warm season grasses occurring in October and highest sporulation around cool season grasses occurring in June. Typically, in temperate ecosystems, colonization levels are found highest in late spring when new root growth is maximum and lowest in late summer and fall when plants start to senesce (Stenlund and Charvat 1994, Brundrett 1991). In upland phosphorus limited ecosystems, most of the seasonal variation in AM colonization levels can be attributed to temporal variation in phosphorus availability and variation in plant requirement for phosphorus during its life cycle . This is one reason why arbuscular numbers are found to vary, with highest abundance in spring when the fungi most likely affect nutrient uptake (Smith and Read 1997). Overall, mycorrhizae have been found to be most important during seedling establishment (Grime et al. 1987), during flowering (Fitter 1989), and during periods of rapid growth (Dhillion and Anderson 1993).

Since the health and stability of the plant soil system in upland habitats largely depends on the roles of mycorrhizae, it is quite possible that mycorrhizae are just as important in wetland habitats. Historically, research on mycorrhizae in wetlands has been limited. Thirty years ago scientists assumed that mycorrhizal fungi did not colonize hydrophytic vegetation (Ragupathy et al. 1990). Now, not only is it well known that these fungi do colonize hydrophytic vegetation, but it also has been found that mycorrhizal fungi are a significant component of wetland ecosystems (Ragupathy et al. 1990; Stenlund and Charvat 1994; Turner and Friese 1998). The distribution and ecological role of mycorrhizas in these wetland ecosystems is, at this time, poorly

understood. In recent studies, researchers have considered either the role of phosphorous levels or soil saturation depth to explain the regulation of mycorrhizal fungal colonization levels in wetlands (Wigand and Stevenson 1997; Cantelmo and Ehrenfeld 1999; Miller and Bever 1999; Thormann et al. 1999; Stevens and Peterson 1995). The appearance of mycorrhizal associations in waterlogged habitats may also be dependent on the types of plant species or even AM fungal species present in the system, but, since wetlands are only recently being examined for mycorrhizae, a lot of questions remain unanswered and definite conclusions have not been drawn (Smith and Read 1997, Miller and Bever 1999).

Perhaps most important in studying mycorrhizae in wetlands is realizing and considering that these symbiotic fungi require oxygen and may not be able to tolerate saturated or inundated soils typical of wetlands. Flooding in wetlands reduces the availability of oxygen in the soil which is usually further reduced by other aerobic microorganisms (Mitsch and Gosselink 1993). Because AM fungi are aerobic organisms, this low oxygen concentration in waterlogged soils could prevent sporulation, germination, and/or even survival of the fungi (Miller and Bever 1999; Miller 2000; Turner and Friese 1998; Cantelmo and Ehrenfeld 1999). Limitation of AM fungi in these soils could also occur due to the accumulation of toxic byproducts produced in anaerobic soils (Mosse et al. 1981). Without adequate oxygen levels (below 0.4% oxygen tension), LeTacon et al. (1983) have shown that spores of *Glomus mosseae* (Nicol. and Gerd.) Gerdemann and Trappe fail to germinate unless first exposed to air. Several AM fungal wetland studies indeed indicate that lower AM fungal colonization levels are found in wetter (less aerated) soils of a wetland gradient. This has been exemplified in tidal saltmarshes (Brown and Bledsoe 1996; van Duin et al. 1989), hummock dominated

wetlands (Cantelmo and Ehrenfeld 1999), fens (Wetzel and van der Valk 1996), freshwater wetlands (Rickerl et al. 1994), and many other wetland types (Keeley 1980; Wolters 1999; Lodge 1989). In many situations it has been found that flooding rather than phosphorus levels control the AM mutualism in wetlands (Miller 2000), and it is believed that as oxygen becomes limiting, there is a shift from a mutualistic association to a more parasitic one or a shift completely away from any association (Brown and Bledsoe 1996, Keeley 1980, Clayton and Bayarj 1984). Other factors that could limit the presence of the AM fungi in waterlogged soils include parasites (Jeffries 1995), lack of propagules (Anderson et al. 1984), or flooding conditions increasing specific root length lessening the plant's need for the fungus (Miller 2000, Rubio et al. 1997).

Interestingly enough, even though AM fungi occur more often in soils that are drier, they are still found in the wettest soils and in hydrophytic vegetation. Ragupathy et al. (1990) indicated that up to 47% of 70 tropical hydrophytes surveyed were indeed colonized by AM fungi. Furthermore, Brown and Bledsoe (1996) found AM fungal colonization levels to be >20% in regions where soil moisture levels exceeded 120%, and Cooke et al. (1993) found colonized roots at soil depths of 42cm where there was no detectable oxygen. It is believed that the maintenance of AM inoculum potential in wetlands highly depends on the presence of wetland plant roots showing a decent amount of oxygen leakage into the rhizosphere or the presence of aerobic microsites within the waterlogged soil providing oxygen for the fungi (Lodge 1989, Miller 2000, Cantelmo and Ehrenfeld 1999). These aerobic microhabitats could help AM fungal spores germinate and colonize a root, and, once colonized, these fungi can survive extensive flooding (Miller and Bever 1999, Ellis 1998). These findings and beliefs suggest that the AM

fungi are able to adapt to extremely low oxygen levels in some way. The fungal adaptations to low oxygen that have been hypothesized include the fungus tapping into the oxygen in the aerenchyma tissue of the plant (Brown and Bledsoe 1996; Miller 2000; Cooke et al. 1993) or using the oxygen that leaks into the rhizosphere from the root (Miller 2000; Cooke and Lefor 1998). Brown and Bledsoe (1996) observed AM fungi in the aerenchymatous tissue of saltmarsh plants, and Keeley (1980) found most mycorrhizal colonization occurring in the main proximal roots of *Nyssa sylvatica* individuals where the majority of root oxygen can be found. As for an oxidized rhizosphere, this could have a twofold positive effect on the AM association – the first and most important effect being the availability of oxygen to the fungi. The second positive effect on the association is based on a correlation between an oxidized rhizosphere and sequestering of available P in this rhizosphere due to oxidation of the soils. It is quite possible that coupling the AM fungi with the stored P in the rhizosphere could be a new mechanism for plant phosphate uptake (Wigand and Stevenson 1997).

Many fungal species appear to be better adapted to certain edaphic conditions (Fitter 1989, Sanders and Fitter 1992), and this could include being better adapted to flooded soils. Miller and Bever (1999) found that in Carolina bay wetlands, certain AM fungal species occurred only in the drier regions of a soil moisture gradient while AM fungi that occurred in the wetter regions were found along the gradient. In this case, water depth was indeed found to be a limiting factor for certain types of AM fungi. This study reveals that the AM fungi in wetlands are not physiologically equivalent to each other in their adaptations to flooded conditions. It also indicates that some kind of adaptation is necessary for the fungi to survive in these wetter areas of the wetlands.

Similar trends of fungal species distribution in wetlands were found in tidal saltmarshes by Brown and Bledsoe (1996).

It has also been found that some biotic and abiotic factors vary with the type and number of fungal species in the mycorrhizal community of a wetland (van der Heijden et al. 1998). For example, in studying wetlands in Illinois, Anderson et al. (1984) found plant cover, spore abundance, plant species richness, and fungal species richness positively correlated with each other and with organic matter content and negatively correlated with pH, Ca, Mg, P, and percent soil moisture. Furthermore, in studying the species of fungi along a moisture gradient, they found one species of AM fungi distributed all throughout, one species only at the dry end, and one species only at the wet end of the gradient. Since AM fungal species are distributed in different areas of a wetland in relation to many abiotic factors and this distribution influences the distribution of other biotic factors, it can be assumed that AM fungi are important to many wetland ecosystem processes yet to be discovered.

The degree of AM fungal colonization in wetlands could also be largely dependent on host plant species (Wetzel and van der Valk 1996, Miller 2000, Keeley 1980). The aspects of the fungus/plant association differs for plants in ways which include interspecific differences in root length colonized, width of vesicles, and occurrence of arbuscules (Sanders and Fitter 1992). The colonization levels in host plants can vary greatly even within a genus. For example, both Anderson et al. (1984) and Miller et al. (1999) concluded that *Carex* species with low to no colonization levels have a specific root phenology not conducive to colonization (as expected by the Baylis hypothesis) (Baylis 1975). In the case of *Carex*, this unsuitable root phenology is the

presence of numerous bulbous root hairs. Other similar conclusions have been made about specific plant species, but interestingly, many opposing reports have also been made. Many species of *Typha* and *Carex* have been found to be highly colonized in some studies (Cooke and Lefor 1998, Wetzel and van der Valk 1996) and in other studies have been found to have no colonization (Rickerl et al.1994, Cornwell et al. in review, Thormann et al. 1999). In these situations, the occurrence of colonization may not necessarily be dependent on the host, but rather the environment that the host is in (Miller et al. 1999). Anderson et al. (1984 and 1994) suggest that some plants have functional mycorrhizae at the dry end and not at the wet end of a moisture gradient, while others may have functional mycorrhizae throughout the entire gradient, including in flooded zones. All in all, this variation in colonization levels of different plants is quite beneficial to a wetland habitat as this can support high species diversity and enhance plant competition (Gange et al. 1993, Wilson and Hartnett 1998).

It has been suggested that colonization levels in wetlands may vary with the season. AM mycorrhizae show seasonal responses in non-wetlands which are often associated with changes in plant phenology and/or phosphorous levels (Smith and Read 1997; Rabatin 1979; Sanders and Fitter 1992). In wetlands, seasonal differences in colonization levels could be due to not only changes in phosphorous levels and plant phenology, but also to changes in the water regime of a particular zone in the wetland (Jurgensen et al. 1997). For instance, many wetlands fed by runoff and precipitation have periods of draw-down where the soil in the upper parts of moisture gradients can experience significant amounts of drying (Mitsch and Gosselink 1993). During these times, mycorrhizal fungi could take advantage of the drier, more aerated soils to

effectively colonize plants. This has been suggested in research by Miller (2000) in which the inoculum potential of soils from different wetness regimes of Carolina Bays was measured. In this study, the wetter soils had the same inoculum potential as the drier soils when placed under drying conditions. This indicates that AM fungal propagules are thriving in the wetter soils but may need dry conditions to establish new associations with wetland plants. Hence, occasional drying may maintain the inoculum potential necessary for new plant colonization thus causing temporal variation in colonization levels. AM fungal colonization could be most important for plant species during drawdown periods by helping plants survive drought stress, compete effectively, and acquire much needed nutrients (Smith and Read 1993; Cooke and Lefor 1998; Van Duin et al. 1989; Brown and Bledsoe 1996).

As before mentioned, the functionality of AM fungi is questionable if arbuscules are not present in the mycorrhizal association. Several wetland studies have noted the absence of arbuscules in the roots of wetland plants, especially the plants found more frequently in the wetter and more anoxic soils. These plants are still colonized by AM fungi, as evidenced by hyphae and vesicles, but appear to have no method of transferring phosphorous to the plant; therefore, the mycorrhizae are determined as non-functional by some scientists (Cooke et al. 1993; Cantelmo and Ehrenfeld 1999; Thormann et al. 1999, Clayton and Bayaraj 1984). On the other hand, Anderson et al. (1984) found that these mycorrhizal fungal associations lacking arbuscules are not necessarily always non-functional. They demonstrated this by using mycorrhizal roots from wetlands with only coenocytic hyphae and no arbuscules to inoculate corn plants and discovered that functional associations and sporulation did occur as a result of the inoculation. Hence, it

has been suggested that these AM fungi in wetlands are functional (and thus mutualistic) when conditions become more suitable to promote the mycorrhizal association as stated previously. Also, it is possible that the mycorrhizal benefit only occurs during certain stages of wetland plant life cycles which have yet to be identified in wetland habitats (Sanders and Fitter 1992). What the AM fungi is doing for the plant in the meantime remains an unanswered question.

Since the mycorrhizal association is postulated to be a functional mutualism at one time or another, it is important both for the plant and the AM fungus for the fungus to be able to persist in the wetter conditions as it awaits the periodic drier conditions to become functional. It has been found that once the association is established, a fungus can survive through flooding conditions as it awaits more amiable conditions to be functional for the plant (Miller 2000, Miller and Bever 1999). Anderson et al. (1984) did note that the variation in functional versus non-functional associations were common in wet sites where conditions fluctuated seasonally. An interesting correlation was discovered by Cooke et al. (1993) between the increase in abundance and species richness of wetland vegetation in wetlands with drawdowns (whether natural or human induced) and the increase in colonization of AM fungi in these drawdown areas. They suggested that the correlation is due to the fungi's capabilities of functioning in these drawdown areas as they would function in a terrestrial environment (where they are known to increase biological diversity). Once functional, these AM fungi could act as an important source of inoculum, as enhancers of species abundance and richness, and/or as alleviators of nutrient, drought, or seedling establishment stress (Turner and Friese 1998; Miller 2000, Cooke et al. 1993). Nevertheless, the nature of the periodic non-functional

association and how important this association is to wetlands both with seasonal fluctuations (marshes and Carolina bays) and without fluctuations (fens and other peatlands) still needs to be assessed.

The relationships between levels of AM colonization and P and soil moisture in wetlands are not very clear. In some cases it appears as if the levels of P in the wetlands are important in determining AM colonization levels (Jurgensen et al.1997, White and Charvat 1999), and in other cases it seems less important and percent soil moisture is more important (Rabatin 1979, Nelsen et al. 1981, Anderson et al. 1984, Miller et al. 1999, Rickerl et al. 1994). Such contradictory findings were even found within one study done by Wetzel and van der Valk (1996). They studied the colonization levels of AM in prairie pothole wetland vegetation in Iowa and North Dakota. They found that the differences in the two locations caused differences in colonization levels that could not specifically be attributed to soil moisture or P levels alone. It appeared that there was no relationship at all between AM colonization levels and available P along a hydrological gradient in North Dakota wetlands while there was some sort of a relationship in Iowa wetlands. They speculated that other environmental factors not measured could be more important in controlling the colonization levels of plants in prairie potholes. The general belief right now is that P is most important in regulating the association in soils that are drier and P limited (<10mg/kg available P) (Rickerl et al.1994, Wetzel and van der Valk 1996, Anderson et al. 1994) while soil moisture is more important in wetter soils (Miller 2000). As expected, colonization levels are lower in soils with higher soil moisture; however, it is still not known if this relationship is due directly to the effects of soil moisture or instead to some other environmental factor (still yet to be determined) that

may vary with soil moisture (Miller 2000, Anderson et al. 1986, Khan 1993, Brown and Bledsoe 1996).

A lot of effort is spent trying to determine what would be a good measurement of mycorrhizal benefit in a wetland, especially since colonization levels are so highly dependent on plant phenology and water levels of the wetland. Benefits are traditionally recognized as an improved access, on the part of the mycorrhizal plant, to limiting soil resources (Johnson et al. 1997). There are two problems with this – many wetlands do not necessarily have limited soil resources and the fungi have to find a way to survive in the flooded soils. Benefits commonly tested for in wetland studies include increased biomass production of mycorrhizal plants (Miller et al. 1987) and increased P in mycorrhizal plants (White and Charvat 1999, Rickerl et al. 1994). These measurements of benefits have shown some positive results. For example, Wigand and Stevenson (1997) did show AM fungi as enhancing uptake of phosphate in a submersed plant, *Vallisneria americana*. As a matter of fact, the P uptake was 85% more for mycorrhizal plants than it was for non-mycorrhizal plants. Furthermore, Miller et al. (1987) demonstrated a positive mycorrhizal response based on increased biomass production in mycorrhizal plants. Those who do not find these benefits assume the association is non-functional or even parasitic, while, in fact, the association could be benefiting the plant in other possibly immeasurable ways. For instance, Newsham et al. (1995) did not find increased P uptake or increased biomass production in the mycorrhizal plants, but was able to show that the plants had increased resistance to root pathogens giving them an advantage over non-mycorrhizal plants. It is this sort of benefit that needs to be examined in wetland ecosystems where the role of mycorrhizal fungi may be quite

different than their role in terrestrial ecosystems.

With all the varying abiotic and biotic factors found and yet to be determined as affecting mycorrhizae in wetlands, studying mycorrhizae in wetlands can be challenging although necessary. Wetland mycorrhizal relationships have been largely ignored until recently because many scientists assumed that these aerobic fungi could not survive in saturated and inundated soils. Much to their surprise, colonization by arbuscular mycorrhizae has been found in all types of wetlands including freshwater marshes (Miller and Bever 1999), salt marshes (Cooke et al. 1993), coastal swamps (Cantelmo and Ehrenfeld 1999), prairie potholes (Rickerl et al. 1994, Wetzel and van der Valk 1996), and fens (Turner and Friese 1998, Thormann et al. 1999). What still needs to be determined is which of the three wetland components (hydrology, soils, vegetation) may have the greatest influence on the occurrence of mycorrhizae in a wetland and may explain why AM fungal colonization levels differ between contrasting wetlands. Assessing and comparing different types of wetlands may lead to answering why and by what means does the mycorrhizal association persist in wetlands (Miller 2000). For example, it has been speculated by Thormann et al. (1999) that fen dominant vegetation will be mycotrophic due to the prevailing low nutrient availability, and marsh vegetation will be non-mycotrophic due to the fluctuating water table and higher availability of nutrients. Examining such speculations could reveal important information about the roles and distribution of AM fungi in wetlands.

Wetland Restoration

Healthy and diverse wetlands, that may partially depend on the mycorrhizal

associations in the soil, are quickly disappearing throughout the U.S.. Restoration of these wetlands is a major area of research and application at this time (i.e., Mitsch and Gosselink 1993, Galatowitsch and van der Valk 1998). Understanding the relationships between mycorrhizal fungal colonization and the gradients/environmental factors in wetlands will only help the success of restoration projects, especially if mycorrhizae are indeed found to be important to plant establishment and survival in wetlands. Assessing and comparing the importance of mycorrhizae in different types of wetlands should help develop restoration techniques that will greatly improve the preservation and restoration of biologically viable and sustainable wetland ecosystems.

Over 90% of wetlands in Ohio have been lost through habitat destruction; thus, it is of prime importance that the remaining wetlands are well described and understood. The need for developing techniques for restoring wetland ecosystems to their original structural and functional states has become vital, especially with current mitigation policies and the increasing development of natural areas (Brown and Bedford 1997). The techniques currently used for restoration projects are questionable and the evaluation of the "finished" project leaves little to be desired. Because of this, there is a high demand for better guidelines for the actual restoration practices and for management practices after restoration has begun (Mitsch and Gosselink 1993, Zedler 1996). Furthermore, there is a demand for thorough investigations of reference wetland sites in order to understand the variables driving healthy biotic communities to 'completely' restore a functional wetland (Smith et al. 1995).

An important consideration in understanding reference wetlands for restoration projects includes understanding the scale at which ecosystem processes are happening.

For instance, on the scale of an individual plant, topographical changes are enough to create microsites with differing nutrient levels, physical structures, and hydrology. Therefore, it might be necessary to create microtopography within a restored wetland to improve plant species diversity and survival (Bledsoe and Shear 2000). Microsites also influence the microbial community of the soil system in a wetland. Processes such as nutrient cycling and decomposition occur at the scale of the microbial community and can be important in determining the plant community and the functional roles of a wetland.

The functional roles of a wetland are, at times, completely dependent on soil microbial communities and soil characteristics; therefore, one key technique for restoring the functional components of a wetland may be the application of donor soils. Donor soils allow the recruitment of diverse and viable native plant communities by taking soils from undisturbed wetlands before they are lost to development and applying these soils to degraded sites. Donor soils would allow this recruitment of plants by adding a viable seed bank and would enhance the functional components of a wetland by adding an active microbial community (Burke 1997, Clewell and Lea 1990). Numerous studies have shown the benefits of using donor soils for restoration of wetlands (Leck 1989, Ray 1998, Stauffer and Brooks 1997). In a study done by the U.S. Fish and Wildlife Service on wetland restoration sites in New York, donor soil application significantly increased wetland plant species number and cover as well as limited the encroachment of a wetland invasive species (Brown and Bedford 1997). Plant species richness and cover was also increased by use of donor soils in a created wetland in Pennsylvania (Stauffer and Brooks 1997). Although many benefits of donor soil have been shown for wetland plant

communities, little is known about how donor soil might affect microbial community functional roles. It is speculated that donor soil enhances bacterial and AM fungi communities which have important implications for soil processes and for plant recruitment success (Wolters 1999, Rowley in prep., Smith and Read 1997).

