



Influence of Changing Water Sources and Mineral Chemistry on the Everglades Ecosystem

By Paul V. McCormick and Judson W. Harvey

Administrative Report

Prepared for the U.S. Fish and Wildlife Service

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U.S. Geological Survey, Reston, Virginia 2007

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Contents

Executive Summary	1
Introduction	3
The Potential Significance of Mineral Chemistry in the Everglades	3
Sources and Measures of Mineral Content	5
Importance of Mineral Chemistry in Peatland Ecosystems	6
Classification and Evolution of Peatlands with Respect to Their Mineral Status	6
Ecological Effects	9
Biogeochemical Processes	9
Vegetation responses.....	10
Causes of vegetation change across mineral gradients	13
Everglades Water Sources, Mineral Chemistry, and Associated Ecological Features	15
Water Sources to the Predrainage and Managed Everglades	15
Influence of Water Source on the Mineral Chemistry of Everglades Peatlands	16
Precipitation	17
Lake Okeechobee Overflows	18
Interactions between Surface Water and Ground Water	18
Role of Ground Water in the Predrainage Everglades	19
Role of Ground Water in the Managed Everglades	20
Canal Discharges	21
Relative Importance of Flows Supplied by Canals and Ground Water	25
Mineral Sources to EAA Canals	26
Natural chemical limits to ombrotrophy in the Everglades.....	27
Loxahatchee Refuge: Case Study of a Rainfall-Driven Everglades Peatland	30
Effects of canal-water intrusion on Refuge water chemistry.....	31
Effects of canal-water intrusion on Refuge soil chemistry	35
Ecological effects of mineral enrichment in the Refuge.....	38
Biogeochemical Processes	38
Responses of Everglades Vegetation	43
Response of Everglades Periphyton	49
Potential Responses of Aquatic Fauna and Food Webs	53
Conclusions: Current Understanding and Information Gaps	53
The spatial extent and chemistry of the historic soft-water Everglades.....	54
The relationship between canal flows and mineral concentrations in Everglades wetlands	55
Ecological effects of increased mineral loading.....	55
Hydrologic measurements and modeling of canal flows and mixing within the Everglades	56
Acknowledgements	56
References Cited	58

Figures

Figure 1. Map of south Florida showing major hydrologic units of the Everglades and the canals (solid lines).....	
Figure 2. Distribution of different peatland types across regional mineral gradients in Sweden. Peatland types are color-coded.....	
Figure 3. Specific conductance of major water sources to the present-day Everglades, including bulk atmospheric deposition, Lake Okeechobee surface water, and canal discharges from major SFWMD pump stations.....	22
Figure 4. Surface-water specific conductance in canals across the Everglades as measured during U.S. EPA surveys.....	23
Figure 5. Patterns of surface-water specific conductance across the Everglades and adjacent wetlands as measured during U.S. EPA surveys.....	24
Figure 6. Relative importance of EAA canals as a source of surface water in WCA 2A as indicated by sulfate:chloride ratios.....	26
Figure 7. Relationship between surface-water specific conductance and water depth at an interior (LOX8) and a canal-influenced (LOX10) monitoring station in the Refuge based on monthly data collected between 1994 and 2004.....	27
Figure 8. Ratios of the concentration of major ions in surface water from an interior Refuge location (LOX8) to that in rainfall. The ratio for Cl ⁻ , which approximates the predicted value if rainfall were the sole mineral source, is shown by the dashed line.....	29
Figure 9. Surface-water specific conductance and total phosphorus across transects monitored by the SFWMD in the southwest corner of the Refuge.....	32
Figure 10. Spatial patterns for surface-water specific conductance across the Refuge and adjacent rim canals.....	32
Figure 11. Temporal (A) and seasonal (B) patterns for the difference in water stage between gaging stations in the western rim canal (S10Dh gage) and the interior (LOX8) of the Refuge for the period 1994 to 2005.....	33
Figure 12. Relationship (with Spearman Rank correlation) between specific conductance at a canal-influenced monitoring station (LOX10) in the Refuge and the stage difference between the western rim canal (S10Dh gage) and the Refuge interior (LOX8), which indicates the potential for canal-water movement into the Refuge.....	35
Figure 13. Changes in available soil mineral concentrations (as estimated by Mehlich-1 extractions) in the 0-30 cm depth increment in three vegetation types in the Refuge interior (open bars) and near the Refuge perimeter (shaded bars).....	35
Figure 14. Relationships between surface-water specific conductance and total Ca and P in the surface-soil-litter layer of sawgrass stands measured by USGS across the Refuge during February 2004.....	37
Figure 15. Relationship between surface-water specific conductance and the sulfur content of live sawgrass measured by USGS across the Refuge during February 2004.....	38

Figure 16. Surface-water sulfate and soil sulfur concentrations measured by USGS at 12 monitoring sites along a 22-km transect across the central Refuge..... 39

Figure 17. Phosphorus and nitrogen fractions in soil cores (0-20 cm depth increment) collected by USGS during August 2004 at 12 monitoring sites along a 22-km transect across the central Refuge..... 40

Figure 18. Decomposition of sawgrass litter incubated for 12 months at 12 USGS monitoring sites along a 22-km transect across the central Refuge..... 42

Figure 19. Abundance of common interior slough-wet prairie macrophyte taxa measured by USGS during 2005 at 12 monitoring sites along a 22-km transect across the central Refuge..... 44

Figure 20. Soil pH and TP measured by USGS across the same transect of 12 monitoring sites surveyed for slough-wet prairie vegetation (see fig. 18)..... 46

Figure 21. Growth response of *Xyris ambigua* to increased mineral loading measured in the laboratory by USGS..... 47

Figure 22. Percent cover of slough-wet prairie and sawgrass habitats calculated by USGS for 14 sites along a 22-km transect across the central Refuge..... 47

Figure 23. Biomass increase of sawgrass seedlings grown in the laboratory by USGS for three months in different soil types amended with different mineral concentrations..... 49

Figure 24. Relative abundance of dominant diatom species across a canal gradient (lowest specific conductance at site 1 to highest specific conductance at site 5 in the Refuge and at a location in the interior of WCA 2A, a minerotrophic peatland adjacent to the Refuge.. 51

Figure 25. Changes in desmid dominance within the periphyton community at nine SFWMD monitoring stations across a water-chemistry gradient (see fig. 8) in the southwest corner of the Refuge..... 52

Appendix 1 - Locations of Refuge sampling sites referenced in report. 67

Tables

Table 1. Examples of peatland classification schemes based on surface-water mineral chemistry as compared to conditions in the A.R.M.....7

Table 2. Sources of Surface Water and Relative Importance of Various Pathways of Water Input, Output, and Exchange within the Central and Northern Everglades¹ 15

Table 3. Median concentrations of major nutrients and dissolved mineral ions for the period 1994-2003 in surface-water samples collected by the South Florida Water Management District at major canal pump stations (S5A and the outflow from STA1W) that affect water quality in the Refuge and WCA 2A and in the interior of WCA 2A (CA215) and the Refuge (LOX8).21

Conversion Factors

Inch/Pound to SI

Multiply	By	To obtain
Length		
inch (in.)	2.54	centimeter (cm)
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)
mile, nautical (nmi)	1.852	kilometer (km)
yard (yd)	0.9144	meter (m)
Area		
acre	4,047	square meter (m ²)
acre	0.4047	hectare (ha)
acre	0.004047	square kilometer (km ²)
square foot (ft ²)	929.0	square centimeter (cm ²)
square foot (ft ²)	0.09290	square meter (m ²)
square inch (in ²)	6.452	square centimeter (cm ²)
square mile (mi ²)	259.0	hectare (ha)
square mile (mi ²)	2.590	square kilometer (km ²)
Hydraulic conductivity		
foot per day (ft/d)	30.48	centimeter per day (cm/d)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$^{\circ}\text{F}=(1.8\times^{\circ}\text{C})+32$$

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:

$$^{\circ}\text{C}=(^{\circ}\text{F}-32)/1.8$$

Specific conductance is given in microsiemens per centimeter at 25 degrees Celsius (μS/cm at 25 °C).

Concentrations of chemical constituents in water are given either in milligrams per liter (mg/L) or micrograms per liter (μg/L).

NOTE TO USGS USERS: Use of hectare (ha) as an alternative name for square hectometer (hm²) is restricted to the measurement of small land or water areas.

Influence of Changing Water Sources and Mineral Chemistry on the Everglades Ecosystem

By Paul V. McCormick and Judson W. Harvey

Executive Summary

Available scientific evidence indicates that inputs of dissolved minerals (Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- , HCO_3^- , and SO_4^{2-}) have increased substantially across large portions of remaining Everglades peatlands as a result of water-management actions and land-use changes during the past century. The ecological effects of increased mineral concentrations have largely gone unnoticed and rarely been considered in conservation efforts. This document synthesizes information from the broader peatland literature and the limited amount of data from the Everglades to indicate the nature and extent of ecological changes caused by increased mineral inputs to the Everglades and to identify additional information that is needed to better understand the influence of mineral chemistry on the ecology of this regional peatland.

Water sources strongly influence peatland mineral chemistry. Ground water and surface runoff typically have higher mineral concentrations than precipitation. Consequently, rainfall-fed or ombrotrophic peatlands often are mineral depleted compared to ground-water-fed or minerotrophic peatlands. Water and soil mineral concentrations explain many differences in the ecology of ombrotrophic and minerotrophic peatlands. Concentrations of major mineral ions can affect peatland fertility by altering the availability of critical nutrients such as nitrogen (N) and phosphorus (P). Mineral chemistry also influences peatland vegetation directly by selecting for plant species best adapted to a specific chemical environment. Many plant species are unable to survive with the low mineral concentrations and associated acidity of ombrotrophic peatlands, while other species exhibit reduced growth and survival in response to increased mineral inputs.

The Everglades peatland originated roughly 5000 years ago as a seasonal wetland on top of mineral-rich limestone bedrock. Climatic shifts produced longer hydroperiod wetlands across large portions of the northern and central Everglades that gradually accumulated peat soils over this bedrock surface, resulting in an ecosystem that was increasingly isolated from bedrock and ground-water mineral influences and more strongly affected by rainfall. Contemporary measurements of rainfall chemistry in south Florida and the low mineral content of water and peat in remaining rainfall-driven portions of the Everglades attest to the mineral depleted nature of this water source. However, even the predrainage Everglades likely had higher mineral concentrations than those in many northern ombrotrophic peatlands due to differences in climate, biota, and the importance of mineral inputs from marine sources.

Reconstructions of historic water budgets indicate that direct rainfall was the primary source of water to much of the Everglades prior to start of drainage efforts in the early twentieth century. Seasonal overflows from Lake Okeechobee and runoff from surrounding seasonal wetlands and uplands provided most of the additional water to the predrainage ecosystem. The mineral content of these other water sources was likely higher than that of rainfall but lower than that of surface flows entering the Everglades today. Wetlands in the southern Everglades naturally have a mineral chemistry more strongly influenced by interactions with mineral-rich bedrock and ground water due to thinner peat accumulations, a greater proportion of infrequently flooded marginal wetlands, and a more transmissive underlying aquifer.

Drainage and water management activities over more than a century have converted much of the remaining Everglades from a rainfall-driven system to one strongly influenced by the chemistry of canal discharges. Waters in major conveyance canals have mineral concentrations more than 50-fold higher than that of rainfall and as much as 10-fold higher than that of surface waters in rainfall-fed areas of the Everglades interior. Spatial variation in mineral concentrations across the northern and central Everglades is due largely to differences in the relative importance of rainfall and canal discharges as water sources. Minerals in canal water come from many sources including runoff from the Everglades Agricultural Area (EAA), Lake Okeechobee water released into canals, and mixing between canal water and ground water in the surficial aquifer. Inputs of minerals from agricultural runoff and deep ground water were not significant in the predrainage system and have increased as a result of farming and canal drainage from the EAA as well as other water management activities that increase vertical exchange between canals and ground water.

The interior of the Arthur R. Marshall Loxahatchee National Wildlife Refuge is one of the last parts of the Everglades without substantial canal-water influences. Refuge surface waters effectively are isolated from underlying bedrock and ground-water mineral inputs by the presence of deep peat soils and water levels that are often equal to or higher than those in surrounding areas. Peats in the Refuge are mineral poor, indicating a lack of mineral-rich water sources during much of its history, and surface-water mineral chemistry across portions of the Refuge interior approximate that which would be expected based on a purely rainfall-driven hydrology.

Drainage waters discharged into conveyance canals that surround the Refuge have increased mineral levels around much of the Refuge perimeter and several kilometers into the interior in some areas. Elevated mineral levels may affect the availability of key limiting nutrients such as P, although initial findings indicate only modest changes in soil nutrient availability due to increasing mineral concentrations. Rather, it appears that availability is mediated by soil microbes, which account for a much higher fraction of stored P and N in areas exposed to canal-water intrusion compared to the Refuge interior. Microbial nutrient stores may be stable under flooded conditions but can be converted into more bioavailable forms during droughts. Increased turnover of nutrient pools through accelerated plant decomposition also has been documented in areas of the Everglades affected by canal mineral loading.