Other soil amendments, besides donor soil, may be useful in wetland restoration. Organic amendments including leaf litter, sludge, mulch, and peat moss have shown to help increase plant species richness, diversity, and plant cover in disturbed wetland habitats (Stauffer and Brooks 1997, Zink and Allen 1998). If mycorrhizal fungi are indeed found to be important in wetlands, then application of mycorrhizae to degraded wetlands could also significantly benefit wetland restoration sites. Mycorrhizal community response to disturbance, such as flooding, differs by habitat depending on the soil characteristics, host plant species, and fungal species (Allen 1991, Miller 2000); therefore, habitat specific guidelines for selection of mycorrhizal species and where to apply the mycorrhizal inoculum would need to be set.

Since the ultimate goal of restoring wetlands is to establish a functional community with high biodiversity (Galatowitsch and van der Valk 1998), restoration scientists need to reach beyond the typical mindset of just re-establishing the plant community. A functional wetland is not just an ecosystem with high plant diversity, it is also has stability and resilience in times of disturbance (Keddy 2000). Furthermore, a functional wetland is not necessarily a fertile (productive) wetland. Oftentimes an infertile wetland can have higher species diversity and many more rare species than a fertile wetland (Moore et al. 1989, Bedford et al. 1999). An infertile wetland can also support a more functional microbial community, especially in regards to mycorrhizal

fungi which are beneficial to plants in infertile habitats (Smith and Read 1997). It is even possible that the higher plant diversity of infertile wetlands could be directly linked to the more functional mycorrhizal community.

Some of the overall functional roles of a wetland include cycling of nutrients, controlling floods, improving water quality, providing animal habitats, etc. (Mitsch and Gosselink 1993, Keddy 2000). Many of these roles are dependent not only on the plant community but also on the soil community. Poor soil characteristics and an unhealthy microbial community in a habitat can easily lead to a poor plant community and loss in ecosystem function (Allen 1991, Brundrett 1991). Therefore, understanding the soil community dynamics of a wetland and applying this knowledge to restoration practices should help scientists more successfully reach restoration goals. The knowledge obtained from soil studies in reference sites, such as the following study, will help set restoration guidelines that are more appropriate for establishing a functional wetland ecosystem.

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Chapter 3

Arbuscular Mycorrhizal Fungal Dynamics in Wetland Habitats: An Assessment of Seasonal and Soil Gradient Effects

INTRODUCTION

Wetland ecosystems are unique habitats that support highly diverse communities of plants and offer numerous functional roles for the environment. Wetlands act as sources, sinks, and transformers of nutrients, and therefore play a large role in ecosystem nutrient cycling. Other functions of wetlands include providing water purification, groundwater recharge, valuable wildlife habitat, and floodwater control (Mitsch and Gosselink 1993). Although wetlands are considered as highly valuable to humans, anthropogenic disturbance has greatly impacted and degraded these ecosystems. Over 50% of the United States' wetlands and 90% of Ohio wetlands have been destroyed and lost (Tiner 1998, Mitsch and Gosselink 1993). Continual development spurs continual wetland mitigation; thus, it is of utmost importance that the remaining wetlands are well described and understood to help with preservation and restoration efforts.

More often than not, the status of a wetland is determined by the health and biological diversity of the plant community present and considers the physical and chemical factors that affect this community. Unfortunately, little attention is given to the other organisms and their functional roles in the wetlands – especially the microorganisms and their important roles in soil processes and nutrient cycling (Cooke and Lefor, 1998; Schneble, 1997). More information is needed on how the soil microbial community is affected by disturbance and how the microbial community can be useful in

reestablishing wetland sites. The health and stability of any plant-soil ecosystem, including wetlands, largely depends on a wide diversity and functionality of soil microbes including arbuscular mycorrhizal (AM) fungi (Bethlenfalvay and Lindermann, 1992).

AM fungi act as alleviators of nutrient, toxic metal, drought, and seedling establishment stress and enhance plant fitness (Allen 1991, Allen 1989, Smith and Read 1997). Hence, AM fungi can have important roles in plant community dynamics such as plant abundance, composition, and diversity in different habitats. These roles have been exemplified in many upland ecosystems, especially grasslands and agricultural areas (Bethlenfalvay and Linderman 1992, Hartnett and Wilson 1999, Allen 1992, Pfleger and Linderman 1994). It is well known that AM colonization of plants in these ecosystems is often limited by available soil phosphate levels, soil moisture levels, and available fungal inoculum. Furthermore, AM fungal presence can be controlled by the plant species present (Smith and Read 1997, Anderson et al. 1984). What is less well known about AM fungi is the factors affecting their presence in wetlands and what their ecological roles may be in wetland ecosystems.

AM fungi have been found in many wetland habitats including salt marshes (Cooke et al. 1993), Carolina Bay wetlands (Miller 2000), coastal swamps (Cantelmo and Ehrenfeld 1999), and fens (Thormann et al. 1999, Wetzel and van der Valk 1996). Until recently, the roles and distribution of wetland mycorrhizal associations were largely ignored since it was assumed that AM fungi could not survive in anoxic conditions and many wetland plant species were found to be non-mycorrhizal (Mosse et al. 1981, Anderson et al. 1984, Mejstrik 1984, Khan 1974). In recent wetlands studies, AM fungi

have been found mainly in soils that are not flooded or have several aerobic microsites (Brown and Bledsoe 1996, Wetzel and van der Valk 1996, Miller 2000, Cantelmo and Ehrenfeld 1999). Interestingly, they have been found in the wettest soils and in hydrophytic vegetation to some extent. Ragupathy et al. (1990) indicated that up to 47% of 70 tropical hydrophytes surveyed were indeed colonized by AM fungi. Furthermore, Brown and Bledsoe (1996) found AM fungal colonization levels >20% in regions where soil moisture levels exceeded 120%, and Cooke et al. (1993) found colonized roots at soil depths of 42cm where there was no detectable oxygen. Survival of AM fungi in these types of conditions may require the fungi to concentrate colonization in areas of the root systems that are well oxygenated (aerenchymatous tissue), to distribute themselves along a moisture gradient, or to thrive in areas that will have a seasonal drawdown.

Sites within a wetland that are more aerobic, or may become aerobic at one time or another, can act as sources of mycorrhizal inoculum for wetland plants. Once AM fungi are able to germinate and colonize a plant, they are able to survive flooded conditions in a wetland (Ellis 1998). The extent of this survival seems to depend on the intensity, frequency, and/or duration of flooding or on the type of fungal or plant species present (Brown and Bledsoe 1996, Wetzel and van der Valk 1996, Keeley 1980, Rickerl et al. 1994, Cooke and Lefor 1998). For example, Miller and Bever (1999) found that certain AM fungal species in the Carolina Bay wetlands may be more tolerant to wet conditions than other species. Their study indicated that the AM fungi in wetlands may have adaptations that are successful in flooded soils.

Many contradictory reports have been made about the mycorrhizal status of wetland plant species. It is often assumed and has been noted that plant members of

Cyperaceae and Juncaceae are largely non-mycorrhizal (Powell 1975, Anderson et al. 1984, Thormann et al. 1999) while other reports indicate significant levels of AM colonization in plants such as *Typha* and *Carex* species (Wetzel and van der Valk 1996, Cooke and Lefor 1998, Stenlund and Charvat 1994). It is not well understood if the variation in colonization levels for specific plant species is related to root characteristics or to environmental factors at the scale of an individual plant (Miller et al. 1999). Furthermore, the mutualistic nature of the mycorrhizal association is questioned in some of these plant individuals because of the lack of arbuscules, points of nutrient exchange between the fungus and the plant. So far, few studies have surveyed the extent of mycorrhizal colonization in wetland plants and the extent of arbuscular presence in these plants (Turner and Friese 1999, Cooke and Lefor 1998, Turner et al. 2000).

In wetlands, the dynamics of AM fungi in time and in relation to nutrient levels are largely unknown. Currently, it is believed that the fungi are mostly influenced by water levels; thus, it is expected that the seasonality of the fungi will correlate with flooding cycles (Wetzel and van der Valk 1996, Brown and Bledsoe 1996). In upland ecosystems, nutrient availability and plant need for nutrients at different times of their life cycle largely regulate the AM fungal dynamics (Demars and Boerner 1995, Anderson et al. 1994, Dhillion and Anderson 1993). However, in wetlands, the relationship between AM colonization and available phosphate does not always exist and is not very clear (Rickerl et al. 1994, Miller et al. 1999). On the one hand, in wetlands that are largely P limited, such as fens, mycorrhizal dynamics might be linked to P levels (Wetzel and van der Valk 1996), while on the other hand, nutrient rich wetlands may have some other edaphic factor largely controlling colonization. Because wetland dynamics are affecting

the distribution of AM fungi, it is likely that the roles of the association are also being affected. These roles could be more or less significant in different wetlands since mycorrhizal response to disturbance events, such as flooding, has been found to differ according to different soil and plant characteristics of a habitat (Allen 1991, Cornwell et al. in review). Assessing mycorrhizal dynamics in different types of wetland habitats may answer questions regarding their survival techniques, roles, and distribution in wetlands. Two contrasting types of wetland habitats that would encompass these questions are fens and marshes, which will be examined in this study. Fen and marsh habitats differ by their seasonal patterns, their phosphorous levels, their soil organic content and their moisture levels. Because all of these factors have been found to influence mycorrhizae in wetlands to some extent, the results of a mycorrhizal study in these two wetlands could reveal useful information about the roles and distribution of AM fungi in wetlands.

The overall objective of this research was to assess the AM gradient and seasonal dynamics in two wetland habitats in order to more fully understand the significance and distribution of AM in these wetlands. The seasonal dynamics were assessed by surveying mycorrhizal colonization levels throughout the entire growing season, while the gradient dynamics were assessed by sampling along a moisture gradient in each wetland site. The primary questions to be addressed in this study are as follows: (1) are AM fungal colonization levels restricted to drier regions of a water gradient? (2) what are the seasonal dynamics of AM colonization in fen and marsh habitats? (3) what are the effects of available P and soil moisture on AM colonization levels? (4) what is the extent of AM colonization in dominant wetland plants of marsh and fen habitats? (5)

what are the differences in the mycorrhizal dynamics between fen and marsh habitats? Information from this research will provide further understanding of the importance of these associations in wetlands and will be useful in establishing appropriate restoration and preservation techniques for marsh and fen wetland habitats.

MATERIALS AND METHODS

Site Descriptions

The sites in this study represent a range of wetland types from saturated fens to inundated marshes. The four sites are Spring Valley Marsh (SV), Gingell Parcel Marsh (GP), Travertine Fen (TF), and Siebenthaler Fen (SF) (Figs 1-5). Spring Valley Marsh is located in Warren County, Ohio and is a marsh. The other three sites are located in Greene County, Ohio (Fig. 1) and consist of a mound fen (SF), a hillside fen (TF), and a wetland with a fen to marsh gradient (GP). The hydrology of all four wetlands is controlled by groundwater, although not from the same aquifer. The climate for this area of Ohio consists of humid and hot summers and cold winters. The greatest amount of precipitation occurs from March to May and a mild seasonal drought from July to September is typical.

Spring Valley Marsh is owned and maintained by the Ohio Division of Wildlife. This marsh is approximately 150 acres and is located adjacent to the Little Miami River (Fig. 1). Prior to the 1940's, the property was farmed extensively. In the early 1940's, the land was converted to a marsh by a muskrat pelt trader. A levy was constructed to the west of the property which let groundwater flood the land. By the 1960's, the Ohio

Division of Wildlife of the Ohio Department of Natural Resources had purchased the land, redesigned the original levy to allow natural vegetation to colonize the area, and built levies for access roads.

Seeps and springs from an aquifer (separate from the main Greene County aquifer) at SV keeps the majority of the marsh flooded throughout the year. The areas of the marsh closer to the dikes and to the levy are not inundated – at best, the soils are only saturated in these areas. Since the marsh consists of Linwood Muck soils (high in clay and organic matter) as designated by the *Soil Survey of Warren County, OH* (1973), the water level remains consistent throughout the year. Currently the Ohio Division of Wildlife does have a water control structure in place; however, the main regulator of water levels has been beavers.

Spring Valley Marsh is the largest, relatively undisturbed marsh in the area and has a diverse plant community of wetland plant species such as *Typha latifolia, Sparganium eurycarpu,* and *Polygonum amphibium*. The research transect at this marsh spanned a 93m gradient with 50m of this gradient flooded (by at least 10 cm) throughout the growing season. The area designated as the dry portion of the gradient for this study was along a dike to the north of the wetland.

Gingell Parcel is a groundwater fed wetland with a fen to marsh gradient. The wetland is 56 acres and is currently owned by the Beaver Creek Wetlands Association. Historically, the wetland area was the bed of the Beaver Creek prior to the channelization of the creek in 1917. Since the 1940's, when farmers stopped maintaining the strict channelization of the Beaver Creek, GP has been inundated with groundwater and occasional floodwater from the creek. The levy built to channelize the Beaver Creek (to

the west) and New Germany-Trebein Road (to the south) act as barriers to water flow in the area. A large fallow field lies to the East of the wetland and creates a smooth topographic gradient into the inundated area of the marsh.

Gingell Parcel consists of both Sloan soils and peatty-muck soils. The inundated area of the marsh is host to Sloan soils (Soil Survey of Greene County, OH, 1978). The silt, characteristic of Sloan soils, is dumped into this area by flooding and remains in the marsh because of the structures impeding water flow. The areas up gradient from the flooded part of the marsh have peatty-muck soils that are very typical of soils around groundwater seeps (Amon, personal communication).

The gradient transect used for this study is 31 meters long and consists of an upland plant community, a fen plant community, and a marsh plant community. The vegetation in Gingell Parcel along the gradient is patchy due to the groundwater seeps and the inundated areas. Where the groundwater seeps into the wetland between 5 and 20 meters, characteristic fen plant species can be found. The areas immediately around the flooded soils, for the last 10 meters of the transect, are dominated by hydrophytic marsh plant species. This area remained flooded for the entire growing season, although the extent of the flooding varied monthly.

Siebenthaler Fen, a 100 acre fen complex, is owned by the Ohio Department of Natural Resources, Division of Wildlife and is along the Beaver Creek corridor just south of Gingell Parcel. This wetland is a mound fen and is composed of several large mounds formed by the groundwater seeps. This site was disturbed in the first half of the 20th century by channelization of the Beaver Creek and placement of drainage tiles and a drainage ditch. At that time, the fen was used as cattle pasture and left fallow for at least

50 years. Since the Division of Wildlife purchased the wetland in the mid 1990's, the elevation of the water level has increased and has permitted wetland plant species growth. SF's plant community is now extremely diverse and patchy throughout the fen habitat.

The soils in this area are Linwood Muck. The surface layer (from the surface to two feet down) is a muck layer and is underlain by six feet of brown and sedge peat. The *Soil Survey of Greene County, OH* (1978) classifies the soil as Sloan in this area; however, the excessive groundwater in the area flushes the silt (which makes up Sloan soil) back into the Beaver Creek. The elimination of the silt results in soil characterized as Linwood Muck. Attempts to drain the fen decades ago exposed the once dominant peat soil to oxygen resulting in the muck layer that remains to this day.

There are no areas of flooding in the Siebenthaler Fen except in rare cases where the Beaver Creek floods over its channels or if the drainage ditch floods. Attempts to remove drain tile in one area of the fen, although unsuccessful, have created a small depression where water may occasionally collect. Because of the numerous mounds, the water gradients at Siebenthaler Fen are patchy. The 117 meter long gradient transect used for this study extends from the drainage ditch levy into the main part of the fen.

Travertine Fen is close to Spring Valley Marsh and is in Greene County, Ohio (Fig 1). It is currently owned by Greene County Park District and has been designated as an Ohio Department of Natural Resources' State Nature Preserve. This wetland is a hillside fen with several running groundwater springs throughout the 21 acres of the preserve. Prior to 1992, when purchased by Greene County Park District, the area was left fallow by private owners. Upslope from the fen (to the east) is a small forest and

beyond that are agricultural fields. To the west of the fen (at the base of the hill) is a levy originally built for a railroad.

The gradient transect for this site is 42 meters long. At the end of the transect (bottom of the hill), the railroad levy causes excess groundwater to pool. This flooded area is largely dominated by *Typha latifolia* and remained flooded by at least 10cm for the entire growing season. The other parts of the transect consist of groundwater seeps that maintain soil saturation throughout the year, a small creek bed of running groundwater, and an upland habitat.

Travertine Fen has very diverse and unique plant communities reflecting the microtopography made by the groundwater seeps and the hummocks found throughout the fen. The soils are also unique and consist of marly deposits that extend from the surface to ten to thirty feet deep and peatty deposits that extend two to six feet below the surface. Other areas of the fen are dominated by limestone cliffs (Jim Schneider, personal communication).

Field Design

Beginning in March 2000 transects were set up for each of the four wetlands. They were aligned according to water gradients so that each transect had an upland habitat end and an end with an obligate wetland plant community (based on Ohio's wetland indicator categories). The length of the four transects varied because of the different sizes of the wetlands. Eight sampling points were selected along each transect to keep sampling number consistent. Sampling of these points began in March and continued once a month through September by using meter squared quadrats.

Sampling in each quadrat consisted of obtaining two sets of four soil cores, identifying plants within and around the quadrat, estimating total percent coverage of live plants, obtaining one plant with roots for mycorrhizal analysis (the dominant species in the area), and, where possible, a water sample. The soil cores were placed in pre-marked Ziploc™ bags for analysis in the lab. Plants that could not be identified in the field were brought to the lab to be pressed and identified.

Soil Analysis

Two sets of soil cores were taken from four random places within each quadrat. Each core was 2.5cm in diameter and 15 to 20 cm deep. One set of soil cores was used to analyze general mycorrhizal colonization levels for each point along the transect (see below) and to analyze soil characteristics. Within 24 hours of collection, these soil samples were analyzed for percent moisture and organic content by using the procedures described by Brower and Zar (1984). These procedures included placing the soils in a drying oven for at least 24 hours at 100° C to determine the percent moisture and ashing the soils in a muffle furnace to determine organic content.

The other set of soil cores was air dried and sent to a soils lab (Balance Labs, Marion, OH) for analysis of several abiotic factors including Bray and Olsen phosphorus, pH, estimated mineralizeable nitrogen, potassium, calcium, magnesium, and cation exchange capacity.

Arbuscular Mycorrhizal (AM) Colonization Analysis

Mycorrhizal fungal colonization levels of roots were analyzed for each sampling site. For the soil cores, plant roots were randomly removed from the soil, rinsed off, and placed in a tissue cassette. For the specific plant specimens taken from each site, roots were randomly removed by scissors and also placed in tissue cassettes. All roots were then stained for the presence of AM structures using trypan blue (Phillips and Hayman 1970) and assayed for colonization using the gridline intersection method (Giovanetti and Mosse 1980; Brundrett et al. 1994).

Water Analysis

One water table well was installed at each sampling point to measure the height of the water table. The water table wells were made out of PVC pipe with fine slits running perpendicular to the length of the water table well. Before they were placed in the ground, sand was added to the bottom of the hole. Sand was also added around the water table wells to keep soil from clogging the slits. PVC pipe caps were placed on top of the pipes to prevent standing water and debris from entering the pipes.

AM Fungal Spore Analysis

In late October and early November, soil cores were collected from all four wetlands for AM fungal spore analysis. The gradient in each site was arbitrarily split into three sections based on soil saturation – dry, intermediate, and wet. Four soil cores were taken at each of three random sampling spots within the designated section.

In the lab the soil was homogenized and then put through a spore extraction by the methods of Ianson and Allen (1986). Spores were stored in formaldehyde acetic acid until analyzed. For enumeration, spores were suctioned onto a gridded filter paper for counting using a dissection microscope.