Increased mineral inputs to the Refuge are correlated with changes in plant and periphyton species composition and related landscape features such as the cover of slough and sawgrass habitat, although specific cause-effect linkages have only begun to be assessed. Recent experiments have demonstrated that some species are adversely affected by mineral enrichment while the growth of others may be encouraged. Fish and aquatic invertebrates also have surface-

water mineral chemistry requirements for survival, growth, and reproduction that may affect their distributions across an Everglades landscape with varying mineral concentrations.

Among the major mineral ions, elevated SO_4^{2-} (sulfate) concentrations may pose the greatest threat to Everglades restoration. Increased sulfate loading to peatlands elicits multiple ecological responses including increased mercury bioavailability and toxicity, shifts in plant species composition due to the production of hydrogen sulfide, which is toxic at high concentrations, and an increase in P availability through a process known as internal eutrophication. Many of these effects have been documented in ongoing field studies in the Everglades.

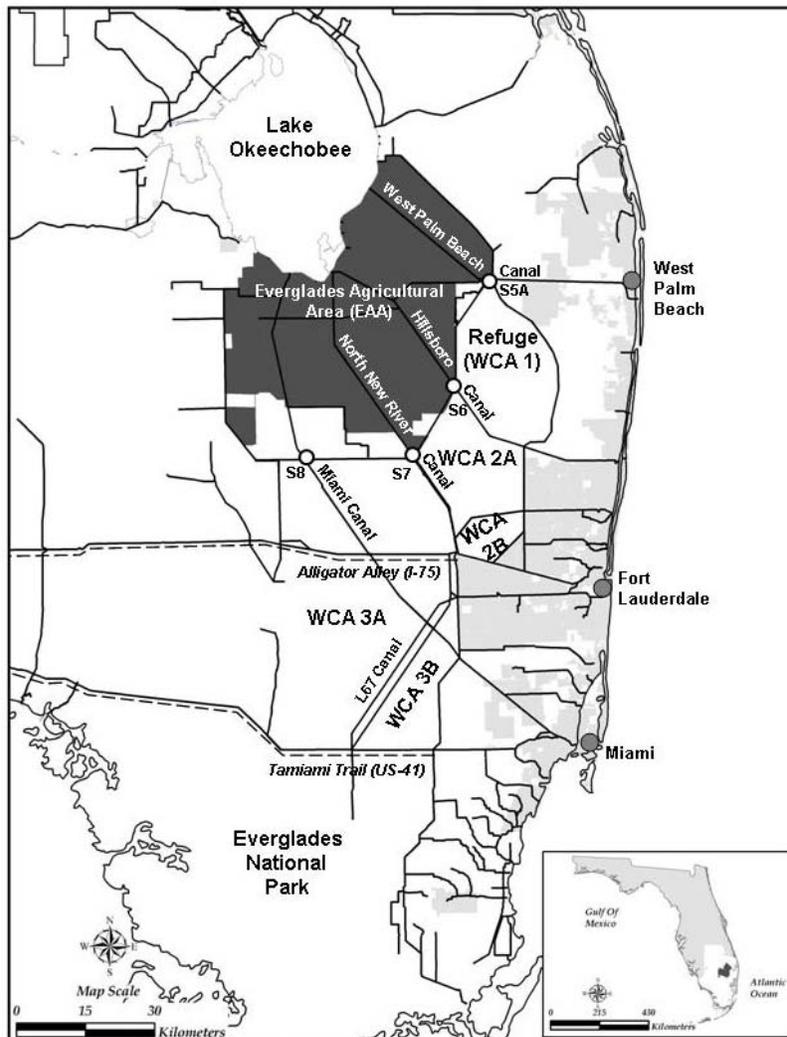
The reliance on canal waters to achieve hydrologic restoration may increase the magnitude and spatial extent of mineral enrichment in the Everglades. The gamut of ecological responses to this change in water chemistry has yet to be determined, although the scientific literature and recent data collected in the Everglades indicate direct effects on nutrient and contaminant cycles, vegetation, and possibly fish and invertebrates. Research and modeling needs on this topic include: 1) chemical and paleoecological analysis of peat profiles to provide a clearer picture of the predrainage mineral chemistry of the Everglades and the extent to which it has been changed during the last century; 2) quantitative data on the relationship between the mineral concentration, duration, and frequency of canal inputs and the transport and accumulation of different elements in soils and vegetation; 3) studies that fill the many data gaps on the ecological effects of mineral enrichment; and 4) improved hydrologic measurements and models to identify water management strategies that would minimize intrusion of canal waters into relatively well preserved rainfall-driven areas such as the interior of the Refuge that do not require additional hydration.

Introduction

Four fundamental aspects of hydrology – water sources, depths, and the duration and timing of flooding – are among the most important determinants of wetland structure and function (Mitsch & Gosselink, 2000). Efforts to restore the Everglades face the challenge of understanding cumulative effects of human alterations of these hydrologic features on the ecology of this large (10,000 km²) subtropical wetland (Fig. 1). The overarching goal of the Comprehensive Everglades Restoration Plan (CERP) is to “get the water right” by restoring the quantity, quality, timing, and delivery of water to the remaining Everglades in order to sustain critical ecological processes and populations. In doing so, the plan faces the inescapable problem that the water sources available for hydrologic restoration differ chemically from historical flows into the Everglades. An increased understanding of how chemical differences in predrainage and present-day flows affect the ecology of the Everglades and the potential outcomes of restoration efforts is, therefore, a critical part of the overall restoration process.

The Potential Significance of Mineral Chemistry in the Everglades

The Everglades developed over the past 5000 years in response to a rainfall-driven hydrology. The predominance of rainfall as a water source was responsible for the characteristic seasonal pattern of flooding and drying, associated depth and flow patterns, and water-chemistry conditions including low concentrations of limiting nutrients such as phosphorus (P) and more abundant minerals such as calcium (Ca). Water management actions over more than a century have converted much of the remaining Everglades from a rainfall-driven system to one strongly



influenced by canal discharges. These discharges originate as runoff from agricultural lands, water releases from Lake Okeechobee (the water chemistry of which has itself been affected by agricultural influences), and ground-water discharge into the regional network of drainage and conveyance canals. Changes in water sources to the managed Everglades not only have altered the timing and connectivity of water flows, but also have increased inputs of nutrients and minerals.

Figure 1. Map of south Florida showing major hydrologic units of the Everglades and the canals (solid black lines) and pump stations (white circles) that supply water to this wetland. Urban areas along the southeast coast are shown in light gray shading and the Everglades Agricultural Area is shown in darker shading. Major roads across the Everglades are shown as dashed lines with road names in italics.

Despite the CERP’s broad goals, most planning efforts have focused on restoring patterns of depth and duration of surface water in the Everglades. The chemical suitability or “quality” of these deliveries is gauged largely with respect to concentrations of a few pollutants including P,

pesticides, and mercury (Hg). Little attention has been paid to the broader implications to Everglades chemistry and ecology of these restoration strategies, which will rely principally on canal discharges as a water source. In particular, potential ecological effects of increasing mineral concentrations – an important factor influencing peatland ecosystems – have yet to be assessed in the Everglades.

The extent of hydrologic and landscape changes in south Florida precludes the complete restoration of water chemistry to predrainage conditions across the Everglades. However, despite more than a century of human impacts, parts of the Everglades retain water-chemistry conditions that approximate the historic rainfall-driven condition. The Arthur R. Marshall Loxahatchee National Wildlife Refuge (Fig. 1) is perhaps the best example. As we discuss in this paper, certain ecological characteristics of the Refuge peatland are known to depend on its mineral-depleted chemistry, and the broader peatlands literature suggests other potential linkages as well. Although this northernmost impoundment of the remaining Everglades has received significant canal discharges for several decades, portions of the wetland interior appear to have remained relatively isolated from these flows. Concerns have been raised by scientists and resource managers that water-management changes associated with Everglades restoration projects will promote increased intrusion of canal waters into the Refuge and alter its ecological characteristics.

The influence of mineral chemistry on the ecology of subtropical peatlands such as the Everglades has received little attention. By contrast, the ecological significance of water and soil mineral concentrations in temperate and northern peatlands is well established and provides an important basis for classifying these systems. Minerotrophy represents one of 3 major environmental factors – the others being hydrology and fertility (as related to the availability of limiting nutrients such as nitrogen (N) and P) – that explain ecological patterns within and among peatlands (Malmer, 1986; Heikkilä, 1987; Wheeler & Shaw, 1995; Bridgham and others, 1996; Wheeler and Proctor, 2000; Økland and others, 2001). The purpose of this paper is to: 1) review the literature on peatland mineral chemistry and its ecological influences as it may relate to mineral relationships in the Everglades; 2) synthesize available data on mineral sources and ecological effects from the Everglades with a focus on the Refuge; 3) identify data gaps and corresponding research needs to better characterize these effects in remaining mineral-poor areas such as the Refuge.

Sources and Measures of Mineral Content

Freshwater ecosystems exhibit great variation in their mineral chemistry as a result of both natural and human influences. Seven ions account for nearly all of the dissolved minerals in freshwater. These include the cations calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), and potassium (K^+) and the anions bicarbonate (HCO_3^-), sulfate (SO_4^{2-}), and chloride (Cl^-). Natural sources of these ions include deposition from precipitation and dry fallout, transport of minerals dissolved from soils and shallow bedrock, and, in ecosystems such as the Everglades, upward transport of minerals from the deeper parts of the surficial aquifer where relict seawater was trapped during an earlier geologic time period. Human activities affect mineral concentrations in downstream waters by introducing new mineral sources into the watershed, for example, through wastewater discharges, the application of fertilizers or road salts, and by altering hydrology in ways that affect the magnitude of inputs from natural sources such as ground water. As will be discussed, human activities that have increased mineral loads to the Everglades include the

drainage of peat soils, which has led to land subsidence and increased ground-water discharge, fertilizer applications, and ground-water pumping for irrigation within the watershed.

Several fundamental chemical properties of water are based on its mineral content. The terms *soft water* and *hard water* commonly are used to distinguish waters containing relatively low and high mineral concentrations, but refer more specifically to levels of Ca^{2+} and Mg^{2+} , which are the dominant cations in most freshwaters. The *alkalinity* of freshwater, which measures its ability to neutralize acidity and maintain a circumneutral or basic pH, usually is determined by concentrations of the bicarbonate anion and a related form, carbonate. The *conductivity* of water, defined as its capacity to conduct electrical current, indicates the total concentration of major ions dissolved in solution and provides a convenient measure of mineral content. Conductivity can be measured quickly and accurately in the field using portable equipment, and is normally reported as *specific conductance*, which corrects for the effect of temperature on conductivity and maintains a constant proportionality with mineral content for measurements obtained at different times and locations. The international unit for specific conductance is Siemens per centimeter or S/cm. Measurements are often reported in units of $\mu\text{S}/\text{cm}$ since most freshwaters have low specific conductance ($\ll 1 \text{ S}/\text{cm}$).

The measurement of specific conductance alone provides information about the total mineral content of water but not its mineral composition. Individual mineral ions contributing to conductance have very different chemical properties. Thus, information on the concentrations of individual ions can be critical to predicting ecosystem effects. When conductance is determined by mixing just two water sources, each with a reasonably homogeneous mineral composition, precise relationships between specific conductance and the concentrations of major ions can be developed. This is the case across much of the Everglades, where conductance is determined largely by the mixing of mineral-rich canal water with mineral-poor rain water. Thus, specific conductance provides a useful surrogate for concentrations of major ions in surface waters across the Everglades.

Importance of Mineral Chemistry in Peatland Ecosystems

Classification and Evolution of Peatlands with Respect to Their Mineral Status

The importance of water sources to peatland mineral chemistry is well established (e.g., see Moore & Bellamy, 1974; Wheeler & Proctor, 2000). Peatlands receive water inputs from ground water, surface runoff from adjacent uplands, and precipitation in different proportions. The importance of these three sources to peatland hydrology is determined by several factors including climate, topography, and the stage of peatland development (e.g., the depth of peat accumulation). Depending on local geology, ground water and runoff can acquire substantial quantities of mineral as they pass through bedrock and soil. By contrast, precipitation usually is depleted in major ions. This difference in the mineral chemistry of source waters accounts for the widely documented relationship between peatland hydrology and mineral chemistry.