Statistical Analysis

All statistical analyses were performed using SPSS Base 10.0 (SPSS 10.0; SPSS, Inc, 1999). Site, month, and gradient effects of AM colonization levels were analyzed using one-way and two-way analyses of variance (ANOVAs). To verify that the equal variance assumption was met, Levene's equal variance test was performed at 5% level of significance, and residual plots were examined to verify that the normality assumption was met. Percent mycorrhizal colonization data did not meet the ANOVA assumptions; therefore, this data was arcsine square root transformed.

For each site, AM colonization data was analyzed by two-way ANOVAs to evaluate the effects of gradient, month, and the interaction between gradient and month, if any. Sites were taken separately due to the results of PCA analysis and a one-way ANOVA indicating the large abiotic differences between the wetlands. To analyze the effect of gradient on AM colonization levels, the water levels of each wetland were individually split into three groupings – wet (the highest 33% water levels), intermediate (the middle 33% water levels), and dry (the lowest 33% water levels). After running ANOVAs, pairwise differences among samples were determined by using Bonferroni's test. In addition to the above analyses on AM colonization data, a two tailed t-test was

run to compare inundated sites to non-inundated sites throughout the entire sampling period (all months and sites acted as replicates).

Due to unbalanced data (highly variable sample sizes), percent AM colonization of specific plant species was not analyzed using an ANOVA. Instead, this data is presented graphically. Placing these plant species into wetland indicator status categories for Ohio balanced the data so that comparing the percent AM colonization among indicator categories was statistically possible. The effect of presence of *Typha latifolia* (cattails) was evaluated by comparing plots where *Typha latifolia* was selected for AM colonization analysis to plots where another species was selected. This data was analyzed using a Kruskal Wallis Rank Test where the factor was presence of *Typha latifolia* and the dependent variable was percent AM colonization of plant species selected. A Kruskal Wallis Rank Test (used for nonparametric data) was also performed to evaluate a site effect on %AM colonization of *Typha latifolia*.

The soil variables measured (phosphorus, % moisture, organic matter, etc.) and individual AM fungal structures (arbuscules, vesicles, spores, and hyphae) were not normally distributed and the variances were not homogeneous across the treatments; therefore, the variables were converted into ranks and statistical analyses were performed via Kruskal Wallis tests and Spearman's Rank Correlations. Kruskal Wallis test was used to determine the significance of site and gradient on the soil variables. Because significant site effects were present, analyses of correlations between the soil variables and percent AM colonization were performed using Spearman's Rank Correlations. Individual AMF structures and relationships with water level, moisture, and available

phosphorus were analyzed using Spearman's Rank Correlations by site. Spore numbers were analyzed using Kruskal Wallis test for gradient effects.

RESULTS

Arbuscular Mycorrhizal Analysis (Soil samples)

Arbuscular mycorrhizal (AM) fungi were found at all sites and in all months. Colonization was indicated by the presence of aseptate hyphae, arbuscules, vesicles, and/or endospores. Total AM colonization levels varied from 0% in scattered locations to 76% in Travertine Fen (TF) in April. Siebenthaler Fen's (SF) highest colonization level was 51% in April, Gingell Parcel's (GP) highest was 33% in April, and Spring Valley's (SV) highest was 50% in March.

Arbuscules were found in all parts of the water gradient in all wetlands (Fig 6). Colonization levels indicated by the presence of arbuscules ranged from 0% in scattered locations to 10% in both SV and TF. Vesicles and endospores were also present at all sites with colonization levels ranging from 0% to 39% for vesicles and 0% to 10% for endospores (Fig 6). Endospores, vesicles, and hyphae, which were by far the most dominant mycorrhizal structures, were present throughout the entire study while arbuscules were only present through June. All of these structures, just like total colonization, were affected by months with the highest occurrence in March and April and lowest occurrence in August and September.

Total AM fungal colonization was the only colonization data statistically analyzed. Before determining effects of month and gradient on total colonization, the

colonization data were analyzed by site. It was found that the four wetland sites varied significantly ($F=4.961$, 3 df, $p=0.002$) by the levels of total AM fungal colonization found in roots from the soil cores. According to Bonferroni pairwise comparisons, GP had significantly ($p<0.05$; $\mu = 11.45\%$) lower colonization levels than either SF ($\mu = 18.42\%$) or TF ($\mu = 19.96\%$). SV ($\mu = 12.54\%$) also had lower colonization levels than the two fens, however these levels were not significantly lower (Fig 7).

The total AM spore population in the soil ranged from 0 spores/g of soil in the GP wet site to 2 spores/g of soil in the SV wet site (Fig 8). Three distinct species were distinguished in the study sites and were tentatively labeled as *Glomus* species 1, 2, and 3. Species 1 was found to be most dominant in SF, GP, and TF while species 1 and 2 were both dominant at SV. SF's and TF's wettest areas were solely colonized by species 1 while both species 1 and 2 were found in the intermediate and dry parts of the water gradient. A few spores of species 3 were found in both of these wetlands in the non-flooded soils. SV's wet end was dominated by species 1 and species 2. A few spores of species 3 was found in the wetter areas of SV, however, this species was more abundant in the drier soils where species 1 and 2 were also abundant. GP did not have any spores present at the wet end of the gradient and had only species 1 present at the intermediate and dry parts.

Because of site differences in spore abundances, SV's spore data was evaluated separately from the other three sites. TF, GP, and SF all had a significant gradient effect on spore number ($\chi^2 = 13.470$, df = 2, P = 0.001), with the wet and middle parts of the gradient having the lowest numbers of spores (Fig 8). There was no significant gradient

effect for SV, but it is important to note that spore numbers were higher at the wet end of the gradient.

Soil, Plant, and Water Characteristics of the Wetlands

Soil characteristics by site and by gradient are given in Table 1. All variables were significantly influenced by site ($p<0.001$). Only phosphorus, pH, percent soil moisture, and magnesium were significantly affected by gradient ($p<0.001$). Phosphorus and percent soil moisture values by month are shown in Figure 9. The trends are split into sites due to both variables having significant site effects. Month does have a significant ($\chi^2 = 13.377$, df = 6, P = 0.037) effect on phosphorus with May having the highest values and July having the lowest values. The effect of month on moisture is largely dependent on site and shows no overall trends among the sites.

Plant characteristics (species diversity and percent cover) by site and by gradient are also presented in Table 1. By site and by gradient, only species diversity was significant ($\chi^2 = 56.362$, df = 3, P = 0.0001 and $\chi^2 = 26.429$, df = 2, P = 0.001 respectively). The largest values for species diversity, by site, were at SF and, by gradient, were at the dry end.

Water level measurements by water table wells were made and then divided up into thirds for each site. This resulted in "dry", "intermediate", and "wet" designations of the gradient. SF always had the lowest water levels for all months and SV had the highest water levels for all months but May (Fig 10). SV, GP, and TF all had relatively consistent water levels throughout the sampling season while SF showed the greatest drop in water levels towards the end of the sampling season.

Effects of Soil P and Moisture on AM Colonization (Soil Samples)

Grouping all four sites together, neither available phosphorus levels nor percent soil moisture had a significant correlation with total %AM colonization (rho = 0.001, p = 0.988, n = 224 and rho = -0.044, p = 0.510, n = 224 respectively). Evaluating sites separately, there were no significant correlations between available soil phosphorus extracted by Bray's method and AM colonization levels (Table 2). However, available soil phosphorus that was extracted by Olsen's method (a more rigorous extraction commonly used for soils with basic soils and high Ca, as characteristic of GP and TF) was significantly ($p<0.05$) positively correlated with AM colonization levels in both GP and TF. With soil moisture, AM colonization levels significantly ($p<0.05$) rose at SF; however, at TF, AM colonization levels were significantly ($p<0.05$) higher with lower soil moisture. Other sites, although not significant, showed AM colonization negatively correlated with percent soil moisture.

Soil phosphorus levels and colonization levels were further assessed at TF and GP where there were significant correlations. Available phosphorus showed a significant ($p<0.10$) positive correlation with AM colonization levels at the wet end of GP and at both the dry and intermediate sections of the gradient in TF. Furthermore, available phosphorus and AM colonization levels in TF for the months of March through May were significantly positively correlated (rho = 0.769, p = 0.026, n = 8; rho = 0.830, p = 0.011, n = 8; rho = 0.651, p = 0.081, n = 8 respectively).

Separate AM fungal structures were analyzed via Spearman Rank's Correlations by site. In no cases were any of the structures correlated with available phosphorus at the

four wetland sites. It was found that arbuscules, vesicles, and hyphae were positively correlated with water levels and moisture for SF, however, these same structures were negatively correlated with water levels and moisture for TF ($p<0.05$). AT GP, hyphae was the only AM structure found to have a significant correlation with water levels and soil moisture ($p<0.05$), and the correlation was negative. Hyphae were also the only AM structure with a significant correlation at SV and this, too, was a negative correlation with water levels ($p<0.05$).

Effects of Gradient and Month on %AM Colonization (Soil Samples)

All sites had month as a significant effect on %AM colonization with April having the highest values (Table 3, Fig 11). The general trend was a significant decrease in total AM fungal colonization levels throughout the sampling season. September showed the lowest colonization levels for SV and SF, while August showed the lowest colonization levels for TF and GP.

Both TF and SV had gradient position (based on water levels) as a significant effect on %AM colonization (Table 3). In both sites, the drier part of the gradient had the highest colonization levels while the wet part had the lowest colonization levels. At TF (Fig 12) the intermediate and wet parts of the gradient did not differ significantly in their effects on %AM colonization (mean difference = -0.0585, SE = 0.033, $p = 0.086$) while the dry end did differ significantly ($p<0.05$). For SV, multiple pairwise comparison tests do not show significance between any pairs for gradient. This was most likely due to large overlaps in the spread of data for each one of the gradient locations. Furthermore, although the dry part of the gradient had the highest means for %AM colonization, it

happened to have the lowest median. GP showed similar trends to TF and SV (higher colonization in the dry part of the gradient); however, this trend was not significant at GP. Gradient also did not have an effect on SF. Surprisingly, the wettest part of the gradient in SF had the highest mean %AM colonization.

There were no interactions between month and gradient for any of the sites. In evaluating GP for month and gradient effects, it was discovered the data did not pass Levene's Test of Equality of Error Variances. The parameter estimates were stable for this site; thus, it was predicted that the unequal variances were due to numerous 0% colonization levels in the later part of the sampling season.

Effect of Inundation on %AM Colonization (Soil Samples)

Each monthly transect point for all four wetlands was defined as being inundated or not. To be classified as inundated, there had to be some level of standing water at and around that sampling point. In every month there were points that were inundated; however, inundation of the soils did not occur in every site (SF soils were never inundated). Running t-tests on this data indicated that %AM colonization is significantly lower in the inundated parts of the wetlands ($t = 2.863$, $df = 222$, $p = 0.05$, means = 0.3889 and 0.3045).

Arbuscular Mycorrhizal Analysis (Plant Samples)

Eighteen different species of plants within the four wetland sites were analyzed for the presence of mycorrhizae. Each site had between 5 to 8 species selected for analysis depending on the size of the plant communities that the transect crossed. All

eighteen species showed presence of arbuscular mycorrhizae to some extent during the sampling season. Table 4 lists the species selected for analysis and their mycorrhizal status. Since the presence of arbuscules typically indicates a truly functional mycorrhizal mutualism, plants that were colonized by arbuscules are also indicated in Table 6.

As in the analysis of soil samples, total %AM colonization of specific plant species selected did drop off as the sampling season continued. This data is not statistically presented due to unbalanced data and low sample numbers. Statistical analysis of species effect was also not possible. Figure 13 portrays an error bar graph with bars indicating 95% confidence intervals for average %AM colonization of plant species. This figure illustrates that *Typha latifolia* had solidly higher %AM colonization levels than *Carex stricta, Eleocharus erthrypoda, Alliaria officinalis, Caltha palustris* and *Acorus calamus*. When analyzing the specific plant colonization levels of *Typha latifolia* versus all other plants sampled (using a Kruskal Wallis test), %AM colonization is significantly higher for *Typha latifolia* ($\chi^2 = 9.026$, df = 1, p = 0.003). Further Kruskal Wallis tests indicate that %AM colonization of *Typha latifolia* is relatively the same among all sites in this study ($\chi^2 = 2.052$, df = 3, p = 0.562). *Typha latifolia* also had the highest %vesicle colonization (39%). Vesicles were present at all sites and in all months, but the presence of them, as well as endospores, was largely dependent on plant species.

When plants were clumped into their wetland indicator status categories using the National Wetland Plant List (Resource Management Group, Inc. 1992), data became balanced so that an ANOVA was possible to evaluate effect of wetland indicator status on plant specific total %AM colonization. The results indicate that there is no significant effect (p = 0.307) of indicator status on % colonization; however, facultative species had

the highest %AM colonization while upland species had the lowest %AM colonization (means were16% and 10% respectively and highest values at any one time were 36% and 22% respectively). Obligate wetland species had the second lowest mean %AM colonization (28%) and facultative upland had the second highest mean (34%).

Because roots were collected from both a general soil core and from a specific host plant at each sampling point, comparisons could be made between the colonization levels of the general and specific plant species roots located in any one sampling point. It was interesting to find that in some cases %AM colonization of soil samples was zero while %AM colonization of specific plant samples was nonzero. For instance, in August both *Carex comosa* and *Typha latifolia* had 14% AM colonization at GP, while the general roots from their locations had no colonization. At SV in March, *Sparganium eurycarpu* had 88% AM colonization while the other roots in the same area only showed 25% AM colonization. On the other hand, *Carex hystericina* at SF in March had 0% AM colonization while the roots from the soil core in that location showed 40% AM colonization.

DISCUSSION

The presence of AM fungi are known to influence plant competition, diversity, and abundance in terrestrial environments (Allen 1991, Smith and Read 1997), yet little is known about the AM fungal roles and distributions in wetlands. Our study examined spatial and temporal variation within different wetland habitats to provide a better assessment of environmental influences upon AM colonization in wetlands. In this study

we found unexpected trends and patterns of mycorrhizal dynamics in wetlands. Arbuscular mycorrhizal (AM) fungi were found at all four wetlands, within both fen and marsh habitats, and at all gradient locations within each wetland. Furthermore, arbuscules were found in all gradient locations indicating functionality of the mycorrhizal association (Smith and Read 1997). Although mycorrhizae were ubiquitous, several trends in AM colonization were apparent at these sites that both supported (Wetzel and van der Valk 1996, Miller et al. 1999, Miller 2000, Turner et al. 2000) and contradicted recent mycorrhizal wetland literature (Rickerl et al. 1994, Miller et al. 1999, Thormann et al. 1999).

Seasonal and Water Gradient Effects

The presence and degree of AM colonization in this study is strongly associated with the time of year. This temporal variation is the overriding dynamic for the role of AM fungi in the fen and marsh habitats. Seasonality of mycorrhizal associations is commonly found in terrestrial environments and is related to available phosphorus, temperature, plant phenology, and soil moisture (Demars and Boerner 1995, Anderson et al. 1994, Rabatin 1979). In wetlands, however, seasonality of AM colonization levels are usually assumed to occur only in wetlands that experience drawdown, which provide an opportunity for oxygenated soils (Brown and Bledsoe 1996, Miller and Bever 1999). Results of this study indicate that the AM fungi were controlled by temporal dynamics which were not related to drawdowns, soil moisture levels, or available P levels in any of the wetlands. Therefore, it is speculated that the seasonality of the fungi in these systems is largely tied to plant phenology indicating that the fungi are most important (and maybe

only important) at times of maximum new root growth in early spring. The presence of arbuscules (the mycorrhizal structure indicating functionality) only in the spring further supports this conclusion. It is important to note that all gradients in all wetlands showed similar seasonal trends of mycorrhizal colonization, and this trend was also apparent for specific plant species assessed. Similar findings for this AM fungal temporal trend in all parts of a water gradient have been found in other wetlands (Miller 2000, Turner and Friese 1998). These studies also indicated that AM fungal temporal dynamics are controlled by plant phenology rather than water levels or soil available P.

Flooding conditions have been found in many cases to negatively influence the level of AM colonization in wetlands (Cantelmo and Ehrenfeld 1999, Miller and Bever 1999, Jurgensen et al. 1997, Stevens and Peterson 1996, Cooke and Lefor 1990). This has been related to decreased oxygen concentration (Saif 1981, Keeley 1980), toxic by-products of anaerobic metabolism (Mosse et al. 1981), low redox potential (Khan 1993), nonmycorrhizal plant species (Anderson et al. 1984, Miller et al. 1999, Khan 1974), higher calcium levels, (Anderson et al. 1984), higher soil and water phosphorus levels (Wetzel and van der Valk 1996, Thormann et al. 1999), higher moisture content (Rickerl et al. 1994, Anderson et al. 1984), and higher pH (Wetzel and van der Valk 1996). Our results indicate that gradient also has a significant negative effect on AM colonization for at least two of the wetlands and that inundation in all sites has a significant negative effect on colonization. The wetter end of the gradient for all of our sites had higher pH, Ca, and soil moisture values which could be interacting with low oxygen conditions to further limit the AM fungi. However, it is not clear if AM colonization in this study or in other studies are indeed responding to one of the individual environmental factors listed

above or to a combination of some or all of them in the flooded soils. Nonetheless, AM fungi (including arbuscular structures) are found in flooded and saturated conditions, as evidenced by our results. All sites in this study, except Siebenthaler Fen (SF), show decreased colonization levels with higher soil water levels. The findings that colonization is higher at the wetter gradient end in SF is significant because, unlike the other sites, SF never had inundated soils at the wet end of the gradient. Instead, the soils at this part of the gradient were saturated, not flooded, suggesting that AM colonization is more largely controlled by flooding than by soil saturation. Literature has indicated that AM fungi in wetlands are present in wet soils by way of aerated roots or aerated soil microhabitats, the second of which is more likely in saturated soils than in flooded soils (Brown and Bledsoe 1996, Wetzel and van der Valk 1996, Turner et al. 2000).

Soil Moisture and Phosphorus Effects

All wetland sites combined, there were no associations between soil moisture or phosphorus and AM colonization levels. When sites are taken separately, small associations are revealed which include higher soil moisture levels with higher colonization levels at SF, higher soil moisture levels with lower colonization at TF, and higher colonization with higher phosphorus values in P deficient wetlands (TF and GP). Variation among the sites for the effects of soil moisture on colonization are most likely due to SF's soils never being subjected to flooding. Furthermore, the soils at SF dried up significantly more than the other three sites (as indicated by soil water levels). The significance of the AM fungi responding positively to higher soil moisture levels at SF needs further study. The results for soil moisture negatively affecting colonization at TF

support recent literature for wetland ecosystems (Lodge 1989, Wetzel and van der Valk 1996, Jurgensen et al. 1997, Miller et al. 1999). The other two sites, SV (a marsh) and GP (a fen to marsh gradient wetland), showed no correlation between AM colonization levels and soil moisture. Recent literature has shown that mycorrhizal dynamics in wetlands can be largely controlled by plant species present, flooding, fungal species present, and/or some other unknown environmental factor (Miller and Bever 1999, Stevens and Peterson 1996, van Duin et al. 1989, Clayton and Bagyaraj 1984). It is quite possible that one or all of these factors drive the mycorrhizal dynamics of SV and GP more-so than soil moisture or available phosphorus.