Peatlands receiving ground-water discharges generally are classified as minerotrophic peatlands or *fens* and often have comparatively high concentrations of major ions (and a correspondingly high specific conductance) as determined by the underlying geology. High mineral concentrations also confer a circumneutral or basic pH to these wetlands. Peatlands fed

solely by precipitation are classified as ombrotrophic peatlands or *bogs* and have surface waters that are mineral depleted and have low specific conductance and pH. Fens can be classified further based on the degree of ground-water influence and corresponding mineral status. For example, transitional peatlands or *poor fens* have intermediate concentrations of minerals, reflecting a hydrology influenced by both ground-water and precipitation inputs, while *rich fens* are those receiving large inputs of mineralized ground water. Examples of classification systems developed for peatlands across different regions of Europe and North America are shown in Table 1.

Table 1. Examples of peatland classification schemes based on surface-water mineral chemistry as compared to conditions in the A.R.M. Loxahatchee National Wildlife Refuge, a rainfall-driven Everglades peatland. Units for all ions are in mg/L.

Peatland location and classification	pH	HCO₃⁻	Cl⁻	SO₄²⁻	Ca²⁺	Mg²⁺	Na⁺	K⁺
Refuge interior	6.3	12.21	16.20	0.40	5.14	1.37	9.69	0.42
English peatlands (Bellamy, 1967):								
Hydro mire type 1	7.5	237.90	14.18	38.42	80.16	7.30	11.50	1.96
Hydro mire type 2	6.9	164.70	17.73	48.03	64.13	4.86	9.20	3.13
Hydro mire type 3	6.2	61.00	17.73	33.62	24.05	4.86	11.50	0.78
Hydro mire type 4	5.6	24.40	17.73	24.02	14.03	2.43	11.50	1.56
Hydro mire type 5	4.8	6.10	10.64	24.02	6.01	1.22	6.90	2.74
Hydro mire type 6	4.1	0.00	14.18	19.21	4.01	1.22	6.90	1.56
Hydro mire type 7	3.8	0.00	10.64	14.41	2.00	1.22	4.60	1.56
Swedish peatlands (Sjörs, 1950):								
Extreme rich fen	7.7	140.30	7.09	19.21	36.07	10.94	4.60	0.78
Transitional fen	5.8	54.90	3.55	1.44	18.04	0.24	1.15	0.39
Intermediate fen	4.8	36.60	0.35	2.88	12.02	0.36	1.84	0.39
Transitional poor fen	5.5	6.10	1.42	1.92	2.00	0.36	1.38	<0.39
Intermediate poor fen	4.4	0.00	1.06	2.40	1.20	0.36	1.84	<0.39
Extreme poor fen	3.9	0.00	2.13	3.36	1.40	0.24	1.15	<0.39
Moss (bog)	3.8	0.00	1.42	6.24	0.80	0.61	2.07	0.39
Northwest Canada (Nicholson and others, 1996):								
Extremely rich	6.5	--	--	--	57.00	11.70	7.50	--

fen								
Moderately rich								
fen	6.4	--	--	--	19.60	4.60	7.30	--
Poor fen	4.9	--	--	--	8.70	2.50	4.10	--
Bog	4.2	--	--	--	1.70	0.40	5.10	--

The above classification scheme can be applied to peatlands worldwide when used to indicate the primary water source. However, the chemistry of a particular peatland type can exhibit significant variation among regions. Ground-water mineral concentrations are quite high in areas such as south Florida that are underlain by calcareous rock but are much lower in areas with non-calcareous bedrock (e.g., Bridgham & Richardson, 1993). Precipitation chemistry varies regionally depending upon the influence of mineral sources such as marine aerosols in coastal areas or dust from mineral-rich soils in continental regions (Almquist & Calhoun, 2003; Damman, 1995; Glaser, 1992). Thus, there is no absolute correspondence between peatland water source and water chemistry. In northwestern Europe, for example, where the bog-fen classification system originated and has been most intensively studied, mineral and pH levels vary considerably within each peatland type and exhibit overlap between categories such as bog and poor fen (Wheeler & Proctor, 2000). However, some of this variability is due to human disturbance (for example, draining, burning, and acid deposition) rather than natural forces.

Peatlands are dynamic ecosystems that can exhibit natural changes in their mineral chemistry over time in response to climatic fluctuations and autogenic processes that control mineral inputs from different water sources. Northern peatlands often evolve towards ombrotrophy as peat accumulates, the wetland surface becomes isolated from the underlying bedrock and the influence of ground-water discharges, and precipitation exerts increasing control over hydrology and chemistry (Moore & Bellamy, 1974). An extreme endpoint of this trajectory is a raised bog, where the peat surface has risen above the elevation of the surrounding landscape and water is derived solely from precipitation. Studies of temperate peatlands such as pocosins also indicate a successional trend towards a more mineral-poor state as peat accumulations reduce contact between plant roots and underlying mineral soils, although this trajectory can be reset by fires that reduce peat depths (Christensen and others, 1981; Richardson & Gibbons, 1993). Large peatlands can encompass a variety of successional states and trajectories and contain mineral gradients produced by local variation in water sources. Within a 780 ha undisturbed Minnesota peatland, for example, Glaser and others (1990) described five landform types, each with a characteristic mineral chemistry and vegetation community. Variation in mineral content (for example, Ca²⁺ concentrations between <1 and 45 mg/L and pH ranging from <4 to >7) within the peatland was determined to result from mixing between mineral-rich spring waters and precipitation. Paleocological analyses revealed multiple successional pathways within this peatland, including the shift from ombrotrophic bog to rich fen, which contrasts with the typical pathway described above. Thus, peatland succession does not always proceed towards ombrotrophy despite continued peat accumulation.

Ecological Effects

Biogeochemical Processes

Peatland mineral chemistry exerts strong control over biogeochemical processes that regulate nutrient cycling and productivity. The gradient from ombrotrophy to minerotrophy has been described as one of increasing fertility that includes some of the lowest (e.g., ombrotrophic *Sphagnum* bogs) and highest (e.g., minerotrophic fens dominated by robust taxa such as *Scirpus* and *Typha*) productivity ecosystems in the world (Moore & Bellamy, 1974). Early studies concluded that peatland mineral gradients paralleled those for commonly limiting nutrients such as N and P, and the hypothesis was raised that a shortage of minerals such as K and Ca might contribute to lower productivity in ombrotrophic systems. Primary production measurements across bog-fen gradients are consistent with the notion of greater primary production in fens versus bogs (Malmer, 1986).

Recent syntheses have questioned the relationship between peatland mineral concentrations and site fertility. Wheeler & Proctor (2000) concluded that mineral and fertility gradients in central European peatlands are largely independent. While soil nutrient content and fertility invariably were low in mineral-poor peatlands, they varied widely among mineral-rich peatlands. However, the concordance of these two gradients may be greater in regions where anthropogenic nutrient loading exerts less influence on peatland nutrient status (Økland and others, 2001). Available information indicates that with the exception of K, major minerals such as Ca generally do not limit peatland primary production (Bridgham and others, 1996; Bedford and others, 1999). As in other wetlands, peatland production is most often constrained by the availability of N or P. The more important effect of mineral chemistry on peatland fertility may be through its influence on the availability of limiting nutrients such as N and P as well as micronutrients such as iron (Fe).

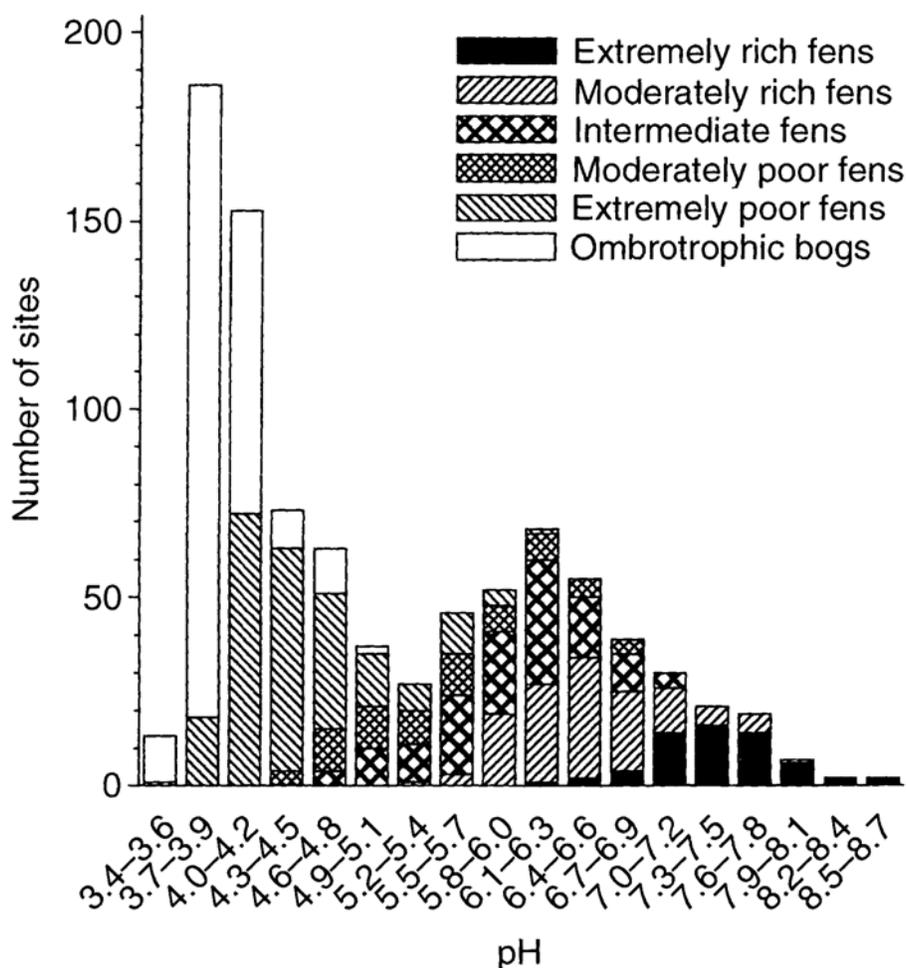
Total soil nutrient concentrations in bogs often are lower than in fens due to lower external inputs (an exception being in regions affected by high atmospheric N deposition from human sources; Aerts and others, 1992). The relationship between total nutrients and nutrient availability, however, is considerably more complex due in part to mineral and pH effects. For example, concentrations of extractable soil N, P, and K can be higher in bogs despite similar or lower total nutrient concentrations (e.g., Waughman, 1980). Pore-water concentrations of dissolved nutrients in bogs also have been found to be similar to or higher than those in fens (Schwintzer & Tomberlin, 1982; Vitt and others, 1995). With respect to N, vegetation patterns across mineral gradients may be more closely related to the ionic form rather than amount of available N. Shifts in available N from NO_3^- to NH_4^+ with increasing acidity, for example, may favor species capable of NH_4 uptake at low pH (Kinzel, 1983). Primary production in calcareous fens can be strongly P limited despite high soil total P (TP) due to high concentrations of dissolved Ca, which co-precipitates phosphate from solution at high pH (e.g., Verhoeven & Arts, 1987; Boyer & Wheeler, 1989). Higher concentrations of extractable aluminum (Al) and Fe in more minerotrophic soils also can bind phosphate and reduce P availability (Richardson, 1985; Wassen & Barendregt, 1992). Inhibition of bacterial growth and a consequent reduction in bacterial immobilization of P were hypothesized to contribute to higher pore-water phosphate concentrations at low (pH < 4.5) soil pH (Wilson & Fitter, 1984). Thus, while total nutrient levels in bogs are typically lower than those in fens, patterns of nutrient availability and their relationship to plant growth are less predictable (e.g., Bridgham and others, 2001).

Comparisons of nutrient mineralization rates across peatland mineral gradients provide a somewhat different picture of nutrient availability than do instantaneous measures of dissolved or extractable nutrients. These rate processes ultimately are constrained by both the nutrient content and decomposability of plant litter as influenced by plant species composition and by ambient environmental conditions. Litter decomposition rates have been found to be lower in bogs than in fens, and this pattern has been related to the dominance in bogs of *Sphagnum* mosses, which have a low nutrient content and decay-resistant tissue. However, the rate of decay of standard organic materials (e.g., standardized strips of cellulose) also is lower in bogs than in fens (Farrish & Grigal, 1988; Verhoeven and others, 1990), indicating that environmental factors such as low pH also may limit decomposition. Nutrient turnover rates can be expressed on the basis of soil mass, soil volume, or total soil nutrients, and each of these corrections have somewhat different but ecologically significant meanings. For example, Verhoeven and others (1990) concluded that the biomass decomposition rate was lower in bogs than in fens while the turnover rate of the nutrient pool was higher. They attributed this pattern in part to the nature of decomposition in *Sphagnum* mosses, which concentrate a large fraction of their nutrients in the relatively decomposable growing tip and, thus, exhibit rapid nutrient release upon decay. Mineralization of soil N but not P increased along an ombrotrophic-to-minerotrophic wetland series when expressed as a rate per unit soil volume (Updegraff and others, 1994; 1995), indicating a larger pool of plant-available N in fens. However, rates of turnover of both nutrient pools in bogs and poor fens equaled or exceeded those in more minerotrophic peatlands, indicating that there is a potentially smaller but more labile pool of nutrients in more acidic, mineral-poor peatlands. Bridgham and others (2001) expanded this assessment by including estimates of nutrient supply rates using ion-exchange resins and concentrations of soil-extractable nutrients and arrived at a similar conclusion.

Among the major mineral ions, sulfate enrichment from anthropogenic sources including the burning of fossil fuels and fertilizers has been shown to have some of the most dramatic effects on peatland biogeochemical processes. Sulfate serves as an electron acceptor for certain classes of anaerobic bacteria known as sulfate reducers, which are limited by the availability of this ion in most freshwater wetlands. Reduction of sulfate yields hydrogen sulfide, which is toxic to wetland plants at high concentrations (Lamers and others, 2002). Sulfate reducing bacteria also are responsible for converting elemental Hg to the bioavailable form methyl-Hg, resulting in significant bioaccumulation and health concerns in peatlands such as the Everglades that are exposed to high Hg deposition rates. Increased sulfate loading can cause “internal eutrophication”, a process whereby adsorbed P is released to the soil pore-water either through competition for anion binding sites on the peat surface (Beltman and others, 2000) or the complexation of Fe to produce Fe-S, which precludes storage of P in Fe-P complexes (Lamers and others, 2001). Interestingly, elevated concentrations of Cl⁻, an ion that is generally considered to be largely inert from an ecological perspective, can exert the same competitive binding effect on P in peat soils (Beltman and others, 2000).

Vegetation responses

Regional surveys of temperate and northern peatlands across Europe and North America have documented broad, predictable relationships between vegetation composition and mineral gradients (e.g., Sjörs, 1950; Waughman, 1980; Malmer, 1986; Vitt and others, 1990; Wheeler & Shaw, 1995), and plant communities have been used to classify fens according to their mineral



status in many regions. Vegetation patterns within peatlands also are aligned with mineral gradients generated by local variation in the relative importance of precipitation and ground-water inputs (Grootjans and others, 1988; Glaser and others, 1990; Boeye & Verheyen 1994). The strength of regional relationships was illustrated by Sjörns & Gunnarsson (2002), who compiled water-chemistry and vegetation data from 889 sites in central and northern Sweden (Fig. 2). Peatland mineral status was defined based on surface-water pH, which was correlated strongly with Ca^{2+} concentrations and specific conductance. Vegetation was classified into community types based on *a priori* information on their occurrence across mineral gradients (Sjörns, 1950). These data show predictable but overlapping distributions of community types across regional mineral gradients and support the widely held view that there are no absolute limits to the presence of different community types with respect to pH or other chemical variables across these gradients. Observed variation in these regional relationships may reflect the general rule that species are more tolerant of variation in environmental factors such as

Figure 2. Distribution of different peatland types across regional mineral gradients in Sweden. Peatland types (e.g., bog, poor fen, rich fen) were defined based on plant species composition. Peatland mineral concentrations were indicated from surface-water pH, which was strongly correlated with specific conductance. Reprinted from Sjörns and Gunnarsson (2002) with permission.

mineral chemistry in the center of their geographical distribution than near the edge (Økland and others, 2001).

Wetland plant species differ considerably in their tolerance to mineral concentrations and can be loosely grouped into 3 general categories: 1) those restricted to mineral-poor waters; 2) those restricted to mineral-rich waters; and 3) those that appear indifferent to mineral concentrations. In prairie pothole wetlands, which span a specific-conductance range of greater than three orders of magnitude, certain species had relatively narrow tolerances (a range of a few hundred $\mu\text{S}/\text{cm}$) while others exhibited a much broader distribution ($>$ two orders of magnitude) (Walker & Coupland, 1968; Stewart & Kantrud, 1972). Bridgham and others (1996) noted that common plant species occur across a wide range of mineral conditions and that species with more exacting mineral requirements generally are not the dominant species in most habitats. Still, the loss of sensitive species in response to changes in peatland mineral status is important from a conservation standpoint with respect to the maintenance of local and regional floristic diversity.

Vegetation patterns across mineral gradients have been explained based on the tolerances of individual plant species to low soil and water mineral levels. The extremely low mineral content and pH in bogs is stressful to many vascular plants and represents a barrier to colonization for those species without special adaptations. This constraint is evidenced by regional surveys showing that common bog species also occur in fens whereas the reverse is not true. The flora of bogs thus tends to be impoverished compared to that of fens and can be distinguished based on the absence of fen indicator species (e.g., Wheeler and others, 1983; Malmer, 1986; Glaser and others, 1990; Glaser, 1992; Wheeler & Shaw, 1995). For example, Glaser and others (1990) identified 53 vascular plant species across a rich fen-bog gradient in the Lost River peatland of northern Minnesota. Only one of these species, the sedge *Eriophorum spissum*, was restricted to bog habitat while a few others were most common in bogs. By contrast, 15 species were restricted to rich and/or extremely rich fen habitat. Accordingly, species richness was considerably higher in the rich and extremely rich fens than in the bogs and poor fens.

Although the number of fen indicator species is greater, some species have been shown to exhibit limited tolerance to minerotrophic conditions (Jeffries & Willis, 1964) and strongly prefer or are restricted to bog or poor fen habitats. Several studies have illustrated this pattern for sedges (Cyperaceae), a group that is distributed globally across all peatland types. A total of 69 sedge species were identified in a survey of a broad range of peatland types in Maine, including bogs, extremely poor fens, and poor to moderate-rich fens (Anderson and others, 1996). The pH optima of the 21 most commonly encountered species ranged between 3.98 and 7.93 and the Ca^{2+} optima ranged between 0.10 to 21.92 mg/L. Four species of the genus *Eriophorum* and three species of *Carex* exhibited optima below 4.40 for pH and 1.80 mg/L for Ca. While none of these species was restricted to bogs, their abundance declined with increasing mineral levels and pH and all were absent from moderately-rich fens. A survey of undisturbed portions of the Red Lake peatland complex in Minnesota identified 20 species of *Carex*, one of which exhibited a strong preference for bog habitats, three of which were indicators of poor fen conditions, and two of which were restricted to rich fen habitats (Wheeler and others, 1983). Common *Carex* species in Japanese peatlands exhibited contrasting distributions between bog (pH $<$ 5.5) and fen (pH $>$ 5.0) habitats, with some species being restricted to either bogs or fens and others exhibiting broad habitat tolerances (Nakamura and others, 2002).

Regional variation in plant distributions with respect to minerotrophy has been widely reported, indicating that environmental requirements can vary throughout a species range. The most widely documented pattern is for many plant species to exhibit increased tolerance of mineral-depleted conditions in maritime climates. Tansley (1939) documented this pattern for two common species, *Cladium mariscus* and *Schoenus nigricans*, which are confined to rich fens in continental Europe but occur in poor fens and even bogs near the coast. Similar patterns have been documented for other species (Malmer, 1986). Various explanations have been proposed for this reproducible pattern including increased mineral loading to coastal bogs from sea spray and the ameliorating effect of “flushing” from increased precipitation on the extreme acidity of these peatlands. Glaser (1992) documented analogous shifts in species occurrences in bogs across climatic gradients in eastern North America. Maritime bogs had a more diverse flora than those in the continental interior and one-third of the species found in the maritime bogs were restricted to fens or other mineral-rich habitats in the interior. However, in contrast to previous studies in Europe, these shifts could not be related to differences in bog chemistry and, in some cases, may be related to hydrologic differences instead (Santelmann, 1991). Thus, caution should be exercised when extrapolating vegetation-mineral relationships among regions and assigning cause and effect based on pattern alone.

Causes of vegetation change across mineral gradients

While numerous studies have documented a close correspondence between vegetation and mineral gradients, few have directly examined the mechanisms underlying these relationships. Most studies have been correlative in nature, and because peatland mineral gradients typically encompass changes in multiple elements as well as associated changes in pH, it is difficult to isolate specific chemical-ecological relationships from such information. Mineral gradients also may coincide with other influential gradients such as those for limiting nutrients and hydrology, making the task of teasing apart mechanistic relationships still more challenging.

Studies in both wetland and upland habitats indicate that vegetation patterns across peatland mineral gradients are the product of multiple effects of both mineral concentration and pH on plant physiology and competitive ability. Considerable attention has focused on the effects of Ca on plant distributions among soils of differing mineral content. Calcium is an essential plant nutrient, but when accumulated in excess can impair physiological functions related to osmotic balance, enzyme activity, and nutrient uptake (Kinzel, 1983). Controlled experiments (e.g., Steele, 1955; Bradshaw and others, 1958; Jeffries & Willis, 1964) have shown that variation in Ca concentration could explain the distribution of some plants across soil mineral gradients. While many species exhibit broad tolerances to Ca, others have been classified as either *calcifuge* species that are intolerant of high Ca concentrations or *calcicole* species that are restricted to Ca-rich soils due to their high Ca requirement. Growth of calcifuge species may be limited in calcareous soils as a result of direct Ca toxicity (Jeffries & Willis, 1964; Marrs & Bannister, 1978) or Ca-induced deficiencies in P, K, or Fe (James, 1962; Grime, 1965; Jeffries and others, 1969; Waters & Pigott, 1971). Field fertilization experiments in peatlands rarely have found Ca to be a limiting nutrient, even in ombrotrophic habitats (Bridgham and others, 1996). However, the absence of certain species from low Ca soils has been attributed to symptoms such as reduced K uptake caused by Ca deficiency (Jeffries &

Willis, 1964), which may contribute to a poor competitive ability of these species in mineral-poor habitats (Marrs & Bannister, 1978).

Soil pH exerts a strong influence on plant growth through its effect on nutrient availability and uptake and the solubility of toxic metals. At extremely low pH (<3), the high concentration of H⁺ ions itself may impact plant growth. However, within the range of pH levels documented in most peatlands, indirect effects just mentioned likely prevail. For example, Rorison (1960) found no differences in growth rates of a calcicole species when grown in artificial solutions with pH adjusted to either 7.6 or 4.6, whereas water extracted from an acidic soil was found to be toxic. Vegetation patterns across mineral gradients suggest two critical pH limits at a pH near 4, which separates bogs from fens, and a pH near 6.8, which separates poor fens from rich fens. While these thresholds are somewhat arbitrary (Sjörs, 1950), they do suggest different effect mechanisms depending on the pH range. Metal toxicity can be an important factor limiting plant growth in bog environments with high metal concentrations. The solubility and associated toxicity of Al is completely dependent upon pH, with soluble forms present below pH 5 and predominant below pH 4. Rorison (1960) demonstrated experimentally that poor calcicole growth in low pH soils was a consequence of Al toxicity. Calcifuge species appear to possess Al-chelating systems or other detoxification mechanisms that permit growth in the presence of high concentrations of soluble Al (Grime & Hodgson, 1969). The toxicity of Fe and Mn also increases at these low pH values when combined with the low redox potential in flooded soils. Iron toxicity was determined to be an important factor explaining the absence of certain fen species from more acidic habitats (Snowden & Wheeler, 1993). Forms and availability of N and P vary across a broad pH range due to multiple processes. Low pH (<5.5) inhibits nitrification, resulting in a shift in available N forms from NO₃⁻ to NH₄⁺ (Morris, 1991). The capacity to utilize NH₄⁺ as a N source may favor the dominance of certain species under low pH conditions (Kinzel, 1983). High pH (>7) acts in conjunction with high Ca to decrease P availability due to the formation of insoluble Ca-P compounds in rich fen soils, and primary production in these environments have been shown to be strongly P limited as a result (Boyer & Wheeler, 1989).

Chemical factors other than Ca and pH also have been suggested as influences on vegetation patterns across mineral gradients. Increased bicarbonate concentrations (alkalinity) in soil porewater may retard ion uptake and root growth of calcifuge species (Kinzel, 1983). Floristic differences between maritime and continental bogs have been correlated with Mg and Na concentrations (Glaser, 1992), although the causal nature of this relationship has not been established. Undoubtedly, multiple factors act in concert to affect species' growth and distributions. For example, Clymo (1962) showed experimentally that the distribution of a calciphilic species of *Carex* across a peatland mineral gradient could be explained both by its requirement for Ca and its susceptibility to Al toxicity at lower pH.

Whereas floating and emergent macrophytes obtain their inorganic C for photosynthesis from the atmospheric CO₂ pool, submerged aquatic vegetation (SAV) is dependent on dissolved inorganic C (DIC) as the sole C source. The forms of DIC are strongly affected by pH, and SAV species vary in their ability to utilize these different sources (Wetzel, 2001). Pagano & Titus (2004) documented differential growth responses of three SAV species to DIC enrichment in a soft-water, acidic (pH = 6.0) environment. Positive responses of *Elodea canadensis* and *Utricularis vulgaris* to DIC enrichment were indicative of C limitation, whereas the absence of any response from *Eriocaulon aquaticum* indicated that this characteristic soft-water taxon is

well adapted to the DIC environment of acidic habitats. Measured responses were consistent with the distribution of these species among aquatic habitats of differing pH. Thus, surface-water pH can play an important role in shaping vegetation communities in wetlands containing submerged plant species.