Because AM fungi increase fitness and growth of plants through enhanced uptake of nutrients (Lewis and Koide 1990, Smith and Read 1997), AM colonization levels are largely associated with available phosphorus (P) levels in the soil. It has been found in terrestrial ecosystems that increasing levels of available P will significantly reduce colonization because the plant will no longer need the fungus for nutrient uptake (Hayman and Mosse 1971, Koide 1993). Furthermore, it has been found that at very low levels of P (~<2pmm) both the AM fungus and the plant are P limited; thus, initially, higher levels of P will increase colonization by the fungus (Bolan et al. 1984, Koide and Li 1990). In wetlands, the associations found between P and colonization levels have been rather contradictory. Many studies have demonstrated the correlation, especially in the lab (White and Charvat 1999, Wetzel and van der Valk 1996, Tang et al. in review), while others lack evidence to support the correlation (Miller 2000, Miller et al. 1999). In some studies, the low levels of colonization in flooded soils are assumed to be related to the higher P availability in these anoxic/reduced soils, therefore diminishing the need for

AM fungi (Turner et al. 2000, Rickerl et al. 1994). This study does not support this assumption since P was actually less available at the wettest locations of all wetlands assessed. Interestingly, the AM fungi were not found to be correlated with soil available P except in very discrete instances. Only certain locations in Travertine Fen and Gingell Parcel (both P limited systems) had AM fungal colonization levels correlated with P. In TF, colonization levels were found to be higher with higher P for March through May in the dry and intermediate parts of the gradient. This is most likely due to the extremely low available P conditions at this site, which were probably magnified in March through May when the fungal association is most important for P uptake for the P limited plants. In GP, the wet end of the gradient showed a positive correlation between P and colonization. Because the wetter ends of all sites in this study had lower available P than elsewhere in the wetlands, the positive correlation at GP is probably also due to very low P availability.

It is possible that the scale at which AM fungi and plants are responding to P is so small in wetlands as to be generally overlooked in typical soil tests. For instance, Wigand and Stevenson (1997) have suggested that the mycorrhizal fungi are possibly responding to P sequestering within the oxygenated rhizosphere of wetland plants and could be helping the plant uptake this P. Seeing as many wetlands are dominated by plants that have been found to oxygenate their rhizosphere in flooded conditions (Armstrong 1978, Steinberg and Coonrod 1994), the link between AM fungi and the rhizosphere could be very important in controlling the mycorrhizal and plant community dynamics of wetlands. Furthermore, the possibility of an oxygenated rhizosphere helping AM fungi to survive in anoxic conditions has been suggested and needs further

experimental study. If it is only the rhizosphere dynamics that control AM fungi in wetlands, then minute and precise measurement devices need to be designed and assumptions about colonization levels and P levels need to be re-evaluated. The presence of arbuscules with the lack of correlation between colonization levels and P in our study indicates that the AM fungi in marsh and fen habitats must be involved in phosphorus enhancement at a microscopic scale such as that suggested by Wigand and Stevenson (1997).

Site Mycorrhizal Comparison

Interestingly, even though the four sites in this study show significant abiotic differences, mycorrhizae were ubiquitous. It was found that AM colonization levels were higher in the two strictly fen habitats (although not by much) which meets assumptions in recent literature that mycorrhizae will be more limited by marsh-like conditions (Turner et al. 2000, Thormann et al. 1999). This study indicates that, even though the fen habitats had higher colonization, both fen and marsh habitats are amiable to AM fungi and the fungi could have important implications for plant community dynamics in both types of wetlands. It is possible that the marsh habitats assessed could have higher levels of colonization than found in this study in years where the wetlands experience drawdowns due to drought. When this study was done, the marsh habitats did not show signs of drawdown, which has been noted in previous years. Miller (2000) found that AM colonization rose in plots that underwent seasonal drying and Brown and Bledsoe (1996) found that mycorrhizae were abundant in the channel site of a saltmarsh where there was frequent tidal inundation and retreat, leaving the soils periodically oxygenated. This

drawdown is assumed to be important in providing temporal availability of oxygen to the AM fungi and in allowing the association to become more functional (Cooke et al. 1993, Anderson et al. 1986, Miller 2000). Even without this drawdown, however, marsh habitats did support functional mycorrhizal associations (as indicative by the presence of arbuscules) which is in opposition to the findings of Thormann et al (1999). In their study, along a peatland gradient in Canada, they found that marsh vegetation was largely non-mycorrhizal and speculated this was due to the higher surface-water nutrient concentrations and fluctuating water levels of the marsh habitat.

Plant Community Dynamics and Species Effect

All plant species assessed in this study did show colonization levels of at least 10% at one time or another. The specific dynamics of the AM association in these plants add to the growing body of contradictory literature describing the mycorrhizal status of wetland plants. For instance, in this study, *Carex* species were found to be either lightly or moderately colonized depending on the wetland and depending on the location within a wetland. These results do support recent wetland studies involving the positive mycorrhizal status of *Carex* species (Miller et al. 1999, Turner et al. 2000, Wetzel and van der Valk 1996), although it also contradicts other reports of *Carex* species being nonmycorrhizal (Thormann et al. 1999, Khan 1974, Powell 1975, Anderson et al. 1984). Miller et al. (1999) surveyed 23 species of *Carex* and found 16 of these species to be mycorrhizal. Furthermore, they suggested that *Carex* species in their wetlands were either non-mycorrhizal, obligately mycorrhizal, or facultatively mycorrhizal depending on edaphic conditions. Our findings support that the mycorrhizal status of *Carex* may

largely be influenced by edaphic conditions; however, the data does not support the findings of Miller et al. (1999) who classify *Carex stricta* as a non-mycorrhizal species.

Typha latifolia was found to have the highest colonization levels of all plants in all wetlands. Once again this adds to a growing body of contradictory literature. Thormann et al. (1999), Anderson et al. (1984), and Rickerl et al. (1994) all found *Typha* species to be nonmycorrhizal while others have found it to be mycorrhizal, even in flooded conditions (Turner et al. 2000, Tang et al. in review, Stenlund and Charvat 1994). These contradictory reports could largely be due to the wetland soil factors influencing mycorrhizal associations more-so than the actual plant species being nonmycorrhizal. Two of the reports finding *Typha* species to be nonmycorrhizal (Thorman et al. 1999, Rickerl et al. 1994) took samples of the plant individuals only once (in July). Seeing as results from this study indicate significant seasonal effects on AM fungi with colonization levels highest in March and April and continuously declining after that, it is very possible that the *Typha* plants found in those other studies are mycorrhizal at times during the growing season when the plants were not sampled. Furthermore, some plants growing in locations with no flooding or with occasional drawdowns have been shown to be mycorrhizal in these locations at times when drawdown occurs and nonmycorrhizal in saturated or flooded soil conditions (Rickerl et al. 1994, Anderson et al. 1984, Lodge 1989). This signifies the need to sample seasonally throughout the wetland habitat to fairly assess the mycorrhizal condition of specific wetland plant species.

Many studies have speculated that AM fungi are surviving in flooded soils via tapping into the oxygen in the aerencyhma of plant tissue (Miller 2000, Keeley 1980), and Brown and Bledsoe (1996) have even found morphological evidence for this. The

observation that AM fungi are colonizing species such as *Typha* and other monocots in the flooded areas of the study sites indicates that the AM fungi may indeed be using these plants to survive anoxic conditions. *Typha* and other monocots are known to develop extensive aerenchyma (Steinberg and Coonrod 1994, Mitsch and Gosselink 1993, Crawford 1989) in which the AM fungi could survive. All but one of our sampling points had *Typha latifolia* heavily colonized by AM fungi. Potentially, *Typha latifolia* is acting as a propagule agent in which the fungi can survive during periods when the association is non-functional.

Many of the plants assessed in this study were moderately or heavily colonized by AM fungi. It is significant that some of these plants also showed the presence of arbuscules in the first three months of sampling. Arbuscules are known to be the site of phosphorus exchange from the fungus to the plant and indicate that the fungi are acting as mutualists for the plants (Smith and Read 1997). All but one of the species at TF were found to have arbuscules, indicating plant benefit in this very P deficient wetland. In this location, because the fungi are enhancing plant nutrition via the arbuscules, AM fungi have significant implications for plant competition, succession and diversity in fens (van der Heijden et al. 1998, Newman and Reddell 1988). The plants in the marsh habitats did not have as many arbuscules as those in fen habitats which could indicate that the AM fungi may support the mutualism via other morphological features or in environmental conditions not found during this study.

Wetland AM Fungal Spore Dynamics

Many recent studies have found spore numbers to decrease with soil moisture/wetness (Miller 2000, Miller and Bever 1999, Anderson et al. 1984, Brown and Bledsoe 1996, Khan 1974). Our data for TF, GP, and SF support these findings. SV is an exception in that higher spore numbers were found in the wettest location. This result is similar to the results of Rickerl et al. (1994) who found spore numbers to be higher in wetter soils in South Dakota peatlands. It is speculated by that study that, in flooded soils, spore formation was either stimulated or germination was inhibited by the anoxic conditions of the soil resulting in low spore numbers. The wet soils at SV in this study did experience flooding for the entire sampling period, thus the abundance of spores here could also be due to stimulation of spore formation or inhibition of germination. It has been found by Le Tacon et al. (1983) that, without adequate oxygen levels (=below 0.4% oxygen tension), spores of *Glomus mosseae* (Nicol. and Gerd.) Gerdemann and Trappe fail to germinate. Why this may have an influence for AM fungi in SV and not in the other sites where flooding also occurred is unknown at this time. It is possible that the differences in the type of fungi found at the wet end of the gradients have a significant factor on these results and indicates that different AM fungal species show a certain amount of ecological plasticity in their response to environmental conditions. Furthermore, as suggested by Miller and Bever (1999), AM fungi are not similar in their tolerance to flooded conditions, potentially explaining our finding that certain fungal species were more relegated to the dry soil while others were distributed throughout the dry-wet gradient.

The formation of AM associations, even in wetlands, is dependent upon the

availability of inoculum (Smith and Read 1997). Miller (2000) has shown that flooded soils have the same inoculum potential as dry soils if placed in the appropriate conditions (drier conditions). If spores indeed are restricted by flooded soils and could not serve as a primary inoculum source, there is potential for aerated roots of wetland plants, such as *Typha latifolia,* serving as inoculum sources in these flooded soils. In this study, the high levels of colonization in the springtime indicate that there is a significant source of inoculum in the soils of both fen and marsh habitats. This source could be spores in the driest soils, but, with spore numbers so low in the flooded soils, they are unlikely to be the source of inoculum in flooded soils. The majority of the flooded soils did have *Typha latifolia* plants, some of which had the highest levels of AM fungal colonization and, therefore, could be the key to the success of AM fungi colonizing in flooded soils.

In summary, our data indicates that wetland plants are mycorrhizal under a wide range of edaphic and moisture conditions. Furthermore, the data presented establishes that the colonization levels of AM fungi in wetlands are closely tied to specific plant species and plant phenology in which case each distinct wetland with a distinct plant community will have distinct mycorrhizal dynamics. The AM association is probably also regulated in wetlands by many interrelated factors associated with water levels. Although there were few correlations found between fungal colonization and P levels, there were indications of a mutualistic, functional relationship suggested by the presence of arbuscules. Since arbuscules were found at all gradient locations, we suggest that AM fungi are functional in all parts of fen and marsh wetland habitats at certain times. More likely than not, the functional relationship will be found at times when root growth is maximum, as in this study, and/or when wetland conditions are more conducive to the

AM fungi.

Because our data indicates a strong seasonal dynamic controlling the association in all gradient locations and in all plant species assessed, we suggest that future studies sample wetlands over a span of time to more fully understand the dynamics of mycorrhizae in wetlands. Since our results indicated locations where the soil samples revealed no AM colonization while specific plants indicated some colonization (and vice versa), we also recommend that both the soils and the plants are evaluated for the presence of mycorrhizae. Although the exact role of AM fungi in wetlands is still not fully understood, the results from this study imply that they are a significant component of the plant community. Because the AM fungi were found to be functional in these wetlands, it is expected that they are influencing plant diversity and competition by enhancing nutrient uptake, seedling establishment, and/or resistance to root pathogens (Newsham et al. 1995, Lewis and Koide 1990, Gange et al. 1993). Because of these implications, AM fungi should be considered in plans to restore wetlands to a functional status and should be a significant component of studies assessing reference wetland dynamics.

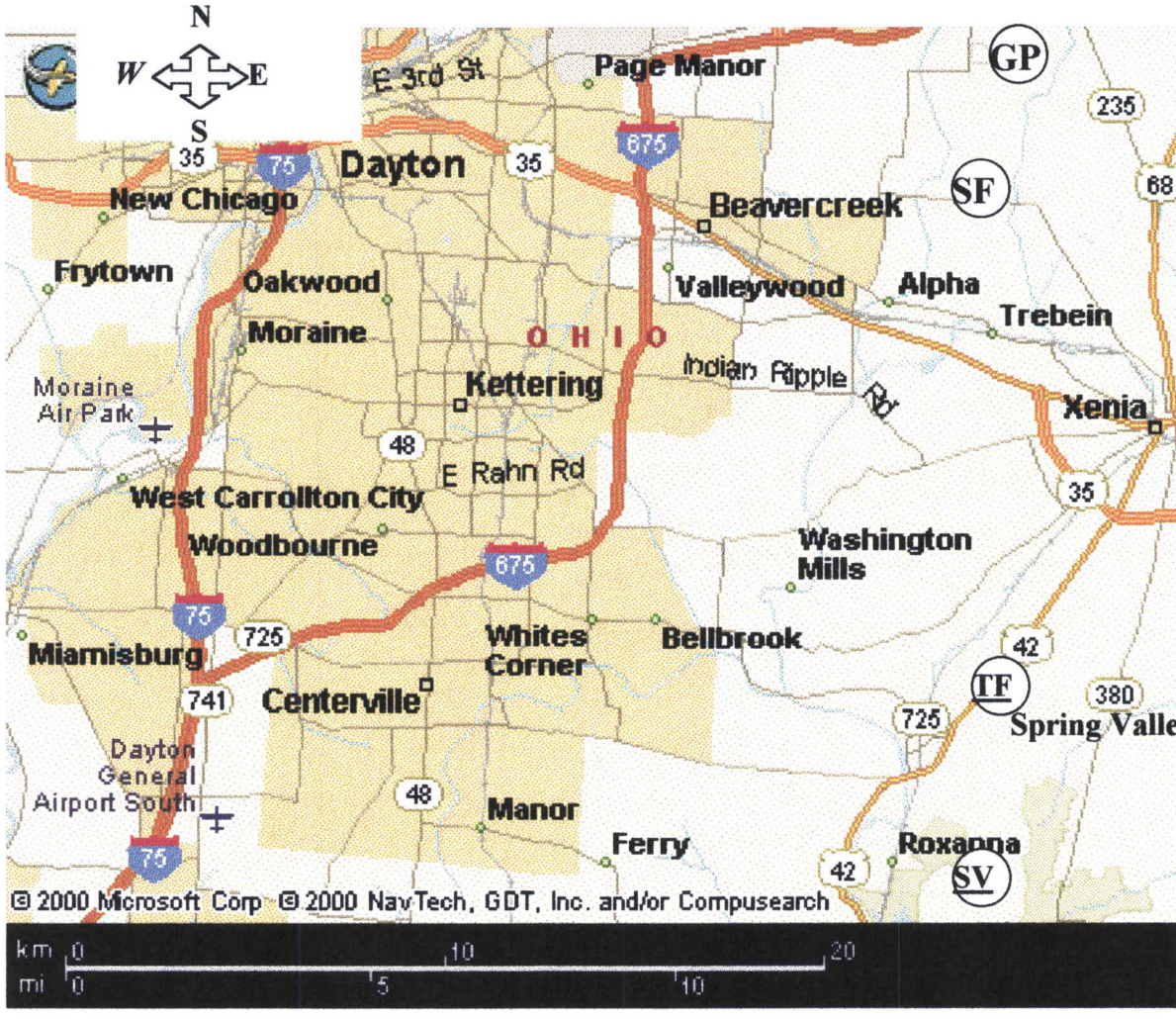

Fig 1: Map of the location of the four wetland sites. Site abbreviations are surrounded by circles.

Figure 2: Picture of Spring Valley Marsh Site in June, 2000.

Figure 3: Photograph of Gingell Parcel Site in June, 2000.

Figure 4: Photograph of Travertine Fen Site in June, 2000.

Figure 5: Photograph of Siebenthaler Fen Site in August, 2000.

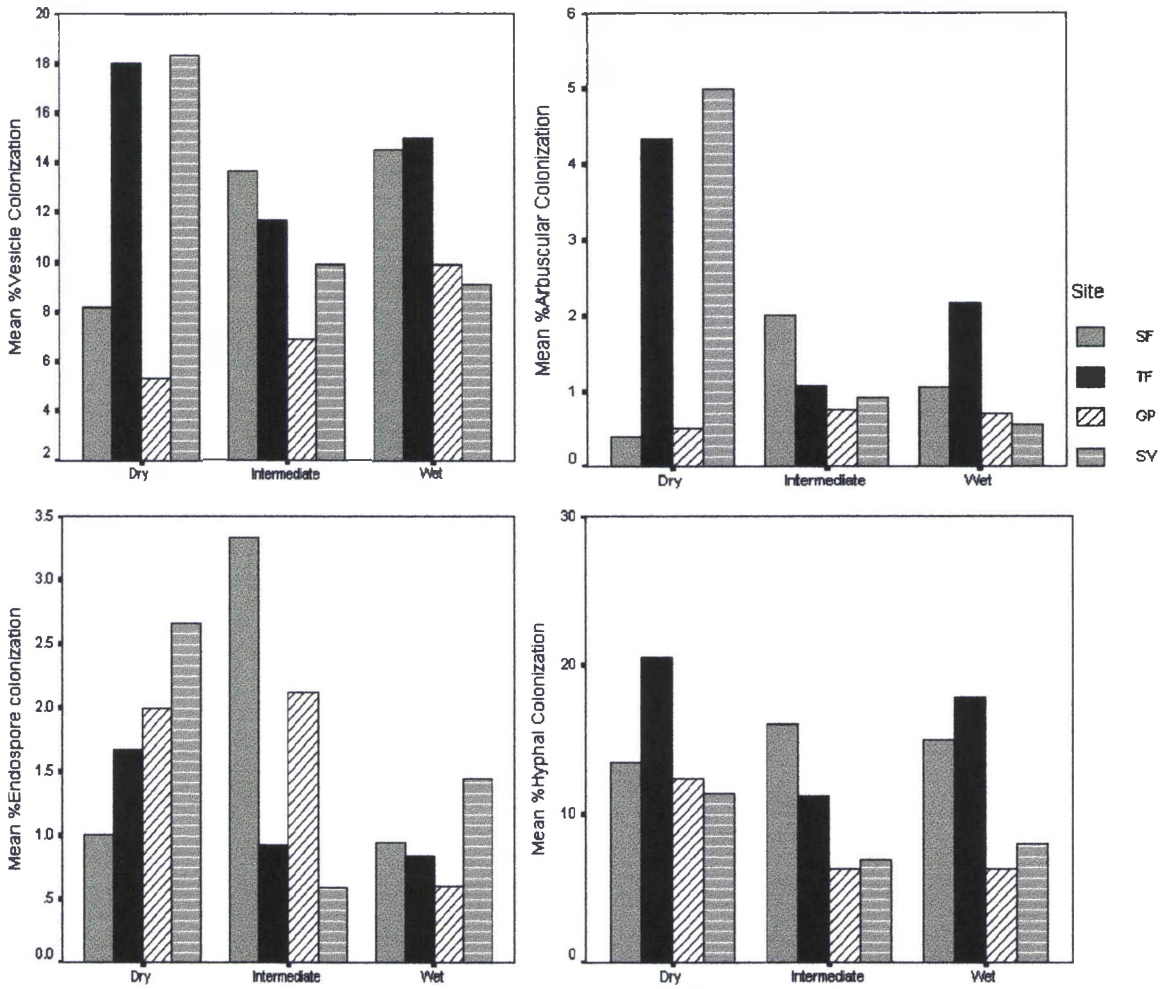

Fig 6: Mean percent colonization for individual AM fungal structures by site and by gradient location. Colonization levels are an average for all months. However, %AM colonization from March through June only is used for arbuscular data due to the infrequency of arbuscules after June.