Everglades Water Sources, Mineral Chemistry, and Associated Ecological Features

Water Sources to the Predrainage and Managed Everglades

Direct rainfall was the primary source of water to the predrainage Everglades, with additional contributions originating as episodic overflows of Lake Okeechobee, seasonal runoff from infrequently flooded wetlands and low-lying uplands at the margins of the Everglades, and exchange with ground water in the underlying sand and limestone aquifer. At present, the most reliable information about water sources to the predrainage Everglades comes from the South Florida Water Management District’s (SFWMD) efforts to simulate the hydrologic response of the predrainage ecosystem using the Natural Systems Model (NSM v 4.5) (SFWMD, 2006). The NSM bears a close relationship with the South Florida Water Management Model (SFWMM) (SFWMD, 2003), which is the primary model used to guide hydrologic modeling efforts of the Central and Southern Everglades Restudy of Everglades hydrology (U.S. Army Corps of Engineers, 1999). The “Restudy” provided the basis for much of the CERP.

The NSM uses the most current estimates of predrainage topography, vegetation distribution, flow-resistance characteristics of vegetation, tidal and inflow boundary conditions, along with other factors. It should be emphasized that the NSM model does not actually attempt to simulate the hydrology of the predrainage system. Rather the model is run with the standard 31-year input series of precipitation data and evapotranspiration functions used for what is referred to as the 1995 base run of the SFWMM (SFWMD, 1999). The NSM results, therefore, have great value because they allow meaningful comparisons between the current managed system and the natural system under identical model input conditions for climate.

Water inflows to the northern and central Everglades determined from the NSM (predrainage landscape) and SFWMM (current landscape) models are summarized in Table 2.

Table 2. Sources of Surface Water and Relative Importance of Various Pathways of Water Input, Output, and Exchange within the Central and Northern Everglades¹

Interior Ground-water Exchange	Model	NSM v. 4.5 Predrainage ²	SFWMM v. 3.5 Managed ⁴		
Landscape Condition		1,000 acre-feet per day	Percent of total inputs	1,000 acre-feet per day	Percent of total inputs
Inputs					
Precipitation		6018	84	3450	66
Lake overflow		606	8	227	4
EAA Drainage		---	---	907	18
Marginal Inflows		571	8	614	12
Net ground-water discharge		<1	<1	<1	<1
Outputs					
ET		5471	76	3350	64
Marginal Inflows		1853	26	1005	19
Net ground-water recharge		18	<1	823	16

¹Results were summarized from South Florida Water Management District model runs made using Natural Systems Model v. 4.5 and South Florida Water Management Model v. 3.5 (all runs dated April 4, 1999) that were accessed December 20, 2006 from the web at <http://www.sfwmd.gov/org/pld/restudy/hpm/>, and from calculations made using results from Harvey et al (2005). The boundaries of the central and northern Everglades are defined as the historic or remnant areas of contiguous emergent wetlands lying between Lake Okeechobee wetlands to the north and Everglades National Park to the south. The boundaries are delineated by the South Florida Water Management District (South Florida Water Management District, 1999 and 2006). The NSM model includes the northernmost portions of the predrainage Everglades that were later converted to agriculture (EAA), whereas the SFWMM uses as its boundaries the Water Conservation Areas as represented in the SFWMM model. Dashed table entries are not applicable. The estimates of interior ground-water exchange are based on direct measurements of ground water and surface water exchange fluxes in the interior parts of the managed central Everglades (Harvey and others, 2004).

System boundaries are defined as the historic (NSM) or remaining (SFWMM) areas of contiguous emergent wetlands lying between Lake Okeechobee to the north and Everglades National Park to the south. The NSM model includes the northernmost portions of the predrainage Everglades that were later converted to agricultural lands known as the Everglades Agricultural Area (EAA), whereas the SFWMM boundaries correspond to the Water Conservation Areas (WCAs) (see Fig. 1). These boundaries are formally defined by the SFWMD (1999; 2006). Precipitation provided approximately 84% of the water to the predrainage system while runoff and Lake Okeechobee overflows each contributed 8% of the total input. Net discharge and recharge to ground-water areas outside of the Everglades were negligible in the predrainage system (< 1%), whereas the internal exchange that occurred between surface water and ground water in the wetland interior accounted for 3% of inflows.

The importance of precipitation as a water source to the Everglades decreased in the managed system (from 84 to 65% of total water input) as a result of canal drainage, subsidence, and water routing to achieve water conservation and supply goals. A new source of water, inflow of drainage waters from the EAA (18%), became a significant input. The importance of runoff from marginal areas increased slightly (from 8 to 12%) while the percentage of inputs from Lake Okeechobee decreased slightly (from 8 to 4%). The net recharge of Everglades surface water increased substantially as a result of management activities (from <1% to 16% of inputs), while exchange with ground water in the wetland interior remained about the same (4% of inputs).

The above summary of water sources to the Everglades is based on the most current and reliable data and modeling information. Nevertheless, caution must be exercised in interpreting these results. In particular, these data are representative of spatially and temporally averaged conditions. Relative contributions from different water sources would be expected to vary considerably among specific locations and years. Also, the spatial distribution of overflows from Lake Okeechobee depends on the specific flow paths that these waters followed through the Everglades. Those flow paths are poorly known, which creates uncertainty as to the relative contributions of different water sources to different locations.

Influence of Water Source on the Mineral Chemistry of Everglades Peatlands

Human activities during the past century have directly and indirectly given rise to several new mineral sources to the Everglades that have increased concentrations of all major ions in

surface discharges. Prior to this period, there is evidence that portions of the predrainage Everglades were developing towards an increasingly mineral-poor state. The Everglades developed on top of limestone bedrock in a shallow trough across south Florida (Gleason & Stone, 1994). Limestone dissolution strongly influenced water chemistry in the early stages of development as evidenced by a layer of calcitic mud or marl underlying peats across much of the present-day Everglades (Gleason and others, 1974). Marl sediments are indicative of seasonally inundated wetlands with water of moderate to high mineral content, such as the marl prairies that presently occur in the southern Everglades. The shift towards a wetter climate in south Florida steadily increased the spatial extent and hydroperiod of Everglades wetlands as well as the rate of peat accretion (Gleason & Stone, 1994). Accumulated peat increasingly isolated the wetland surface from bedrock and ground-water mineral influences and increased the influence of rainfall on surface-water chemistry. The development towards longer hydroperiod and low-mineral conditions is evidenced by peat deposits 1-3 m deep without significant intervening marl layers in the northern and central Everglades. The limited amount of available paleoecological data provides further evidence of a mineral-poor chemistry in these areas prior to drainage and development (Slate & Stevenson, 2000; Winkler and others, 2001). Before subsidence, peat thicknesses typically were 2-3 m in portions of the northern Everglades that are now the EAA. In the northeastern Everglades, which is now WCA 2A and the Refuge, peat generally was >1 m thick and described as a “water lily-dominated peat” with little calcite buildup. Peat generally was <1 m thick in the southern Everglades and contained abundant calcite layers south of the present location of Tamiami Trail (Gleason & Stone, 1994; Renken and others, 2005). Thinner peats in the southern Everglades are consistent with results of soil analysis and dating, which revealed a more dynamic spatial and temporal pattern of peat versus marl formation and indicated a more variable history of hydration and mineral inputs in this part of the Everglades (Winkler and others, 2001).

Precipitation

Contemporary measurements of rainfall chemistry in south Florida illustrate the mineral-depleted nature of this water source. Based on rainfall-chemistry data collected by the SFWMD during the mid- to late 1990s, the median specific conductance of rainfall in the northern Everglades is <20 $\mu\text{S}/\text{cm}$ and median concentrations of all major ions except for Cl^- (median value = 1.5 mg/L) are < 1 mg/L. Contemporary measurements of atmospheric deposition likely overestimate historic mineral concentrations in rainfall and dry deposition as they reflect contamination from local sources (e.g., locally generated dust, trapped insects, and other debris) and human influences such as farming on regional atmospheric chemistry. However, these data clearly illustrate that, in the absence of significant water sources other than direct rainfall, surface waters in peat-building portions of the Everglades would have a mineral-poor chemistry.

The unequal distribution of precipitation along the lower east coast of Florida is one possible reason why portions of the Everglades may have been evolving more toward ombrotrophic conditions. Spatial patterns of annual precipitation also may help explain differences in hydroperiod, depths, and characteristics of peat development in the Everglades. Precipitation generally is higher near the coast than farther inland. The highest average annual precipitation (approximately 160 cm per year) occurs along a band of coast approximately 15 km wide and 130 km long that extends from the southern tip of Florida to as far north as West Palm Beach (Renken and others, 2005). The zone of highest average annual precipitation extends

farthest inland (60 km) in the northeastern part of the Everglades, in the vicinity of the Refuge and northern WCA 2A. Farther south, the band of greater precipitation remains much closer to the coast until reaching the southern end of the lower east coast of Florida where it extends 30-km inland. The result is that the northeastern Everglades, on average, receives greater rainfall than the central part of the Everglades in western Broward County (where average annual precipitation is approximately 125 cm per year). Greater rainfall in the northeastern Everglades may be one reason for the development of the relatively deep and distinctive “Loxahatchee” peat in this part of the Everglades (Gleason and others, 1974).

Lake Okeechobee Overflows

Episodic overflow from Lake Okeechobee was a significant water source to the predrainage Everglades during the wet season. A confining dam now restricts those flows, although Lake Okeechobee water still enters the Everglades in large quantities through water releases to canals that are part of the water-management network. With a specific conductance of approximately 400-500 $\mu\text{S}/\text{cm}$, and relatively high proportional contributions of Mg^{2+} , SO_4^{2-} , Ca^{2+} and HCO_3^- to its ionic balance, Lake Okeechobee’s mineral content currently is higher than surface waters of more rainfall-driven portions of the northern and central Everglades. The lake’s chemistry is influenced by runoff from the Kissimmee River basin and other agricultural lands within its watershed, interactions with marl layers in the lakebed, limestone bedrock, and ground water beneath the Lake, and by back-pumping from the EAA on the south side of the Lake. The current specific conductance of Lake Okeechobee water may be higher than historic levels due to human influences but provides an upper estimate of the influence that lake outflows may have exerted on mineral chemistry at the northern end of the predrainage system.

Interactions between Surface Water and Ground Water

The mineral chemistry of surface waters in the Everglades always has been influenced to an extent by interactions with mineral-rich ground water from the underlying aquifer. Pore water in the top meter of peat and ground water in the top 10 meters or so of the aquifer typically is a calcium sodium bicarbonate-type water or a mixed cation bicarbonate chloride-type water. The source of peat pore water and shallow ground water is recharge of rainfall or surface water that slowly acquires a predominantly Ca^{2+} , Mg^{2+} , and alkalinity (HCO_3^-) signature due to dissolution of shallow aquifer materials. The mineral content of shallow subsurface waters are further increased by vertical mixing that transports Na^+ and Cl^- upward from the bottom part of the surficial aquifer. The specific conductance of shallow ground water in the interior of the northern and central Everglades presently is about 1250 $\mu\text{S}/\text{cm}$, and the specific conductance of peat pore water is intermediate between that of surface water and shallow ground water. In some areas, especially near canals and levees, shallow ground water and peat pore water have a specific conductance that is considerably higher and with larger contributions of Na^+ , Mg^{2+} , Cl^- , and SO_4^{2-} to its mineral chemistry. This chemical signature reflects mixing with deeper ground water (>30 m) containing relict seawater with a specific conductance often above 10,000 $\mu\text{S}/\text{cm}$ and as high as 26,000 $\mu\text{S}/\text{cm}$. Ground water at intermediate depths typically has a specific conductance between 1,250 and 10,000 $\mu\text{S}/\text{cm}$ and a mineral chemistry that reflects the vertical mixing gradient, with calcium sodium–bicarbonate waters near the top, mixed cation-bicarbonate chloride waters at intermediate depths, and sodium chloride-type at the bottom of the surficial aquifer (Howie, 1987; Harvey and others, 2002; Price & Swart, 2006).

Ground water directly to the northwest of the Everglades may have evolved differently than ground water directly beneath the present day Everglades as exemplified by its substantially higher contributions of Mg^{2+} and SO_4^{2-} ions as compared with Ca^{2+} , Na^+ , bicarbonate, and Cl^- ions (Frazee, 1982; Parker and others, 1955). That type of ground water could have evolved as a result of extremely long periods of fresh ground-water storage in contact with the sand and limestone bedrock that produces a mineral-rich ground water that usually is referred to as “fresh formation water”, a water type on its way to evolving to a “connate” ground water. Within the vicinity of the Everglades, fresh formation water and indicators of connate ground water have been detected only in the northern part of the system beneath the EAA and near Lake Okeechobee (Parker and others, 1955; Frazee, 1982; Harvey and others, 2002).

Role of Ground Water in the Predrainage Everglades

Given the absence of measurements of interactions between surface water and ground water in the predrainage Everglades, it was necessary to rely on modern analogs to estimate contributions of ground-water exchange to the water budget in Table 3. A 5-year time series of hydrologic measurements, made far from the direct influence of levees and canals, was recently completed in the central part of WCA 2A (Harvey and others, 2004) and provides a reasonable data set from which to infer fluxes in the predrainage landscape. In central WCA 2A vertical water exchange across the ground surface occurs as a result of surface water and ground water moving vertically back and forth through peat and shallow ground water. The 1-m layer of peat and the top 8 m of the underlying aquifer where active exchange occurs is referred to as the “interactive layer of surface- water and ground-water exchange” (Harvey and others, 2005a; 2005b). The time-averaged exchange flux of surface water and ground water in the interactive zone was estimated for the period 1997 to 2002 in central WCA 2A, and found to be approximately 0.02 cm/d (Harvey and others, 2006). In the absence of historical data, this flux is assumed to be a reasonable estimate of “interior ground-water exchange” for both the managed and the predrainage Everglades as shown in Table 2. In the predrainage Everglades, that flux would have been influenced by pulsed flows of surface water originating as overflow from Lake Okeechobee or from large but isolated rain events in the northern Everglades. The modern analogy for those pulsed flows is the surface-water gravity waves that are released from water-control structures and move rapidly south through the WCAs. Ground-water discharge tends to occur in the relatively dry areas of the wetland prior to the arrival of a gravity wave, while ground-water recharge tends to occur in the wetted areas once the gravity wave has arrived (Harvey and others, 2004). It is important to note that exchange fluxes between surface water and peat pore water are greater than those between surface water and the underlying aquifer. The exchange flux with the 1-m layer of peat pore water is approximately an order of magnitude greater (0.2 cm/d) compared with ground-water exchange (Harvey and others, 2005a). The greatest fluxes occur in the very shallow surface layer (in the top 7 cm of peat) where exchange is approximately 3 cm/d (Harvey and others, 2005b).

Calculations using data from Price and others (2003) suggest that surface-water exchange with ground water in the underlying aquifer in the southern Everglades may be three times higher than that in the central and northern Everglades, or approximately 0.06 cm/d (Harvey and others, 2006). There are several reasons why ground-water exchange in the interior wetlands probably has always been greater in the southern Everglades. The higher proportion of short hydroperiod wetlands in the southern Everglades compared to areas farther north would tend to

enhance infiltration of precipitation into the peat and bedrock. These shorter hydroperiod wetlands generally have thinner peat accumulations (Gleason and others, 1974), which offer less resistance to subsurface vertical flow. Finally, the greatest transmissivity in the underlying aquifer occurs in the southern Everglades (Fish & Stewart, 1991; Harvey and others, 2002; Renken and others, 2005). The greater interactions between surface water and ground water in the southern Everglades may contribute to a more mineral-rich surface water compared to the central and northern Everglades, with calcium bicarbonate-type waters being common (Price & Swart, 2006). Surface-water specific conductance in the most mineral-rich freshwater areas of Everglades National Park rarely exceeds 400-600 $\mu\text{S}/\text{cm}$ (Joffre Castro, Everglades National Park, pers. comm.), which probably represents an upper limit for the effect that interactions between surface water and shallow ground water had on the mineral chemistry of any part of the predrainage ecosystem.

Role of Ground Water in the Managed Everglades

Water management inadvertently has increased the extent of interactions between surface water and ground water in the Everglades, beginning with the first efforts to drain the wetland by dredging canals in the early 1900s. Surface-water and ground-water interactions probably were a relatively small component of water budgets in the predrainage Everglades compared to the managed Everglades (Table 2). Smaller exchanges between surface water and ground water in the predrainage landscape were due in part to weaker driving forces for vertical flow on the very flat predrainage landscape that had not yet been altered by subsidence and the construction of canals and levees. Furthermore, the resistance to vertical flow probably was greater in the predrainage system due to the relatively continuous cap of undisturbed peat that was a meter or more in thickness and possessed a hydraulic conductivity much lower than the aquifer beneath (Harvey and others, 2004). Progressive drainage efforts through the 1950s led to oxidation and peat subsidence in the northern Everglades, which fundamentally changed the general direction of horizontal ground-water flow and increased the vertical component of this flow (Miller, 1988; Harvey and others, 2002). These effects have been particularly pronounced along the boundaries of the WCAs and in the large area of wetlands that was drained and then developed for agriculture in the EAA. Dependence on canals for drainage in the EAA increased throughout the second half of the 20th century as the wetlands converted to agriculture continued to subside due to peat oxidation (Renken and others, 2005). Loss of peat, and entrenchment of canals >5 m into the top part of the surficial aquifer in many locations brought surface waters into closer contact with mineral-rich ground waters (Harvey and others, 2002) (also see section *Canals Discharges* below).

Water management in the WCAs involves using levees and water-control structures to conserve water during dry periods. Storing water in the conservations areas keeps water levels relatively high in the wetland on the upstream side compared to the downstream side of the levee. Abrupt water-level differences created by levees produce the driving force for relatively deep vertical exchange of ground water. Differences in hydraulic head across the levees cause underflow beneath the levees that brings deeper, mineral-rich ground water to the surface in the downstream wetland (Harvey and others, 2002; Harvey and others, 2004; Harvey and others, 2005a). Underflow beneath the levees of the eastern margin of the managed Everglades has had the overall effect of increasing ground-water recharge in the managed Everglades compared to the predrainage Everglades (Table 3).

Table 3. Median concentrations of major nutrients and dissolved mineral ions for the period 1994-2003 in surface-water samples collected by the South Florida Water Management District at major canal pump stations (S5A and the outflow from STA1W) that affect water quality in the Refuge and WCA 2A and in the interior of WCA 2A (CA215) and the Refuge (LOX8). All units are in mg L⁻¹ except for specific conductance, which is in units of $\mu\text{S cm}^{-1}$

Parameter	S5A Pump Station	STA1W Outflow Pump	WCA2A Interior	Refuge Interior
Total Phosphorus	0.112	0.023	0.005	0.008
Total Kjeldahl Nitrogen	2.5	2.3	2.2	1.2
Specific Conductance	1006	1056	936	92
Alkalinity	226	237	222	12
Cl ⁻	137	156	140	15
Ca ²⁺	79	70	59	5
Na ⁺	95	115	94	10

In addition to storing water behind levees, another part of water management operations that affects surface and ground water interactions is the use of high-capacity pumps to move water in canals. These operations locally increase vertical driving forces beneath the canal bottoms in the aquifer that cause discharge of deeper ground water (Miller, 1988; Krupa and others, 2002). One effect of pumping is to increase rates of movement of ground-water solutes from deep in the surficial aquifer (> 8 m), which brings dissolved minerals from deeper layers in the aquifer into surface waters (Miller, 1988; Krupa and others, 2002).

Canal Discharges

Canal waters are an important source of water to the managed Everglades ecosystem. The most significant sources of the water to the main conveyance canals flowing into the Everglades (the Palm Beach, Hillsboro, North New River, and Miami canals shown in Fig. 1) include water releases from Lake Okeechobee, runoff of rainfall and soil water from agricultural fields in the EAA, and ground-water discharge to canals within the EAA (Miller, 1988; Harvey and others, 2002). The median specific conductance of surface waters in the main canals ranges between 700-1100 $\mu\text{S/cm}$ (Fig. 3), more than 50-fold higher than that of rainfall and twice that of current levels in Lake Okeechobee, which also is exposed to elevated mineral loads from human sources. Specific conductance decreases from north to south across the Everglades canal network (Fig. 4), and this trend likely is caused by progressive dilution with rainwater and surface waters in the WCAs with increasing distance from the mineral sources in the north.

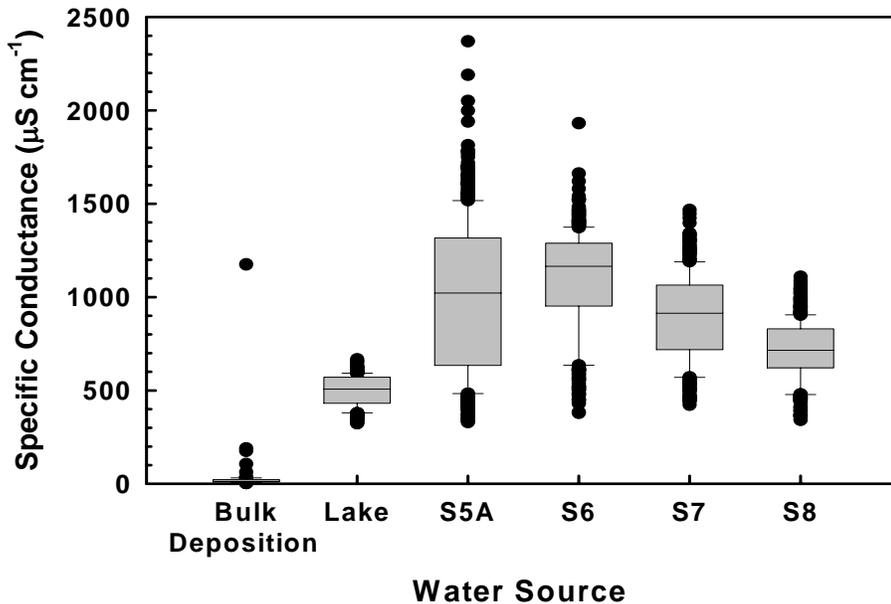


Figure 3. Specific conductance of major water sources to the present-day Everglades, including bulk atmospheric deposition, Lake Okeechobee surface water, and canal discharges from major SFWMD pump stations. The top, mid-line, and bottom of each box represent the 75th, 50th (median), and 25th percentiles of data, respectively; the upper and lower vertical lines represent the 90th and 10th percentiles, respectively; circles show data points outside the 10th-90th percentile range. All data are from SFWMD sampling stations. Lake and pump station data were collected between 1994 and 2005 and bulk deposition data were collected between 1994 and 1999.

Canal waters are discharged through a number of water-control structures on the north and west side of the Everglades, and also from control structures along the canals that traverse the Everglades. The influence of those focal points for discharge of mineralized water is evident from spatial maps of surface-water conductivity in the Everglades wetlands generated from the Regional Environmental Monitoring and Assessment Program (REMAP) conducted by the U.S. Environmental Protection Agency (Fig. 5). Areas strongly influenced by these discharges have a specific conductance near 1000 $\mu\text{S}/\text{cm}$ while those with a rainfall-driven hydrology typically have values as low as 100 $\mu\text{S}/\text{cm}$ or less.

The influence of canal discharges on mineral concentrations in the WCAs is influenced by topographic slope, vegetative resistance to flow, and the location and orientation of interior canals and other pathways for water flow such as airboat trails. As a result, while mineral-rich canal discharges might account for as much as half of the water flowing through both the Refuge and WCA 2A over the past several years (Carl Fitz, SFWMD, pers. comm.), the effect of these discharges on mineral levels in the interior of these wetlands differs dramatically. Canal waters entering WCA 2A from the north are forced southward as sheetflow during times of high water (Harvey and others, 2005a). By contrast, rim canals encircling the Refuge convey canal water southward, in the general direction of the topographic gradient, which reduces the potential for these waters to move into the Refuge. Thus, the interior of the Refuge tends to retain a water chemistry more similar to that of rainfall, whereas the chemistry in the interior of WCA 2A reflects that of mineralized canal water (Table 3). A different situation occurs in WCA 3A, where the major conveyance canals pass through the wetland's interior. The canal levees have regularly spaced cuts that allow for some hydration of the wetland. However, the