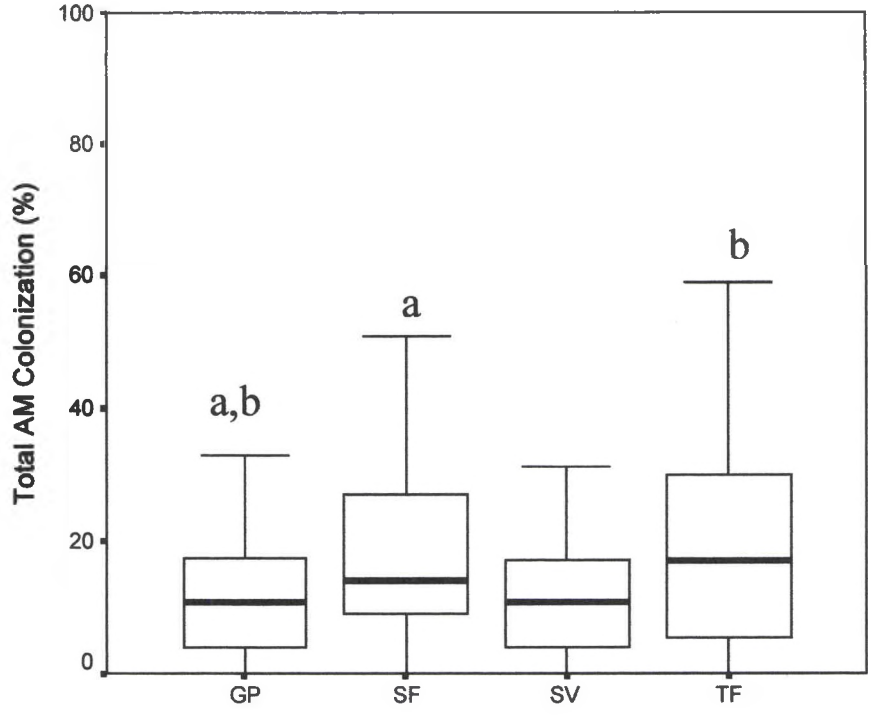

Fig 7: Boxplot of the total AM colonization levels for the four wetland sites. Horizontal black line in the box marks the median of the colonization levels. The hinges of the box indicate the 25th and 75th percentiles. Whiskers indicate the largest/smallest observed value that is not an outlier for each case. Letters that are similar indicate significance between the two sites ($p<0.05$). Median values are for colonization levels for the entire sampling season.

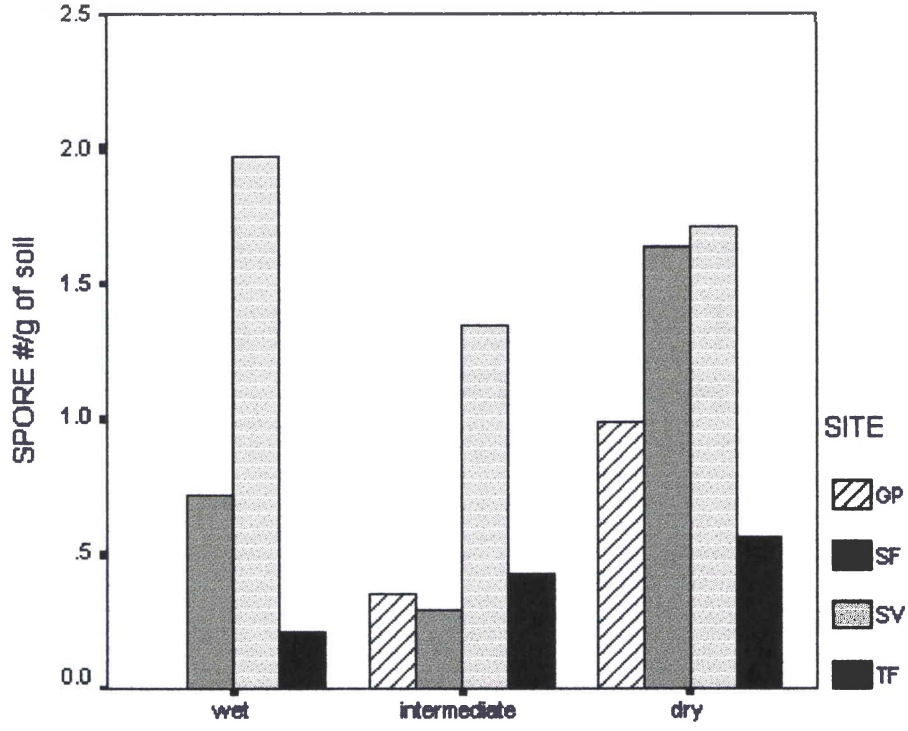

Fig 8: Mean spore numbers per gram of soil found at each part of the gradient in each wetland.

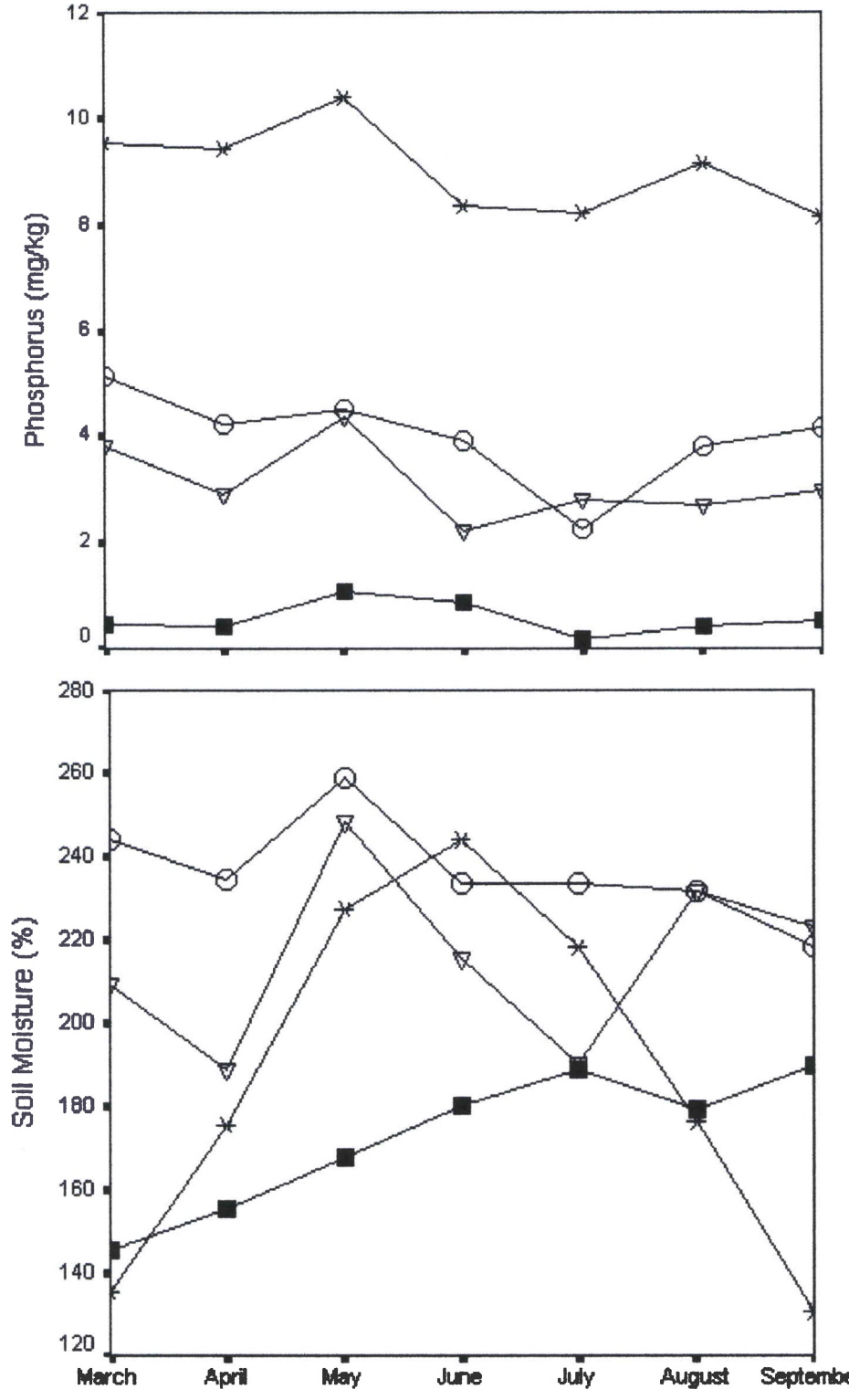

Fig 9: Mean soil available phosphorus and soil moisture levels for each month by each site. Sampling points along the transect were averaged. SF = circle, TF = square, GP = upside down triangle, SV = star.

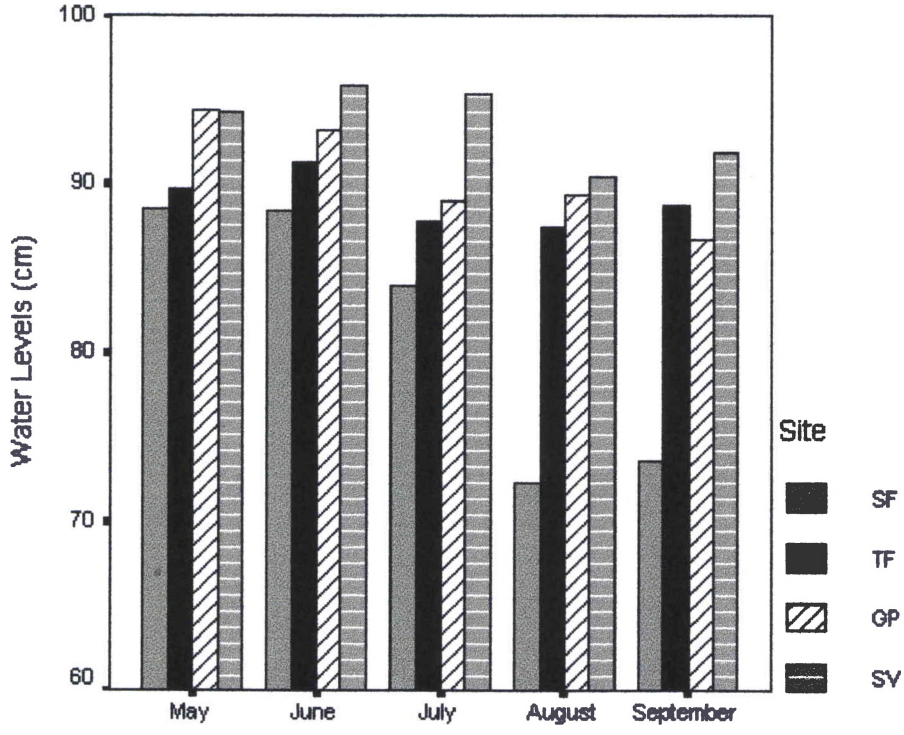

Figure 10: Water levels for each site in May through September. 100cm = soil saturation to the surface and all other water values (<100cm) indicate saturation below the soil surface.

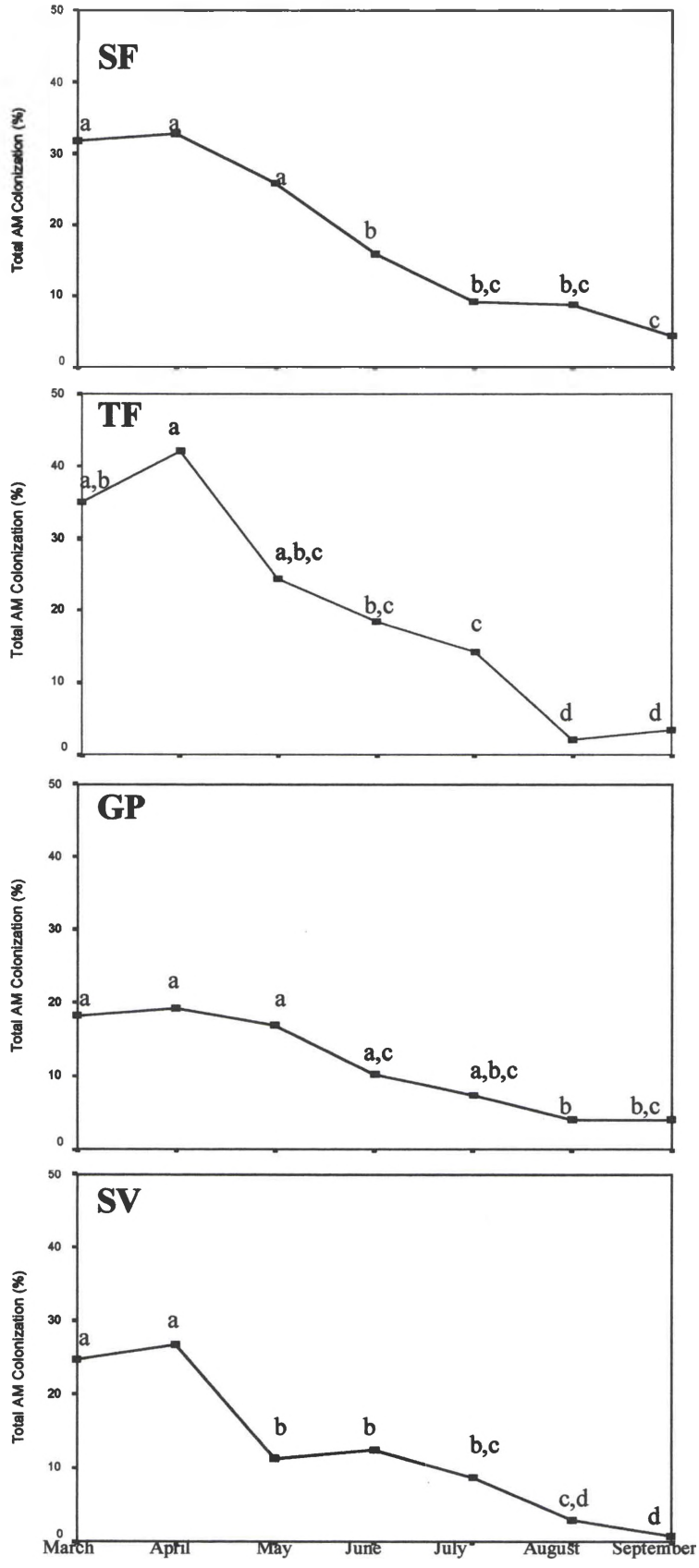

Fig 11: Mean monthly readings of total %AM colonization for each wetland site. Dissimilar letters indicate statistical significance ($p<0.05$) between months within each site.

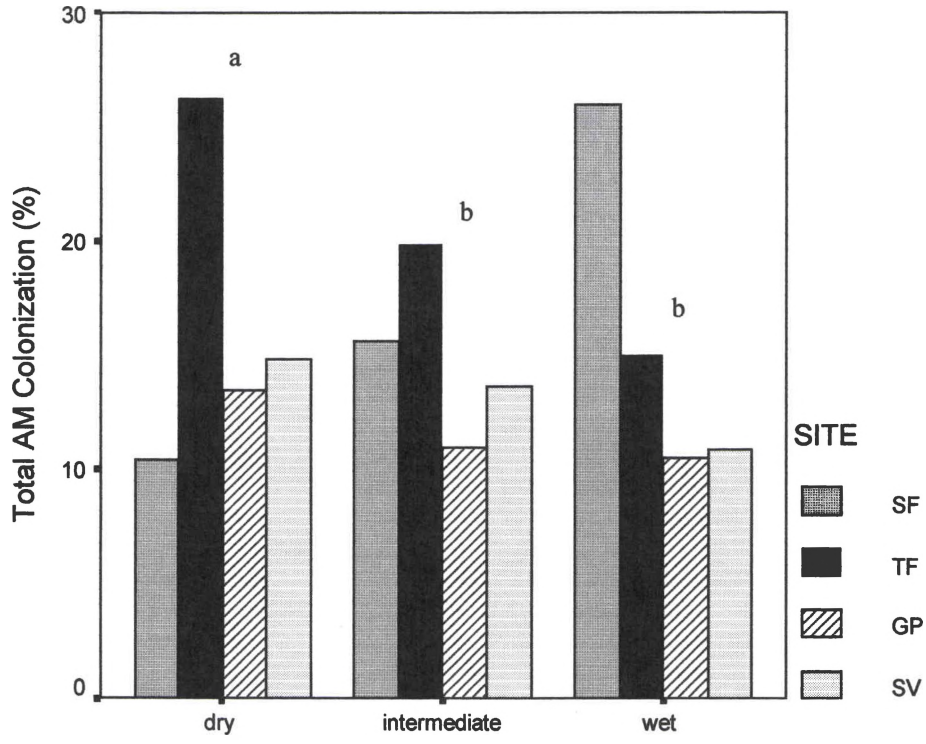

Fig 12: Mean gradient values of total %AM colonization for all sites. Dissimilar letters indicates statistical significance ($p<0.05$) between gradient locations.

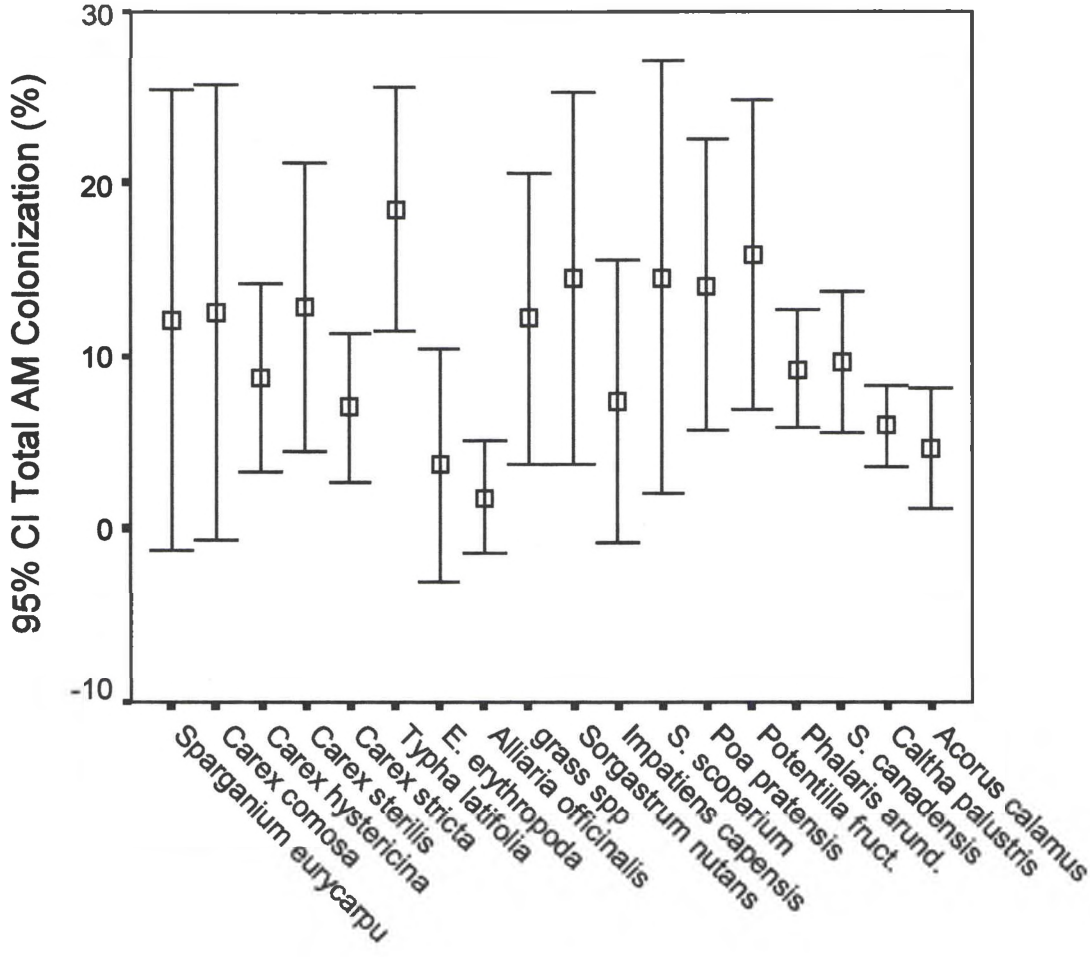

Fig 13: Error bar graph of %AM colonization of specific plant species selected for mycorrhizal analysis. Bars indicated 95% confidence interval. Boxes indicate mean %AM colonization for the data on each particular plant species.