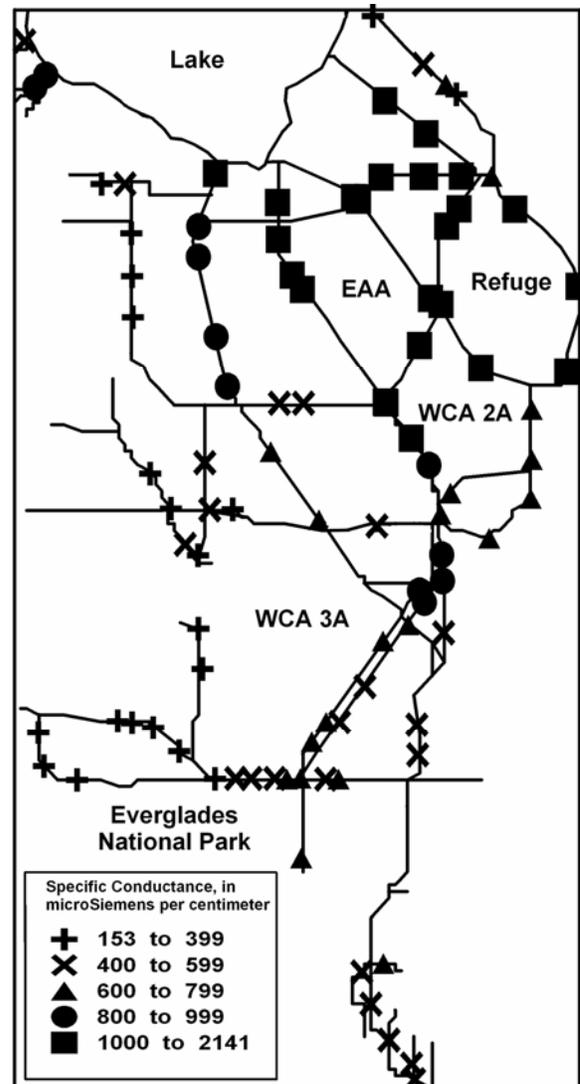
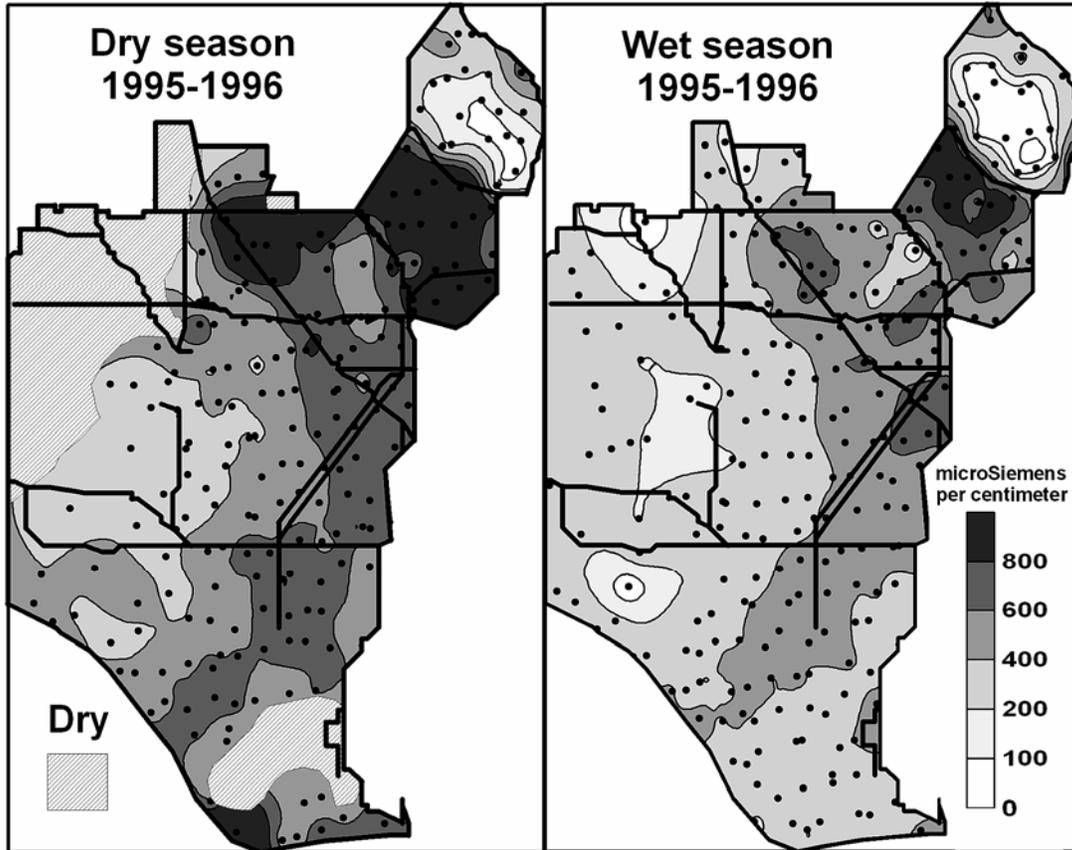


Figure 4. Surface-water specific conductance in canals across the Everglades as measured during U.S. EPA surveys. Symbols show specific conductance (see legend in lower left corner) at 99 sampling locations selected using a probabilistic sampling design described in Stober and others (1998). Fifty locations were sampled during September 1993 and an additional 49 were sampled during September 1994. See Fig. 1 for a more detailed regional map. This figure was modified from Stober and others (1998) with permission.



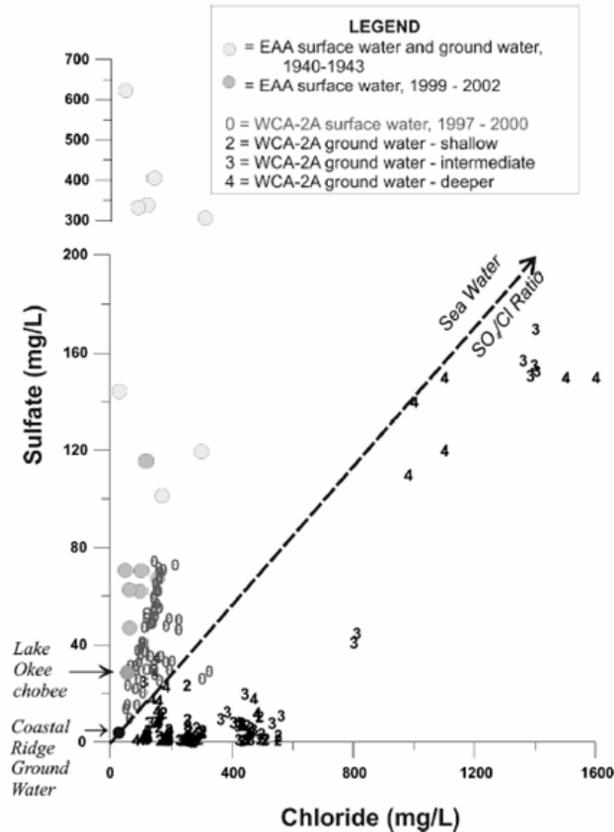
relatively large size of WCA 3A acts to reduce the influence of canal water on the surface-water

Figure 5. Patterns of surface-water specific conductance across the Everglades and adjacent wetlands as measured during U.S. EPA surveys. A total of 500 sampling locations (black dots on the maps) were selected using a probabilistic sampling design described in Stober and others (1998). One-hundred and twenty-five of these locations were sampled during each of the following months: April 1995, September 1995, May 1996, and September 1996. Data were combined for dry season (April, May) and wet season (September) sampling surveys and analyzed by kriging to describe spatial patterns of specific conductance. This figure was modified from Stober and others (1998) with permission.

chemistry of the wetland interior. Future changes in the routing of canal waters through the Everglades include the rerouting of agricultural drainage through treatment wetlands known as Stormwater Treatments Areas (STAs) that discharge waters into parts of WCAs that in the past were not directly exposed to canal waters. Further changes may include removal of a substantial portion of levees in some areas that may include backfilling of associated canals. In addition to altering patterns of hydration and sheetflow in the WCAs, these modifications undoubtedly will cause some changes in the fate of mineral-rich canal water as it moves into the interior wetlands. Some areas that were relatively isolated from mineralized canal waters in the past likely will have increased exposure in the future.

Relative Importance of Flows Supplied by Canals and Ground Water

Water-budget data indicate that on average approximately 18% of Everglades surface water is supplied by canal discharges (Table 3). In WCA 2A, the dominant source of canal water is from canals that traverse the EAA (Fig. 6). The similarity between the ratio of sulfate to chloride in Everglades surface waters and EAA canal waters is an indicator that EAA canal water is a primary source for Everglades surface water (Fig. 6). Discharge of shallow ground water cannot explain high sulfate to chloride ratios in WCA 2A surface waters because the ratios are substantially lower in the underlying ground water beneath WCA 2A, which tends to have a



sulfate to chloride near or below a seawater ratio (Fig. 6). A sulfate:Cl⁻ ratio near that for seawater is expected in deeper ground water beneath WCA 2A, which contains relict seawater in

Figure 6. Relative importance of EAA canals as a source of surface water in WCA 2A as indicated by sulfate:chloride ratios. Water sampled in canals, shallow drainage ditches and in ground water in the EAA in the 1940s (Parker and others, 1955), and more recent sampling in EAA canals (Chen and others, 2006), is characterized by a sulfate:chloride ratio substantially higher than sea water (including relict sea water stored in the surficial aquifer beneath the Everglades). Surface waters sampled between 1997 and 2000 in WCA 2A had sulfate:chloride ratios more similar to EAA canal waters than to ground water from shallow and intermediate depths in the sand and limestone layers of the surficial aquifer beneath the wetland (Harvey and others, 2000; 2002; 2005a). These data support the interpretation that EAA canals are a major water source to surface waters in the northern Everglades.

the bottom part of the surficial aquifer. A similar ratio would be expected in shallow ground water if upward mixing of minerals occurs from the deeper aquifer. The very low ratio of sulfate to Cl⁻ in shallow ground waters beneath WCA 2A is consistent with removal of sulfate by sulfate reduction in shallow ground water (Bates and others, 2002; Orem, 2004). Note that sulfate to Cl⁻ ratios are higher in ground waters beneath the EAA (Parker and others, 1955), which indicates the need to consider the role of EAA groundwater, along with fertilizer additives used on EAA farm fields, as the primary source of sulfate to EAA canals.

Mineral Sources to EAA Canals

Possible sources of minerals to EAA canals include mineral additives applied with fertilizer to EAA farm fields in addition to minerals naturally present in EAA ground water. The importance of fertilizer has been established through use of environmental tracers that identified fertilizer as a significant source of elevated P and sulfate concentrations to EAA canals and Everglades surface waters. The source of P was identified through correlation with closely associated uranium isotopes in fertilizer (Zielinski and others, 2000). The fertilizer source of sulfate was identified by analysis of the sulfur (S) isotopic composition of canal water, wetland surface water, and various ground waters (Bates and others, 2002; Orem, 2004). The ratio of the isotope ³⁴S to ³²S in sulfate measured in ground water generally was too high to explain the source of sulfate in canals, while the overall concentration of sulfate in shallow ground water beneath the Everglades itself was too low to explain the high concentrations measured in canals. Meanwhile, the isotopic signature of S in fertilizer was very close to that measured in canals. Fertilizer also may be an important source of K⁺ (i.e., potash), which is a major nutrient in fertilizer.

In addition to fertilizer inputs, unexpectedly high levels of sulfate in EAA canal waters could have a partial source in the discharge of the more poorly characterized ground waters from beneath the EAA. There is limited evidence that fresh formation ground water, which could have relatively high concentrations of sulfate and Mg²⁺, exists beneath the EAA (Frazee, 1982; Parker and others, 1955). The amount of sulfate discharged from EAA ground water is not certain. Greater insight into sulfate sources to EAA canals could best be addressed by a new program of sampling ground-water chemistry in EAA wells. Wells sampled more than 50 years ago could be sampled again and compared with previous results (Parker and others, 1955). Ideally a tracer signature could be identified that distinguishes sulfate in EAA canals and in the Everglades that comes from fertilizer additives as opposed to EAA ground water. Use of S

isotopes, uranium isotopes, and water stable isotopes might be helpful for that purpose (Bates and others, 2002).

Distinguishing sources of sulfate in fertilizer additives from EAA ground water could be complicated if 1) ground waters beneath the EAA have been contaminated by fertilizer additives, and 2) dissolution of the same or very similar minerals (i.e., gypsum) is the sulfate source in both fertilizer additives and in EAA ground water.

Natural chemical limits to ombrotrophy in the Everglades

Ombrotrophy in northern peatlands typically is characterized by extremely low specific conductance (< 50 $\mu\text{S}/\text{cm}$), pH (<4.2), and concentrations of major ions such as Ca^{2+} (< 5 ppm) (Moore & Bellamy, 1974; Glaser, 1992; Bridgham and others, 1996; Wheeler & Proctor, 2000) as illustrated in Table 1. Water

chemistry in areas of the Everglades such as the Refuge interior that are believed to be rainfall-driven are characterized by somewhat higher mineral concentrations (e.g., specific conductance of $\sim 100 \mu\text{S}/\text{cm}$ and $\text{Ca}^{2+} \sim 5 \text{ mg}/\text{L}$) and a distinctly higher pH (6-6.5) and are more similar to the European classification of transitional fens (those having some bedrock influence), which have a relatively high pH but somewhat depleted cation concentrations (Sjörs, 1950). This comparison raises the issue of why even purely rainfall-fed portions of the Everglades might have a chemistry that is dissimilar to many other ombrotrophic peatlands. Consideration of the factors controlling water chemistry in these ecosystems provides several possible explanations for this difference.