Table 1: Plant and soil characteristics for the four sites Siebenthaler Fen (SF), Travertine Fen (TF), Gingell Parcel (GP), and Spring Valley Marsh (SV) and the three gradient positions. The values are means ± SE. Sample size for the sites is 56. Sample sizes for the gradient positions are 52 (dry), 46 (intermediate), and 62 (wet). The values for species diversity are the averages found at each sampling location in each wetland.

	Site				Gradient		
Variable	**SF**	**TF**	**GP**	**SV**	**Dry**	**Intermed**	**Wet**
Soil							
phosphorus ($\mu g\ g^{-1}$)	4.00 ±0.231	0.56 ±0.047	3.12 ±0.221	9.04 ±0.673	4.49 ±0.500	5.30 ±0.801	2.77 ±0.413
soil moisture (%)	236.42 ±9.756	172.37 ±10.794	215.24 ±13.057	186.72 ±18.245	149.18 ±12.454	207.23 ±11.895	261.44 ±13.841
organic matter (%)	41.97 ±1.196	17.27 ±1.047	27.20 ±1.978	23.13 ±1.603	27.42 ±2.211	28.57 ±2.100	26.49 ±1.170
calcium (lb/acre)	9912.80 ±35.81	9812.35 ±75.04	9357.73 ±155.73	8375.45 ±217.33	9186.65 ±174.76	9336.07 ±151.20	9534.97 ±114.61
magnesium (lb/acre)	1592.30 ±5.77	777.48 ±40.97	1388.00 ±35.13	1260.85 ±36.01	1308.13 ±56.30	1282.04 ±51.52	1189.48 ±41.94
pH	6.67 ±0.043	7.98 ±0.022	7.32 ±0.052	6.74 ±0.113	7.15 ±0.086	6.972 ±0.115	7.352 ±0.076
potassium (lb/acre)	130.45 ±8.94	51.73 ±3.82	109.60 ±4.80	116.98 ±8.26	118.67 ±8.69	98.37 ±7.38	91.19 ±5.13
Plant							
species diversity	11.95 ±0.43	7.73 ±0.33	7.38 ±0.44	7.30 ±0.44	10.10 ±0.37	8.63 ±0.57	7.29 ±0.33
% cover	77.13 ±3.52	75.50 ±4.22	73.88 ±3.61	77.25 ±3.46	78.75 ±2.87	74.78 ±3.89	74.44 ±2.94

Table 2: Spearman's Rank Correlation summary showing relationships between %AM colonization and Bray available soil phosphorus, Olsen available soil phosphorus, or % soil moisture. Correlation coefficients are done by site. (n = 56)

		% AM colonization	
Site	**Soil Variable**	**Spearman's rho**	**N**
SF	Bray P	0.194	56
	% moisture	0.335**	56
TF	Bray P	0.201	56
	%moisture	-0.354***	56
	Olsen P	0.351***	56
GP	Bray P	0.158	56
	%moisture	-0.157	56
	Olsen P	0.407**	56
SV	Bray P	0.068	56
	% moisture	-0.028	56

***P<0.01, **P<0.05

Table 3: Univariate analysis of variance of the effects of month and gradient on %AM colonization. %AM colonization data was arcsine square root transformed for this analysis. df = degrees of freedom.

Effect	df	Mean Square	F	P
SF				
Month	4	0.0535	5.631	0.002
Gradient	2	0.0172	1.806	0.183
Month*Gradient	5	0.0060	0.628	0.680
Error	28	0.0095		
TF				
Month	4	0.2500	45.445	<0.001
Gradient	2	0.0838	15.258	<0.001
Month*Gradient	8	0.0058	1.048	0.429
Error	25	0.0055		
GP				
Month	4	0.1070	6.537	0.001
Gradient	2	0.0370	2.256	0.126
Month*Gradient	8	0.0129	0.787	0.619
Error	25	0.0164		
SV				
Month	4	0.1260	39.714	<0.001
Gradient	2	0.0160	3.646	0.040
Month*Gradient	6	0.0058	1.830	0.131
Error	27	0.0032		

Table 4: AM status of the specific plant species selected for each sampling point in each wetland. All AM status levels are based on the highest colonization level found in that species at any one time during the study. Lightly = 5-25%; Moderately = 26-55%; Heavily = ≥56%. Wetland indicator status is based on the U.S. Fish and Wildlife Guidelines for Ohio. Sampling point 1 is the driest end of site and point 8 is the wettest end of site. Arbuscule presence is based on highest percentage found during the sampling season. No arbuscules were found after May.

Site	Plant Species	Indicator Status	AM Status	Arbuscule Presence
SF				
1	*Alliaria officinalis*	UPL	lightly	
2	*Solidago canadensis*	FACU	lightly	
3	*Caltha palustris*	OBL	lightly	
4	*Typha latifolia*	OBL	heavily	4%
5	*Carex hystericina*	OBL	lightly	
6	*Phalaris arundinacea*	FACW	lightly	
7	*Poa pratensis*	FACW	moderately	
8	*Carex stricta*	FACW	moderately	
TF				
1	*Sorgastrum nutans*	UPL	moderately	
2	*Schizachyrium scoparium*	FACU	moderately	1%
3	*Potentilla fructicosa*	FAC	heavily	4%
4	*Potentilla fructicosa*	FAC	moderately	2%
5	*Carex sterilis*	OBL	moderately	1%
6	*Carex sterilis*	OBL	lightly	
7	*Typha latifolia*	OBL	moderately	1%
8	*Typha latifolia*	OBL	heavily	11%
GP				
1	*Grass spp.*	UPL	moderately	
2	*Carex stricta*	FACW	lightly	
3	*Carex stricta*	FACW	lightly	
4	*Potentilla fructicosa*	FAC	moderately	
5	*Acorus calamus*	OBL	lightly	
6	*Acorus calamus*	OBL	lightly	
7	*Carex comosa*	OBL	lightly	
8	*Typha latifolia*	OBL	heavily	

Site	Plant Species	Indicator Status	AM Status	Arbuscule Presence
SV				
1	*Grass spp.*	UPL	heavily	
2	*Carex hystericina*	OBL	moderately	
3	*Impatiens capensis*	FACW	lightly	1%
4	*Typha latifolia*	OBL	heavily	
5	*Sparganium eurycarpu*	OBL	lightly	
6	*Carex comosa*	OBL	moderately	6%
7	*Eleocharis erythropoda*	OBL	lightly	
8	*Sparganium eurycarpu*	OBL	moderately	4%

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Chapter 4

Synthesis and Future Directions

Wetlands ecosystems are unique habitats that support highly diverse communities of plants and offer numerous functional roles for the environment and for humans (Mitsch and Gosselink 1993). Even though wetlands are highly valued for their functions, many undisturbed wetlands are lost to development. These wetlands are mitigated so that every acre of original wetland must be replaced with 1.5 acres of restored wetland. Of course, it is not yet known if this replacement value is sufficient for true replacement of the functional ecosystem. Furthermore, these restoration projects, unfortunately, are not always successful and the restored wetland can end up as a non-functional, low diversity ecosystem.

Many techniques are being developed to help improve the success of restoration projects and a large number of these techniques are developed through studying ecosystem dynamics in reference wetlands which are healthy and resilient ecosystems. One area of techniques currently being researched includes re-establishing soil microbial communities in the wetlands (Wolters 1999, Schneble 1997). The soil microbial communities of wetlands have a significant role with nutrient cycling in wetlands and potentially play a large role in plant community dynamics. One potentially important group of soil microbes are the arbuscular mycorrhizal (AM) fungi. For many years it was assumed that AM fungi were not capable of living in wetland ecosystems (Harley 1969, Khan 1974); however, now it is well known that they are colonizing wetland plants and could have a significant role in wetland ecosystem functions (Ragupathy et al. 1990, Wetzel and van der Valk 1996). Hence, this study set out to decipher which temporal and

gradient factors of wetlands regulate AM fungi in hopes to better understand their role in wetland ecosystems.

Generally, it is assumed that flooded soils limit the formation of AM associations in wetlands due to the low availability of oxygen; thus, it was hypothesized that habitats with flooded soils would have very low levels of colonization. Furthermore, it was hypothesized that the colonization levels of AM fungi in wetlands would be regulated by soil moisture, available phosphorus (P), and plant phenology as it is in uplands. Our data indicates that wetland plants are mycorrhizal under a wide range of edaphic and moisture conditions and may be only slightly limited by flooded soils. Interestingly, the AM fungi were not found to be correlated with soil moisture or available P except in very discrete instances. For available P, locations in Travertine Fen (a very P limited system) had AM fungal colonization levels correlated with P. In this wetland, the correlation was positive indicating that, besides just the wetland plants, the AM fungi are also limited by phosphorus levels at TF. Longer term research at this site and thorough evaluation of the phosphorus cycle within the soils and within the plants would provide important information on the AM association and its importance to P deficient fens such as TF. These types of fens tend to have high plant diversity which AM fungi could be promoting by diversifying the plant strategies for nutrient uptake. Investigations are needed in these systems that actually measure the possibility of AM fungi influencing plant diversity through enhanced nutrient uptake.

At Siebenthaler Fen (SF), soil moisture was a significant control of AM fungi with colonization increasing with moisture levels. This was unexpected since higher levels of moisture usually are found with lower colonization levels in wetlands. It is

assumed that this result was due to SF never having flooded soils and possibly being limited by soil moisture. Optimum soil moisture levels for AM associations have been found to be directly correlated with optimum moisture levels for plants in a given ecosystem (Lodge 1989, Stevens and Peterson 1996). It would be interesting to investigate if this holds true for the plants and AM fungi at SF. Another possibility is that AM fungi may have a role in drought resistance for wetland plants should the plants experience very dry soils (relatively speaking).

The significant effect of month (indicating seasonal variation) in this study was largely unexpected. It was hypothesized that the AM fungi would only show temporal dynamics if they were in a habitat experiencing seasonal drawdown. Seasonality of mycorrhizal associations is commonly found in terrestrial environments and is related to soil P, temperature, plant phenology, and soil moisture (Demars and Boerner 1995). In wetlands, however, seasonality of AM colonization levels are usually assumed to occur only in wetlands that experience drawdown, which would provide an opportunity for oxygenated soils (Brown and Bledsoe 1996, Miller and Bever 1999). Results of this study indicated that the AM fungi were largely controlled by temporal dynamics which were not related to drawdowns, soil moisture levels, or available P levels in any of the wetlands. It is speculated that the temporal variation of the fungi in these systems is largely tied to plant phenology which indicates that the fungi are most important (and maybe only important) at times of maximum new root and plant growth in the spring. The presence of arbuscules only in the spring further supports this conclusion. Longer term research, including following colonization levels year round, would help to verify if

AM fungi are most controlled by plant phenology in fen and marsh habitats as opposed to being controlled by abiotic factors.

Finding a large effect of month on mycorrhizae in wetlands suggests the need for research that does not include one time sampling. The current literature is dominated by studies using one time sampling (Wetzel and van der Valk 1996, Turner et al. 2000, Rickerl et al. 1994, Miller and Bever 1999, Cooke and Lefor 1990, Stevens and Peterson 1996, Thormann et al. 1999). The results of this study encourage more thorough evaluation of AM fungi in wetlands over many months, in many locations, and in many wetland plant species. For example, 100% of the plant species sampled in this study showed colonization by AM fungi, and 38% of these species had arbuscules in their cortical cells. Many of these plants assessed have been found by others to be either nonmycorrhizal or mycorrhizal depending on the study. Thoroughly examining the plants, including at different times of the year, might help to clarify this conflicting literature. It is suggested by Anderson et al. (1994) that single plant species may show strong dependence on AM fungi in one situation but not in another which, as indicated by this study, is quite likely in wetland ecosystems. The time differences in colonization and the plant species differences in mycorrhizal status could have important implications for maintaining diversity in wetland habitats.

As stated previously, our results indicated a slight effect of gradient on the colonization levels of AM fungi. However significant this effect is, it is still important to note that the AM fungi are somehow surviving and colonizing wetland plants in flooded soils. Even more important is the presence of arbuscules in the flooded soils indicating functionality of the association. The questions yet to be answered regarding this finding

revolve around the survival of AM fungi in anaerobic environments. Many have speculated that the AM fungi are able to obtain all of their oxygen from the aerenchymatous tissue or the rhizospheres of wetland plants. Brown and Bledsoe (1996) have even found morphological evidence for the AM fungi colonizing within the aerenchyma. Further research is needed to reveal if AM fungi are indeed using plant oxygen to survive in these habitats. The finding that *Typha latifolia* (having high amounts of developed aerenchyma) had the highest colonization levels of all plants at the four sites could be linked to the AM fungi using *Typha latifolia* as a survival mechanism in times of flooding. It is possible that the AM fungi are using this plant species' roots as a propagule source for new colonization events in the springtime. The potential for this should be examined, especially since the typical propagule source, spores, are infrequent in wetland soils (Miller 2000, Brown and Bledsoe 1996) and are typically not viable in the spring (Friese, personal communication).

Many studies, unlike this one, do not find the presence of arbuscules at all and doubt the functionality of the AM association (Cooke et al. 1993; Cantelmo and Ehrenfeld 1999; Thormann et al. 1999). The absence of arbuscules could be tied to many biotic and abiotic factors. In this study, the absence of arbuscules seems to be seasonally controlled indicating the lack of plant need for the association after maximum root and plant growth. Even without the arbuscules, however, the AM fungi are still colonizing wetland plants. This leads to several questions including 1) are the fungi functional without the arbuscules? 2) do the AM fungi possibly have another functional morphology under anoxic conditions? 3) are there factors outside of plant phenology that limit the functioning of AM associations in host plants? 4) is the periodic nonfunctional

association benign or parasitic? 5) what are the cost and benefits to both the plant and fungus for the association in anoxic soils? Answering these sort of questions should clarify the roles and benefits of AM fungi in wetlands. The presence of AM fungi in wetland soils, whether functional or not, indicates that there is, at some time, an advantage of having the association. The plant may be maintaining the AM fungal association simply to ensure benefit should conditions change (such as the soil drying up). It would be interesting to find out if arbuscules do increase in abundance when soils significantly dry up and if nutrient uptake is enhanced at these times.

Even with the many unanswered questions, this research still provides major evidence to the significance of mycorrhizae in wetlands and a better understanding of their seasonal dynamics. The results indicate that the specific type of wetland habitat or plant species does not necessarily exclude AM fungi from a wetland system. AM fungi may turn out to be more important in P limited systems (such as fens); however, this does not mean that significant AM fungal roles will not be found in nutrient rich habitats (such as marshes). Benefits of the association to the plant may include roles well beyond the typical enhancement of nutrient uptake, including, but not limited to, enhancing seedling establishment and flooding survival (Keeley 1980). Therefore, more wetland habitats should be examined in a way to elucidate other benefits of the AM association to the plant community, especially since this will have important implications for reestablishment and persistence of wetland plants in restored ecosystems.

The results of this study clearly indicate the importance of soil gradient and seasonal dynamics of AM fungi in wetland ecosystems. The differences found in spatial and temporal distributions of mycorrhizae in different wetland habitats have important

implications for growth room studies and wetland restoration. Knowing the dynamics of mycorrhizae in reference (undisturbed) wetlands will be helpful in developing successful restoration techniques for degraded and disturbed systems. These restoration techniques will, hopefully, focus specifically on the important role of soil microbial communities in the establishment of fully functional wetland ecosystems.

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Appendix A

Evaluation of Edaphic Factors Distinguishing Marsh Habitats from Fen Habitats

MATERIAL AND METHODS

Field Design

Beginning in March 1990 transects were set up for each of the four wetlands. They were aligned according to water gradients so that each transect had an upland habitat end and an end with an obligate wetland plant community (based on Ohio's wetland indicator categories). The length of the four transects varied because of the different sizes of the wetlands. Eight sampling points were selected along each transect to keep sampling number consistent. Sampling of these points began in March and continued once a month through September by using meter squared quadrats.

Soil Analysis

Two sets of soil cores were taken from four random places within each quadrat. Each core was 2.5cm in diameter and 15 to 20 cm deep. One set of soil cores was used to analyze general mycorrhizal colonization levels for each point along the transect (see Chapter 3) and to analyze soil characteristics. Within 24 hours of collection, this first set of soil samples was analyzed for percent moisture and organic content by using the procedures described by Brower and Zar (1984). These procedures included placing the soils in a drying oven for at least 24 hours at 100° C to determine the percent moisture and ashing the soils in a muffle furnace to determine organic content.

The other set of soil cores was air dried and sent to a soils lab (Balance Labs, Marion, OH) for analysis of several abiotic factors including Bray and Olsen phosphorus, pH, estimated mineralizeable nitrogen, potassium, calcium, magnesium, and cation exchange capacity.

Water Analysis

Where available, surface water was sampled for phosphate levels using a YSI 9000 Photometer (Yellow Springs Instrumentation, Inc). These phosphate levels were not statistically analyzed because of low sample size, but are presented for characterization of the water at the four wetland sites (Table 1).

Statistical Analysis

The soil variables measured (phosphorus, % moisture, organic matter, etc.) were not normally distributed and the variances were not homogeneous across the treatments; therefore, the variables were converted into ranks and statistical analyses were performed via Kruskal Wallis tests to test the significance of site and gradient effects.

Principal components analysis (PCA) summarizes patterns of correlations among observed variables and reduce a large number of variables to a smaller number of factors (components). PCA identifies the most important gradients along which the samples vary with respect to the original variables (Grimm and Yarnold 1995). For this study, PCA with varimax rotation was used to summarize the relationships between edaphic factors in the four different sites and for each month sampling occurred. Varimax rotation, an orthogonal rotation, of the eigenvectors was used to achieve simple structure

of the analysis and to improve the interpretability of the solution (Tabachnick and Fidell, 1989). Sample size was 56 for each month for all variables included in this analysis. All analyses were performed using SPSS Base 10.0 (SPSS 10.0; SPSS, Inc, 1999).

RESULTS

Soil and Water Characteristics

Soil characteristics by site and by gradient are given in Table 2. All variables were significantly influenced by site ($P<0.001$). SF had the highest calcium, potassium, magnesium, % soil moisture and % organic matter levels. Phosphorus levels varied significantly ($\chi^2 = 129.447$, $df = 3$, $P = 0.0001$) by site with SV having the highest levels and TF having the lowest levels (Fig 1). pH levels varied around neutral with SV soils having slightly acidic soils and TF having slightly basic soils. The two variables acting most similarly among the sites were soil moisture and organic matter. Highest values for these variables were found at SF and lowest values were found at TF.

Phosphorus (P) significantly ($\chi^2 = 11.562$, $df = 2$, $P = 0.003$) differed by gradient position with the intermediate section of the gradient having the highest levels of P and the wet section having the lowest levels. Percent organic matter showed a similar trend to phosphorus along the gradient although it was not significant. pH significantly differed along the gradient ($\chi^2 = 6.369$, $df = 2$, $P = 0.041$) with higher pH levels in the wet section of the gradient. Percent soil moisture (significant at $\chi^2 = 30.210$, $df = 2$, $P<0.001$) and calcium levels (not significant) rose as the gradient changed from dry to wet. On the other hand, magnesium showed an opposite trend with significantly higher ($\chi^2 = 7.112$, $df = 2$, $P = 0.029$) values at the dry end of the gradient.

Phosphorus and percent soil moisture values by month are shown in Figure 1. The trends are split into sites due to both variables having significant site effects. Month does have a significant ($\chi^2 = 13.377$, df = 6, P = 0.037) effect on phosphorus with May having the highest values and July having the lowest values. The effect of month on moisture is largely dependent on site and shows no overall trends among the sites.

Water phosphate levels are given in Table 1 for each month within each site. Due to varying water levels, not all points were sampled and some points were not sampled every month. SF water phosphate levels were similar within the intermediate and wet portions of the gradient that were sampled. The values slightly rose in June and July but fell back down by September. The water phosphate levels at TF acted slightly different between the two gradient locations sampled. The intermediate gradient phosphate levels rose steadily until August and then dropped off; however, the wet gradient phosphate levels rose quickly from April to May and then fluctuated throughout the season. GP had similarities between the two parts of the gradient sampled. The levels show an increasing trend from non-detectable levels of phosphate in April to levels around 0.70mg/l by September. Water phosphate levels at SV fluctuated and differed greatly according to the sampling point along the transect. Points 5 and 6 show a tremendous leap in phosphate levels between March and June and a drastic drop off after July.

Principal Components Analysis (PCA)

PCA was used to examine the relationship between patterns of soil characteristics and the different wetlands and also between patterns of soil characteristics and vegetation used for this study. PCA of the soil characteristics resulted in two components with

eigenvalues of 1 which together accounted for 72.059% of the variance of the original set of 8 variables. The first component had high loadings for magnesium, pH, phosphorus, and potassium and accounted for 38.5% of the variance (Table 3). Wetland sample points with high positive component 1 scores were enriched with a higher cation exchange capacity and higher Mg, P, and K contents while having lower pH values which loaded strongest on component 1 (Figure 2). Cation exchange capacity loaded weakly on component 1 and, therefore, was not used in interpreting the component. Along component 1 the marsh areas, including SV and areas of GP, had values grouped around zero. On the other hand, the two true fen areas, TF and SF plot out on opposite sides of the component 1 gradient with TF plotting at negative values of the component and SF plotting at positive values of the component.

The second component had high loadings for calcium, % organic content, and % moisture and accounted for 33.558% of the variance (Table 3). All three of these variables showed enrichment in the same direction (positive direction) along the gradient defined by component 2. Calcium had the highest loading values and, therefore, was the most important variable in defining component 2. Along component 2, the two fens and fen-like area of GP fall out relatively close together while SV and the marsh-like sites of GP fall out anywhere between the fen habitats and the opposite end of the component (Figure 2). Wetland sites with high positive component 2 scores tended to have high organic matter, soil moisture, and/or Ca content. SF sampling points showed high positive values for both principal components indicating that this site was enriched by all soil variables tested except for pH.

Figure 3 portrays the same principal components analysis but separates the points according to vegetation that was sampled within each wetland. Only plants that occurred in more than one location and/or wetland are shown. Component 1 portrays a clustering of *Carex sterilis* and *Potentilla fructicosa* at the negative end. At the positive end of this gradient is *Carex hystericina* while *Typha latifolia* can be found all along component 1. Component 2 produces a clustering of grass species at the negative end and sweet flag closer to the positive end. Most species portrayed in this plot have a rather wide spread distribution along one of the two components.

DISCUSSION

Comparative Dynamics of Wetland Habitats

The four sites in this study did show great variance in environmental factors and the combination of both components I and II of the principal components analysis (PCA) clearly divided the sites into separate entities. Component I was largely related to pH demonstrating that higher levels of available P, CEC, Mg, and K were found with lower levels of pH, as expected (Brady and Weil 2000, Richardson and Vespraskas 2001). This component significantly separated the two dominant fen habitats (SF and TF) which probably were most separated by their large differences in P and pH values. Brady and Weil (1990) found that when pH decreases, there is a decline in the percentage of P linked to Ca and, therefore, greater P availability. This is probably a very significant occurrence in these fen habitats that are highly saturated with calcium carbonates deposits from the groundwater (Turner et al. 2000, Jim Schneider, personal communication). SV was even further separated from TF than was SF largely due to SV having much higher

levels of available P (>9ppm) than TF (<1ppm).

Component II was important in separating locations within sites with higher organic matter buildup and/or calcium carbonate deposits. SF did have the overall highest organic matter content for the 4 sites (placing it on the positive end of component II); however, parts of all wetlands had high organic matter content as indicated by the PCA plot (Fig 2). Some areas of the two wetlands with marsh habitat (SV and GP) demonstrate very low values on component II indicating very low calcium deposits or very low organic matter buildup caused by periodic drawdowns (Richardson and Vepraskas 2001). Although TF had very high base saturation values for Ca (ranging from 83% to 97%), which should place it high on component II, its organic matter content, and thus soil moisture content, was the lowest of all 4 sites. This centered TF's soil characteristics around zero for component II. TF did have a large buildup of peat (i.e. organic matter), however the surface of this fen has a lot of calcium carbonate deposits that obscure the accumulation of organic matter, thus the mineral deposits having a greater effect than peat on the nutrient and mineral dynamics of this wetland.

All sites in this study were groundwater driven; therefore, it is not surprising that the sites have high levels of calcium or that the sites have decreased levels of available P in the flooded soils. Even though it is usually found that P is more available in flooded soils (Mitsch and Gosselink 1993, Richardson and Vepraskas 2001), the higher calcium concentration of the water could be tying up significant amounts of the available P in the soils of this study (Lindsay 1979, Brady and Weil 2000). It is also not surprising that TF has such low levels of P (<1ppm) because the peat at this wetland is extremely calcerous. The high P values in SV are expected as it is a true marsh habitat with soils that are

inundated. Its soils are largely mineral based and will be influenced by seasonal fluctuations in water levels allowing P to become more soluble (Turner et al. 2000, Mitsch and Gosselink 1993).

Plant Community Dynamics

Principal components analysis (PCA) of edaphic factors demonstrated the influences of environmental factors on plant species distributions within the wetlands studied. PCA (Fig 3) of the dominant plant species in the four sites of this study reveals many important patterns. In particular, *Typha latifolia* was found all along both components clearly revealing that these plants are generalists in wetland ecosystems. Their distribution in the PCA plot indicates their tolerance of a wide range of environmental conditions, hence their ability to establish and invade in many wetland types. Within the genus *Carex*, plants were also distributed along both PCA components. However, the four species assessed individually show a very narrow range of tolerance along component I which defines soils by pH, P, CEC, Mg, and K. *Carex stricta* and *Carex comosa* are centered around zero on component I indicating a lack of tolerance to extreme conditions, while *Carex sterilis* data points load where soil is low in P, CEC, MG, and K but has higher pH values. *Carex hystericina* lies at the opposite extreme tolerating higher available phosphorus and possibly less basic soils. All four *Carex* species show a wide range of tolerance along component II which defines soils enriched with organic matter content, calcium, and moisture. Other interesting relationships include *Acorus calamus* which lies around zero on both components indicating low tolerance to extremes, and grass species loading very low on component II indicating

tolerance to low organic matter concentrations (thus also low soil moisture levels) and/or low calcium concentrations.

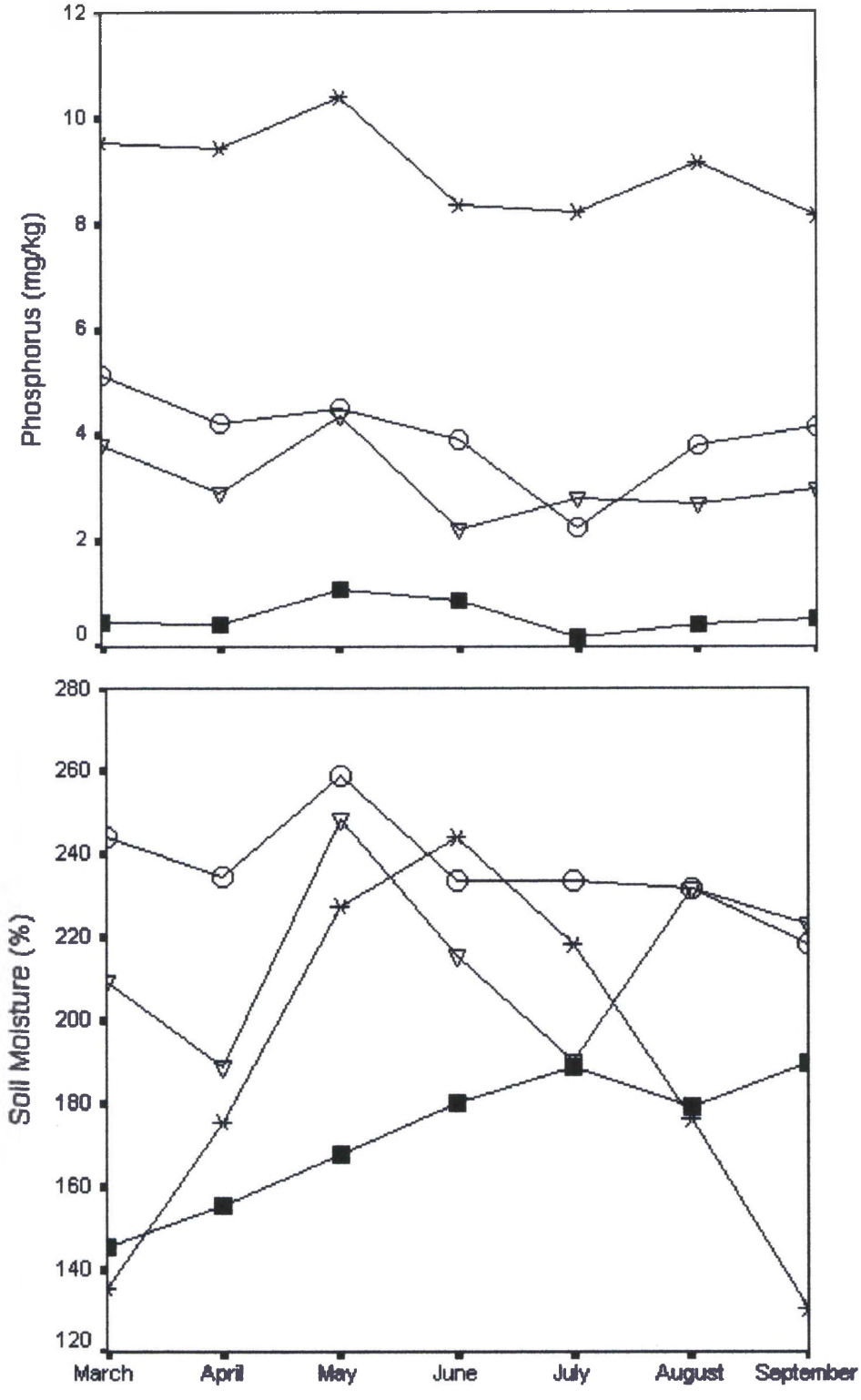

Fig 1: Mean soil available phosphorus and soil moisture levels for each month by each site. Sampling points along the transect were averaged. SF = circle, TF = square, GP = upside down triangle, SV = star.

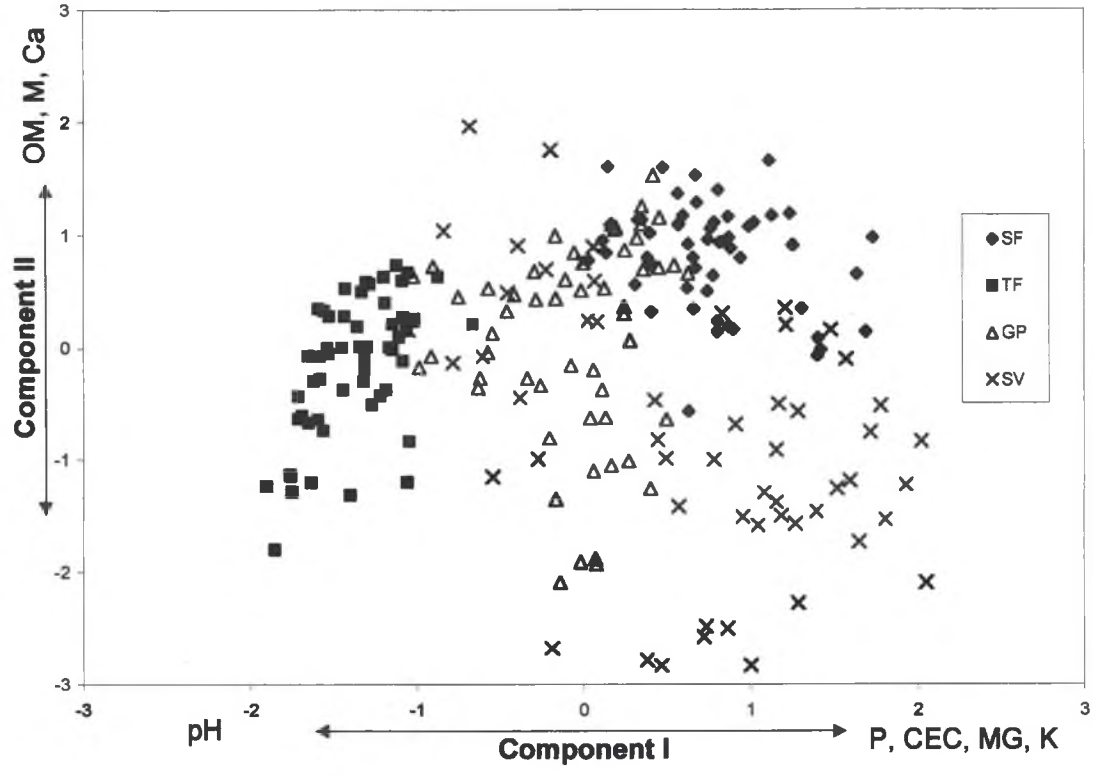

Fig 2: Principal components analysis of soil characteristics from wetland sites in March through September. Points are designated by site. (n = 56 for each site)

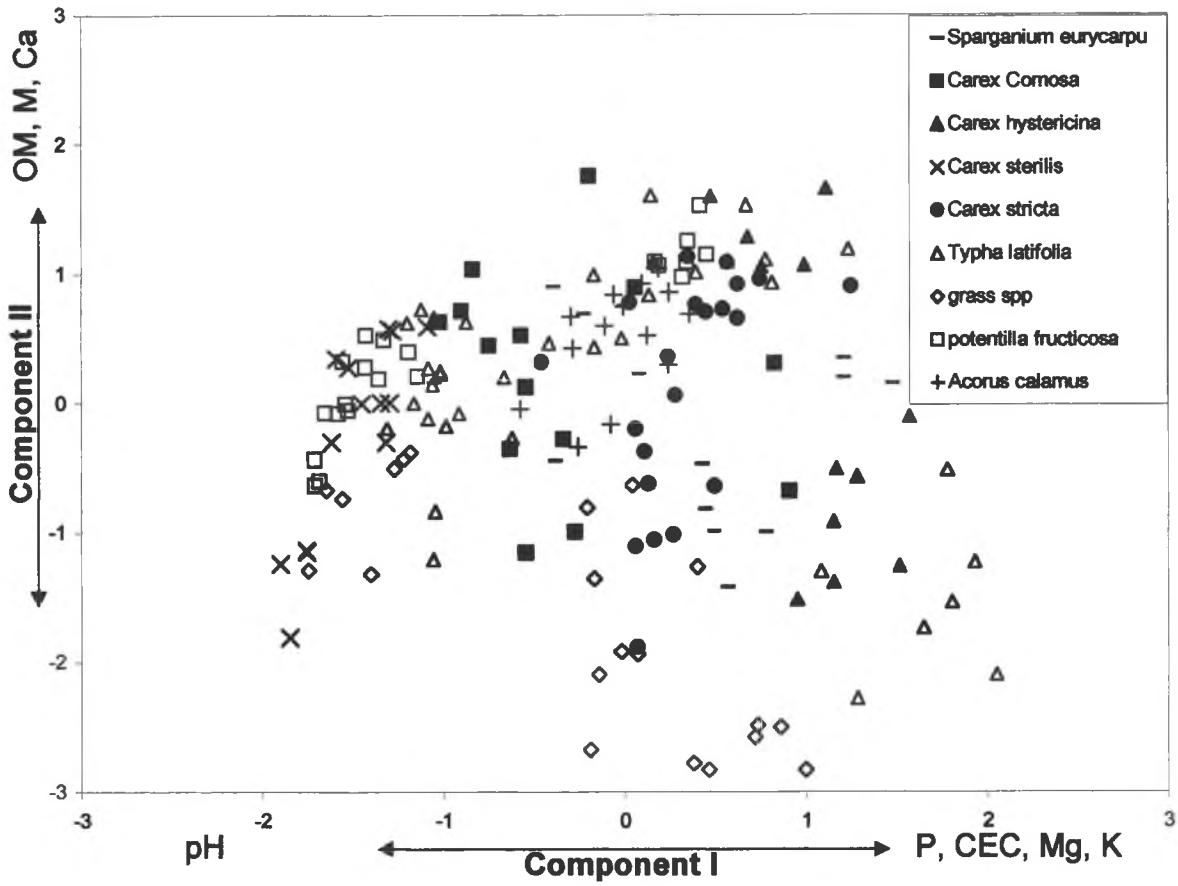

Fig 3: Principal components analysis of soil characteristics from wetland sites in March through September. Points are plotted by the plant species selected in that area. Only plant species that were selected in more than one location are shown.

Table 1: Water phosphate levels as determined by a YSI photometer for each month within each wetland. Locations where samples were taken are indicated by gradient location (dry, intermediate, or wet) and by sampling point location (1 = driest location, 8 = wettest location). Values are given as mg/l PO_4. Due to varying water levels, not all points were sampled and some points were not sampled every month.

LOCATION		Water Phosphate Value by Month						
Site	**Gradient Position**	**March**	**April**	**May**	**June**	**July**	**August**	**September**
SF								
	Intermediate (4)	0.12	0.07	0.36	0.48	0.46	0.28	0.12
	Wet (7/8)	0.16	0.14	0.14	0.34	0.54	0.14	0.20
TF								
	Intermediate (4)		0.16	0.36	0.4	0.56	0.72	0.46
	Wet (6)		0	0.44	0.48	0.28	0.40	0.42
GP								
	Intermediate (5)		0	0.42	0.42	0.48	0.40	0.75
	Wet (8)	0.08	0	0.40	0.30	0.44	0.44	0.61
SV								
	Wet (5/6)		1.03		3.75	4	0.75	0.48
	Wet (7)		0.94	0.38				
	Wet (8)	0.81	0.32	0.40	0.67	0.91	0.94	0.61

Table 2: Plant and soil characteristics for the four sites Siebenthaler Fen (SF), Travertine Fen (TF), Gingell Parcel (GP), and Spring Valley Marsh (SV) and the three gradient positions. The values are means ± SE. Sample size for the sites is 56. Sample sizes for the gradient positions are 52 (dry), 46 (intermediate), and 62 (wet). The values for species diversity are the averages found at each sampling location in each wetland.

	Site				Gradient		
Variable	**SF**	**TF**	**GP**	**SV**	**Dry**	**Intermed**	**Wet**
Soil							
phosphorus ($\mu g\ g^{-1}$)	4.00 ±0.231	0.56 ±0.047	3.12 ±0.221	9.04 ±0.673	4.49 ±0.500	5.30 ±0.801	2.77 ±0.413
soil moisture (%)	236.42 ±9.756	172.37 ±10.794	215.24 ±13.057	186.72 ±18.245	149.18 ±12.454	207.23 ±11.895	261.44 ±13.841
organic matter (%)	41.97 ±1.196	17.27 ±1.047	27.20 ±1.978	23.13 ±1.603	27.42 ±2.211	28.57 ±2.100	26.49 ±1.170
calcium (lb/acre)	9912.80 ±35.81	9812.35 ±75.04	9357.73 ±155.73	8375.45 ±217.33	9186.65 ±174.76	9336.07 ±151.20	9534.97 ±114.61
magnesium (lb/acre)	1592.30 ±5.77	777.48 ±40.97	1388.00 ±35.13	1260.85 ±36.01	1308.13 ±56.30	1282.04 ±51.52	1189.48 ±41.94
pH	6.67 ±0.043	7.98 ±0.022	7.32 ±0.052	6.74 ±0.113	7.15 ±0.086	6.972 ±0.115	7.352 ±0.076
potassium (lb/acre)	130.45 ±8.94	51.73 ±3.82	109.60 ±4.80	116.98 ±8.26	118.67 ±8.69	98.37 ±7.38	91.19 ±5.13

Table 3. Results of principal components analysis for all soil variables (n = 224).

Variable	Component I	Component II
P	0.727	-0.522
% Organic	0.401	0.784
% Moisture	-0.0307	0.774
K	0.736	-0.162
Ca	-0.134	0.829
Mg	0.780	0.403
pH	-0.891	-0.0972
CEC	0.654	0.561
Eigenvalue	3.080	2.685
% Eigenvalue	38.500	33.558
Sum % Eigenvalue	38.500	72.059

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Appendix B

Wetland Sites' Plant Species Lists

Wetland species indicator status according to the U. S. Fish and wildlife guidelines.

SIEBENTHALER FEN PLANT LIST

Scientific Name	Status	Common Name
Actinomeris alternifolia	FAC	Wingstem
Agrimonia parviflora	FAC	Small Flowered Agrimony
Agrostis alba	FACW	Redtop
Alliaria officinalis	FACU-	Garlic Mustard
Apios americana	FACW	Groundnut
Apocynum cannabinum	FACU	Indian Hemp
Asclepias incarnata	OBL	Swamp Milkweed
Aster novae-angliae	FACW	New England Aster
Aster puniceus	OBL	Purple-stemmed Aster
Aster sp.		
Bidens connata	OBL	Swamp Beggar Ticks
Bidens coronata	OBL	Tickseed Sunflower
Boehmeria cylindrica	FACW+	False Nettle
Caltha palustris	OBL	Swamp Marigold
Calystegia sepium	FAC-	Hedge Bindweed
Carex bromoides	FACW	Brome-like Sedge
Carex comosa	OBL	Bearded Sedge
Carex hystericina	OBL	Porcupine Sedge
Carex lupiliformis	FACW+	False-hop Sedge
Carex lupulina	OBL	Hop Sedge
Carex stipata	OBL	Stalk Grain Sedge
Carex stricta	OBL	Uptight Sedge
Carex tribuloides	FACW+	Blunt Broom Sedge
Cephalanthus occidental	OBL	Common Buttonbush
Chelone glabra	OBL	White Turtlehead
Cirsium arvense	FACU	Canada Thistle
Cirsium muticum	OBL	Swamp Thistle
Clematis virginiana	FAC	Virgin's Bower
Cornus amomum	FACW	Silky Dogwood
Cornus stolonifera	FACW+	Red-osier Dogwood
Cuscuta gronovii	NI	Common Dodder
Cyperus strigosus	FACW	Straw-color Flat Sedge
Eleocharis erythropoda	OBL	Bald Spikerush
Elymus villosus	FACU-	Hairy Wild Rye

Elymus virginicus var. virginicus	FACW-	Virginia Wild Rye
Eryngium yuccifolium	FAC	Rattlesnake Master
Eupatoriadelphus macula	FACW	Joe-pye Weed
Eupatorium perfoliatum	FACW+	Common Boneset
Euthamia graminifolia	FAC	Bushy Goldenrod
Galium palustre	OBL	Marsh Bedstraw
Geum laciniatum	FAC+	Rough Avens
Geum rivale	OBL	Water Avens
Glyceria striata	OBL	Fowl Manna Grass
Grass sp.		
Hierochloe odorata	FACW	Vanilla Grass
Humulus lupulus	NI	Common Hop
Impatiens capensis	FACW	Jewelweed
Ipomoea purpurea	UPL	Morning Glory
Iris shrevei	OBL	Southern Blueflag
Juncus dudleyi	NI	Dudley's Rush
Juncus tenuis	FAC-	Slender Rush
Justica americana	OBL	Common Water Willow
Lathyrus palustris	FACW+	Marsh Vetchling
Leersia oryzoides	OBL	Rice Cutgrass
Lobelia siphilitica	FACW+	Great Lobelia
Mimulus alatus	OBL	Winged Monkeyflower
Monarda fistulosa	UPL	Wild Bergamot
Muhlenberia schreberi	FAC	Nimblewill
Panicum dichotomiflorum	FACW-	Panic Grass
Pedicularis lanceolata	FACW	Swamp Lousewort
Phalaris arundinacea	FACW	Reed Canary Grass
Phytolacca americana	FACU+	Common Pokeweed
Pilea pumila	FACW	Clearweed
Poa palustris	FACW	Fowl Bluegrass
Poa pratensis	FACU	Kentucky Bluegrass
Polygonum hydropiper	OBL	Common Smartweed
Polygonum punctatum	OBL	Smartweed
Polygonum sagittatum	OBL	Tear Thumb Arrowleaf
Polygonum scandens	FAC	Climbing False Buckwheat
Rosa palustris	OBL	Swamp Rose
Rosa setigera	FACU	Prairie Rose
Rudbeckia triloba	FACU	Thin Leaved Coneflower
Rumex crispus	FACU	Curly Dock
Rumex orbiculatus	OBL	Great Water Dock
Rumex verticillatus	OBL	Swamp Dock
Scirpus acutus	OBL	Hard-stem Bulrush
Scirpus atrovirens	OBL	Green Bulrush
Solanum dulcamara	FAC-	Bittersweet Nightshade
Solidago canadensis	FACU	Canada Goldenrod
Solidago sp.		Goldenrod

Thalictrum polygamum	FACW	Tall Meadow Rue
Toxicodendron radicans	FAC	Poison Ivy
Triodia flava	NI	Purpletop
Typha latifolia	OBL	Cattail
Urtica dioica	FACU	Stinging Nettle
Valerianella umbilicata	FAC	Corn Salad
Verbana hastata	FACW+	Blue Vervain
Vernonia gigantea	FAC	Tall Ironweed
Viburnum lentago	FAC	Nannyberry

GINGELL PARCEL PLANT LIST

Scientific Name	Status	Common Name
Acorus calamus	OBL	Sweetflag
Actinomeris alternifolia	FAC	Wingstem
Ambrosia artemisiifo	FACU	Annual Ragweed
Angelica atropurpurea	OBL	Great Angelica
Aster puniceus	OBL	Purple-stemmed Aster
Bidens connota	OBL	Swamp Beggar Ticks
Bidens coronata	OBL	Tickseed Sunflower
Caltha palustris	OBL	Marsh Marigold
Calystegia sepium	FAC-	Hedge Bindweed
Carex comosa	OBL	Bearded Sedge
Carex stipata	OBL	Stalk Grain Sedge
Carex stricta	FACW	Uptight Sedge
Chelone glabra	OBL	White Turtlehead
Cirsium arvense	FACU	Canada Thistle
Coreopsis verticillata	NI	Whorled Coreopsis
Deschampsia cespitosa	FACW	Tufted Hairgrass
Eleocharis erythropoda	OBL	Bald Spikerush
Eupatorium perfoliatum	FACW+	Common Boneset
Equisetum arvense	FAC	Field Horsetail
Galium palustre	OBL	Marsh Bedstraw
Galium sp.		Bedstraw
Grass spp.		
Impatiens capensis	FACW	Jewelweed
Leersia oryzoides	OBL	Rice Cut Grass
Nasturtium officinale	OBL	True Water-cress
Pedicularis lanceolata	FACW	Swamp Lousewort
Pilea pumila	FACW	Clearweed
Polygonum amphibium	OBL	Water Smartweed
Polygonum punctatum	OBL	Smartweed
Potentilla fructicosa	FAC	Shrubby Cinquefoil
Rosa palustris	OBL	Swamp Rose
Sagittaria latifolia	OBL	Common Arrowhead
Salix nigra	FACW+	Black Willow
Salix sp.		Willow sp.
Sambucus canadensis	FACW-	American Elder
Scirpus atrovirens	OBL	Green Bulrush
Solanum dulcamara	FAC-	Bittersweet Nightshade
Solidago sp.		Goldenrod
Sparganium eurycarpu	OBL	Burreed
Symplocarpus foetidus	OBL	Skunk Cabbage
Typha latifolia	OBL	Cattail

Valerianella umbilicata	FAC	Corn Salad
Vernonia gigantea	FAC	Tall Ironweed

TRAVERTINE FEN PLANT LIST

Scientific Name	Status	Common Name
Acorus calamus	OBL	Sweetflag
Allium canadense	FACU	Meadow Onion
Allium tricoccum	FACU+	Wild Leek
Andropogon gerardi	FAC	Big Bluestem
Andropogon virginicus	FACU	Broomsedge
Asclepias incarnata	OBL	Swamp Milkweed
Asclepias verticillata	NI	Whorled Milkweed
Aster novae-angliae	FACW-	New England Aster
Bidens coronata	OBL	Tickseed Sunflower
Carex amphibola	FAC	Narrow Leaf Sedge
Carex frankii	OBL	Frank's Sedge
Carex hystericina	OBL	Porcupine Sedge
Carex lupuliformis	FACW+	False-hop Sedge
Carex squarrosa	FACW	Squarrose Sedge
Carex sterilis	OBL	Dioecious Sedge
Carex stipata	OBL	Stalk Grain Sedge
Carex stricta	OBL	Uptight Sedge
Carex suberecta	OBL	Prairie Straw Sedge
Cercis canadensis	FACU-	Redbud
Cirsium altissimum	NI	Tall Thistle
Cirsium arvense	NI	Canada Thistle
Cirsium muticum	OBL	Swamp Thistle
Coreopsis verticillata	NI	Whorled Coreopsis
Cornus Sp.		Dogwood Sp.
Deschampsia cespitosa	FACW	Tufted Hairgrass
Eleocharis erythropoda	OBL	Bald Spikerush
Eleocharis palustre	OBL	Creeping Spikerush
Equisetum arvense	FAC	Field Horsetail
Equisetum laevigatum	FACW	Smooth Scouring Rush
Eupatorium altissimum	NI	Tall Boneset
Eupatorium maculatum	FACW	Joe-pye Weed
Eupatorium perfoliatum	FACW+	Common Boneset
Festuca obtusa	FACU	Nodding Fescue
Fraxinus sp.		Ash
Gentiana clausa	FACW	Closed Gentian
Gentiana linearis	OBL	Narrow-leaved Gentain
Glyceria striata	OBL	Fowl Manna Grass
Grass sp.		
Helianthus tuberosus	FAC	Jerasulem Artichoke
Impatiens capensis	FACW	Jewelweed
Juncus brachycephalus	OBL	Small Head Rush
Juncus diffusissimus	FACW	Slim-pod Rush

Juncus dudleyi	NI	Dudley's Rush
Juncus torreyi	FACW	Torrey's Rush
Leersia oryzoides	OBL	Rice Cut Grass
Lobelia kalmii	OBL	Kalms Lobelia
Lobelia spicata	FAC-	Pale-spike Lobelia
Lysimachia lanceolata	FAC	Lance Leaved Loosestrife
Panicum lanuginosum	NI	Panic Grass
Parthenocissus quinquef	FACU	Virginia Creeper
Pilea pumila	FACW	Clearweed
Platanus occidentalis	FACW-	American Sycamore
Potentilla fructicosa	FAC	Shrubby Cinquefoil
Pycnanthemum pilosum	NI	Hairy Mountain Mint
Pycnanthemum tenuifolium	FACW	Narrow Leaved Mountain Mint
Pycnanthemum virginium	FAC	Virginia Mountain Mint
Rhus sp.		Sumac Sp.
Rhynchospora capillacea	OBL	Needle Beakrush
Rosa setigera	FACU	Prairie Rose
Rubus allegheniensis	FACU-	Common Blackberry
Rubus occidentalis	NI	Black Raspberry
Rudbeckia fulgida	FAC	Orange Coneflower
Rudbeckia hirta	FACU-	Black-eyed Susan
Rumex sp.		Dock Sp.
Salix sp.		Willow Sp.
Schizachyrium scoparium	FACU-	Little Bluestem
Scirpus acutus	OBL	Hard-stem Bulrush
Scirpus americanus	OBL	Olney's Bulrush
Scirpus atrovirens	OBL	Green Bulrush
Scirpus pungens	FACW+	Three Square Bulrush
Silphium trifoliatum	NI	Whorled Rosinweed
Solidago riddellii	OBL	Riddell's Goldenrod
Solidago graminifolia	NI	Lance Leaved Goldenrod
Solidago ohioensis	OBL	Ohio Goldenrod
Solidago patula	OBL	Rough-leaf Goldenrod
Solidago sp.		Goldenrod Sp.
Sorgastrum nutans	UPL	Indian Grass
Sorghum halapense	FACU	Johnson Grass
Thalictrum pubescens	FACW+	Tall Meadow Rue
Toxicodendron radicans	FAC	Poison Ivy
Typha latifolia	OBL	Broad-leaf Cattail
Verbesina alternifolia	FAC	Wingstem
Vernonia gigantea	FAC	Tall Ironweed
Veronica scutellata	OBL	Marsh Speedwell

SPRING VALLEY MARSH PLANT LIST

Scientific Name	Status	Common Name
Achillea millefolium	FACU	Common Yarrow
Agrimonia parviflora	FAC	Small Flowered Agrimony
Allium sp.		Wild Onion
Asclepias incarnata	OBL	Swamp Milkweed
Aster sp.		Aster
Avena fatua	NI	Wild Oats
Bidens frondosa	FACW	Beggar Ticks
Bidens sp.		
Boehmeria cylindrica	FACW+	False Nettle
Bromus sp.		Grass
Carex comosa	OBL	Bearded Sedge
Carex granularis	FACW+	Meadow Sedge
Carex hystericina	OBL	Porcupine Sedge
Carex lupulina	OBL	Hop Sedge
Carex stipata	OBL	Stalk Grain Sedge
Carex vulpinoidea	OBL	Fox Sedge
Calystegia sepium	FAC-	Hedge Bindweed
Chelone glabra	OBL	White Turtlehead
Commelina commmunis	FAC-	Dayflower
Cornus stolonifera	FACW+	Red-osier Dogwood
Cyperus strigosus	FACW	Straw-color Flat Sedge
Daucus carota	FACU	Queen Anne's Lace
Deschampsia cespitosa	FACW	Tufted Hairgrass
Eleocharis erythropoda	OBL	Bald Spikerush
Equisetum arvense	FAC	Field Horsetail
Erechtites hieraciifolia	FACU	Pilewort
Eupatoriadelphus macula	FACW	Joe-pye Weed
Eupatorium perfoliatum	FACW+	Common Boneset
Festuca pratensis	FACU-	Meadow fescue
Galium palustre	OBL	Marsh Bedstraw
Grass sp.		
Hydroctyle ranuncul	OBL	Floating Pennywort
Impatiens capensis	FACW	Jewelweed
Juncus effusus	FACW+	Soft Rush
Kuhnia eupatorioides	NI	False Boneset
Leersia oryzoides	OBL	Rice Cutgrass
Lycopus uniflorus	OBL	Northern Bugleweed
Mimulus ringens	OBL	Alleghany Monkeyflower
Pastinaca sativa	NI	Wild Parsnip
Phalaris arundinacea	FACW	Reed Canary Grass
Pilea pumila	FACW	Clearweed
Plantago lanceolata	UPL	English Plaintain

Polygonum hydropiper	OBL	Common Smartweed
Polygonum punctatum	OBL	Smartweed
Polygonum sagittatum	OBL	Tear Thumb Arrowleaf
Rumex orbiculatus	OBL	Great Water Dock
Sagittaria latifolia	OBL	Common Arrowhead
Salix nigra	FACW+	Black Willow
Scirpus acutus	OBL	Hard-stem Bulrush
Scirpus atrovirens	OBL	Green Bulrush
Scirpus cyperinus	OBL	Woolgrass
Scirpus validus	OBL	Soft-Stem Bulrush
Scutellaria epilobiifolia	FACW	Marsh Skullcap
Setaria glauca	FAC	Yellow Bristle Grass
Silphium terebinthinace	FACU	Prairie Dock
Sium suave	OBL	Water Parsnip
Solidago sp.		Goldenrod
Sparganium eurycarpu	OBL	Burreed
Trisetum pennsylvanicum	OBL	Swamp Oat
Typha latifolia	OBL	Cattail
Urtica dioica	FACU	Stinging Nettle
Urtica procera	NI	Tall Nettle
Verbana urticifolia	FACU	White Vervain
Vernonia gigantea	FAC	Tall Ironweed
Viola cucullata	FACW+	Marsh Blue Violet

CURRICULUM VITAE

Kelly E. Bohrer

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EDUCATION

- BS in Environmental Biology, magna cum laude, *University of Dayton*, 1996.
- Completion of 1 year towards a MS in Ecology/Biology, *Utah State University*, 1997.
- MS in Biology, *University of Dayton*, anticipated graduation – August, 2001.

PROFESSIONAL SOCIETIES

Sigma Xi, The Society for Ecological Restoration, Society of Wetland Scientists, and Beta Beta Beta Alumni.

AWARDS

- Graduate Introductory Lab Outstanding Teaching Award, University of Dayton, 2001
- Environmental Biology Award of Excellence, University of Dayton, 1996.
- Recognition for design and management of Cox Arboretum Environmental Education and Reclamation Project, 1996.
- All American Scholar Collegiate Award, 1993-1996.
- University Scholar and Dean's List, University of Dayton, 1992-1996.
- Nominated for University of Dayton Employee of the Year, 1996.

FELLOWSHIPS AND GRANTS

"A comparative study of the seasonal plant and mycorrhizal community dynamics of fens and marshes in Greene County, Ohio." Graduate Student Fellowship Program, University of Dayton, 2000.

"A comparative study of the seasonal plant and mycorrhizal community dynamics of fens and marshes in Greene County, Ohio." Ohio Biological Survey Small Grants Program, 2000.

GRADUATE TEACHING ASSISTANTSHIPS

- University of Dayton: Taught introductory biology labs for both majors and non-majors. 1999-present.
- Utah State University: Taught introductory biology labs for majors and prepped labs. 1996-1997.

RELEVANT EXPERIENCE

Land Stewardship Technician, 1999.
Five Rivers MetroParks *Dayton, OH*
Coordinated MetroParks covermapping project. Developed and assisted in leading covermapping training programs, covermapped, organized volunteers, and developed covermapping GIS database with Excel, Arc View, and Arc Info.

Project Manager, 1995 – 1996.
Cox Arboretum *Dayton, OH*
Planned, coordinated, and developed a management plan for the reclamation of a

wetland/prairie ecosystem. Included performing vegetation and land use analyses, interacting with public and private sectors for funding and planning, and designing a trail system for environmental education purposes.

Naturalist Intern, 1995.
Cox Arboretum *Dayton, OH*
Developed and implemented environmental education programs for all ages which included hikes, classes, and a summer camp. Worked with volunteers and staff for special programs and events.

RESEARCH ASSISTANTSHIPS

"Animal disturbances in rangeland ecosystems: Soil processes and plant community dynamics." 1996. USDA grant. Carl F. Friese and Tom O. Crist, Principle Investigators.

Tracking movement and documenting habitat use of Sage Grouse in Southwestern Colorado for a habitat improvement plan. 1996. Colorado Division of Wildlife, CO.

TECHNIQUES

Mycorrhizae: AM mycorrhizal root staining, gridline intersection method for root colonization assessment, spore extraction
Soil Analysis: Moisture content, organic content, pH, available phosphorous
Molecular: DNA digests, Cloning, PCR/RTPCR, Gel electrophoresis, Western/Southern Blot
GIS: Arc Info and Arc View
Plant Community Analysis: Diversity and cover, covermapping
Computers: Microsoft Office, SPSS, BioBase; photo editors (with digital cameras)

PRESENTATIONS

Bohrer, Kelly. Seasonal and Soil Gradient Dynamics of Arbuscular Mycorrhizae in Differing Wetland Habitats.
Will be presented at: National Conference for the Society of Wetland Scientists, Chicago, IL, 2001.

Kulik, Mike; ***Bohrer, Kelly***; and Friese, Carl. The Dynamics of AMF spores in four Dayton area wetlands.
Presented at: Stander Symposium, University of Dayton, 2001.

Miller, Ryan; ***Bohrer, Kelly***; and Friese, Carl. A study on soil and water quality in Southwestern Ohio fen and marsh habitats.
Presented at: Stander Symposium, University of Dayton, 2001.

Bohrer, Kelly. A comparative study of the seasonal plant and mycorrhizal community dynamics of fens and marshes in Greene County, Ohio.
Presented at: Ohio Biological Survey Annual Meeting, Columbus, OH. 2000.

Bohrer, Kelly and Carl F. Friese. Development of Conservation Corner: A model for ecological education and restoration at Cox Arboretum and Gardens, Dayton, OH.
Presented at: International Conference for Society of Ecological Restoration, San Francisco, CA. 1999.

Adler (Bohrer), Kelly. Development of a plan for environmental management and education at Cox Arboretum (Conservation Corner).
Presented at: Stander Symposium, University of Dayton, 1996.