Expected concentrations of the conservative ion Cl^- in surface waters of the Refuge interior, calculated based on precipitation chemistry and reasonable assumptions of water losses to evapotranspiration (ET), are consistent with actual concentrations measured as part of routine water-quality monitoring in recent years (Michael Waldon, U.S. Fish and Wildlife Service, pers. comm.). This consistency supports the general belief that water chemistry in this portion of the

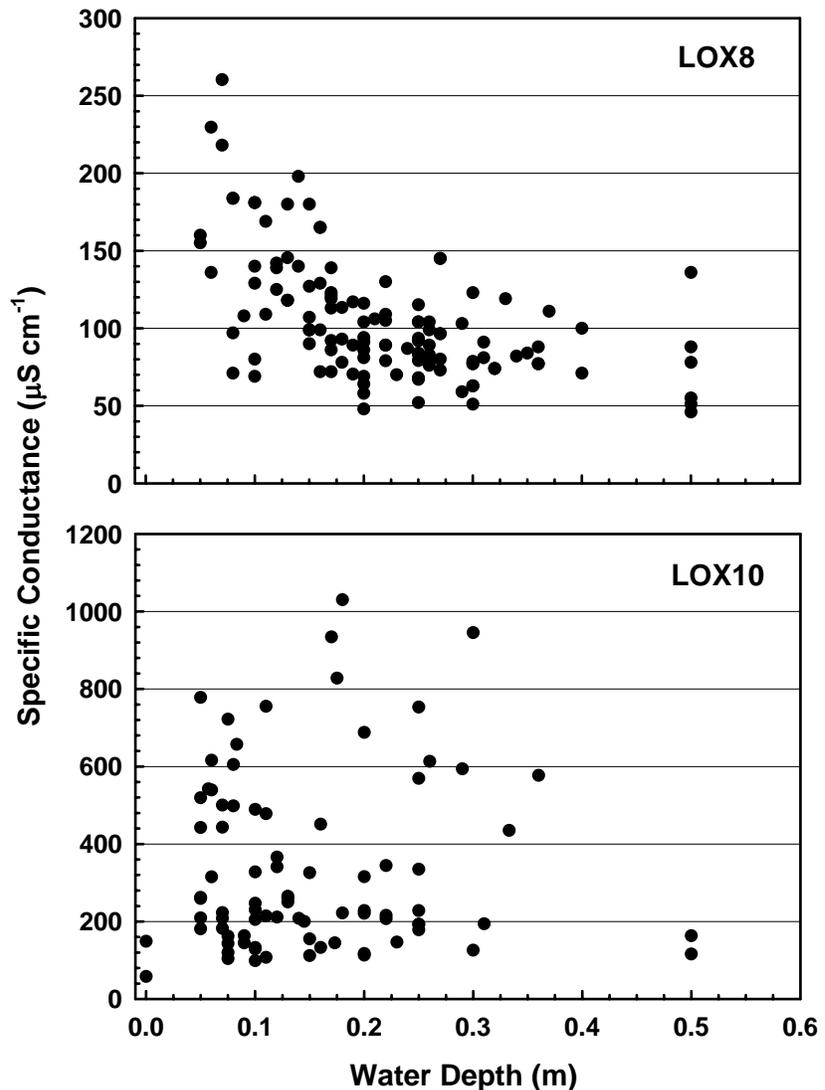


Figure 7. Relationship between surface-water specific conductance and water depth at an interior (LOX8) and a canal-influenced (LOX10) monitoring station in the Refuge based on monthly data collected between 1994 and 2004. See Appendix A for site locations.

Everglades is strongly influenced by rainfall and by the hydrologic balance between precipitation and ET. The effect of seasonal variation in the rainfall:ET ratio on mineral concentrations is evident in the relationship between specific conductance and water stage at an interior monitoring station, LOX8 (Fig. 7). Specific conductance remains low (generally < 100 $\mu\text{S}/\text{cm}$) during the wetter months when precipitation exceeds ET and stages are high, but increases somewhat (approaching 250 $\mu\text{S}/\text{cm}$) during the drier months as stages decline in response to ET that exceeds precipitation.

The balance between precipitation and ET plays a major role in determining concentrations of dissolved minerals in ombrotrophic peatlands and probably contributes to regional differences in the mineral chemistry of these waters. Because of its low mineral content, precipitation typically dilutes concentrations of dissolved minerals in surface waters. By contrast, ET, which is essentially a water distillation process, promotes the concentration of dissolved minerals. In temperate and northern peatlands, annual ET rates typically are just 50-70% of those for precipitation (Mitsch & Gosselink, 2000). In the Everglades, ET and precipitation are balanced (Abteu and others, 2004). Unlike more northerly peatlands, hydrologic characteristics of the Everglades are controlled by a distinct wet season (May-October), during which precipitation exceeds ET, and an extended dry season (November-April), during which precipitation is low but ET rates remain high due to the warm climate and year-round growing season. On this basis alone, mineral concentrations in rainfall-driven portions of the Everglades would be expected to be higher than those in northern peatlands, which have a cooler climate, a shorter growing season and, therefore, lower ET.

Regional influences on the chemistry of atmospheric deposition may explain elevated concentrations of selected ions in Refuge surface waters compared to most ombrotrophic peatlands. Marine influences likely explain elevated concentrations of Cl^- , Na^+ , and Mg^{2+} compared to continental peatlands, while dust from farming and mining operations may be regional sources of Ca^{2+} and Mg^{2+} . Similar factors explained variation in Na^+ , Ca^{2+} and Mg^{2+} concentrations among northern peatlands in North America (Glaser, 1992). Extremely low sulfate concentrations in Refuge waters compared to those in many European peatlands (Table 1) likely are due to prevailing weather patterns and the Everglades' peninsular location, both of which limit contributions from anthropogenic S emissions such as the burning of coal.

The resident flora can exert strong feedback on peatland soil and water chemistry. In particular, the dominance of *Sphagnum* mosses is a key factor responsible for the low pH and conductivity of temperate and northern ombrotrophic peatlands. Organic acids generated by these mosses play a major role in maintaining extremely acidic conditions (pH 3.6-4.2) in bogs (Siegel and others, 2006). *Sphagnum* mosses also possess an extremely high cation-exchange capacity that allows them to concentrate minerals such as Ca and Mg in the dilute environment of these precipitation-fed systems. This process contributes to lower dissolved-cation concentrations than would be expected strictly on the basis of precipitation chemistry and hydrologic relationships such as precipitation:ET ratios. This exchange process also releases H^+ ions into the surrounding water, which may further enhance acidity. The importance of *Sphagnum* to peatland water chemistry was illustrated by Bellamy and Rieley (1967), who documented the conversion of an extremely rich fen to a bog environment following *Sphagnum* introduction. The distribution and dominance of *Sphagnum* is limited in subtropical peatlands (Halsey and others, 2000), and this genus has not been reported from the Everglades. Dominant wetland plant species in the Everglades (for example, *Cladium jamaicense*, *Nymphaea odorata*)

produce peats and other decomposition byproducts that are less acidic than those generated by *Sphagnum* or the woody plants in forested peatlands (William Orem, USGS, pers. comm.).

Even in the absence of keystone taxa such as *Sphagnum*, there are other biogeochemical processes that serve as sinks for dissolved minerals. Extending the Cl^- balance calculations already described to other major ions, it becomes clear that sinks for at least some ions exist within the Refuge. As illustrated in Fig. 8, hydrologic factors can explain concentrations of Na^+ and Mg^{2+} , but not those of other ions. Lower than predicted Ca^{2+} concentrations may result from plant uptake, chemical precipitation within high pH microenvironments within periphyton mats, or may simply be due to slight contamination of rainfall samples collected from the SFWMD monitoring network, which was the source of rain-water chemistry data for this analysis. Concentrations of K^+ and sulfate are considerably lower than anticipated, likely due to plant uptake and microbial reduction, respectively. Lower than expected alkalinity may be due to neutralization by organic acids produced by organic matter decomposition.

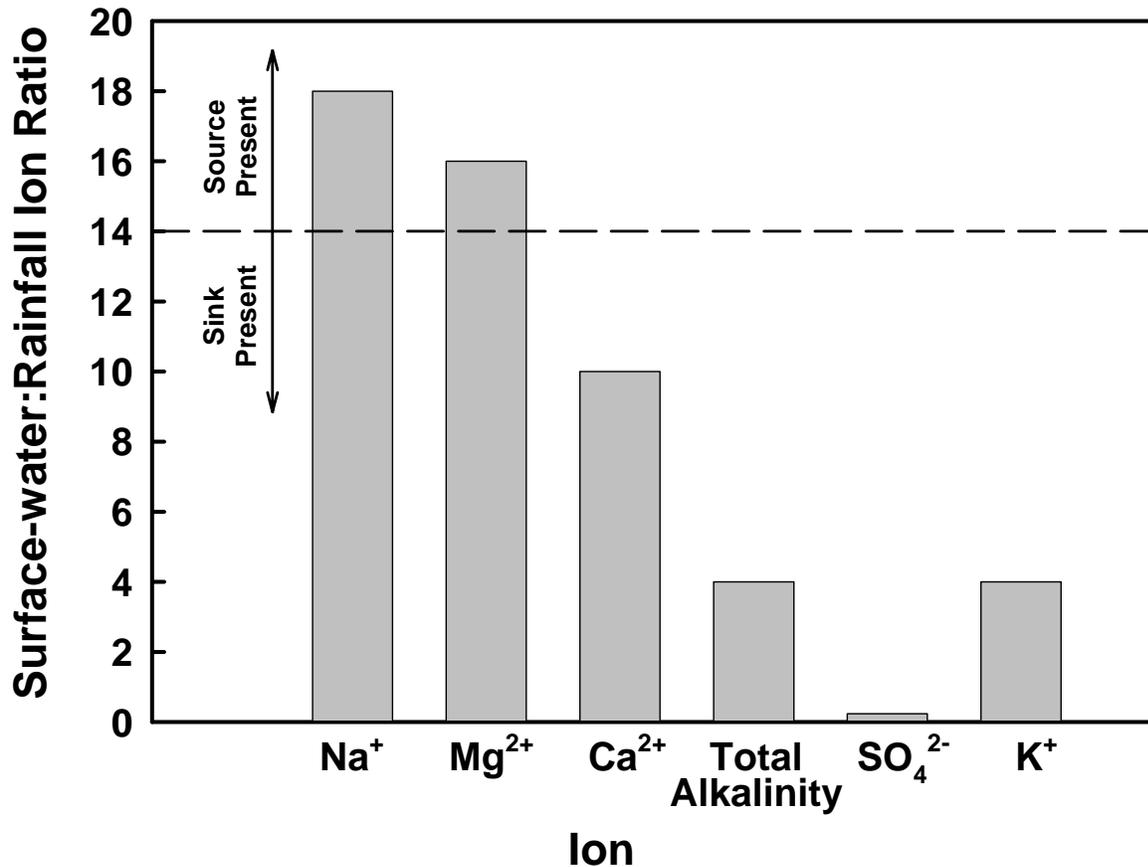


Figure 8. Ratios of the concentration of major ions in surface water from an interior Refuge location (LOX8) to that in rainfall. The ratio for Cl^- , which approximates the predicted value if rainfall were the sole mineral source, is shown by the dashed line. Ionic ratios greater than that for Cl^- indicate the presence of an additional mineral source while lower ratios indicate the presence of sinks for some ions within the wetland.

Lower than predicted Ca^{2+} concentrations may result from plant uptake, chemical precipitation within high pH microenvironments within periphyton mats, or may simply be due to slight contamination of rainfall samples collected from the SFWMD monitoring network, which was the source of rain-water chemistry data for this analysis. Concentrations of K^+ and sulfate are considerably lower than anticipated, likely due to plant uptake and microbial reduction, respectively. Lower than expected alkalinity may be due to neutralization by organic acids produced by organic matter decomposition.

The wetness of the climate may be an important factor moderating acidity in ombrotrophic peatlands. Moore and Bellamy (1974) note that “there is little doubt that the mobility of [peatland] water must be the most important factor” that retards the accumulation of organic acids. For example, Bellamy and Bellamy (1967) explained patterns in the chemistry and vegetation of ombrotrophic peatlands in western Ireland on the basis of the amount and frequency of precipitation. Peatlands in drier parts of the region (<100 cm annual precipitation with a frequency of < 225 rain days/year) were considerably more acidic (mean pH = 4.00) than those in the wettest areas (>125 cm annual precipitation with a frequency of >250 rain days/year) (mean pH = 4.74). They concluded that flushing from rainfall reduced the acidity of these systems. Contributions of bicarbonate ions in bulk deposition also might lend buffering capacity to coastal bogs by increasing alkalinity. Differences in water chemistry between acidic bogs and less acidic fens in northern Japan were explained based on the latter receiving periodic inputs of floodwaters during the monsoon season that ameliorate acidity (Nakamura and others, 2002). Mean annual rainfall in the Everglades is high (~130 cm) and may exert a flushing effect that ameliorates acidity generated by organic acids release during plant tissue leaching and decomposition. Rainfall-driven flows through the predrainage Everglades during the wet season may have had an even greater flushing effect that maintained water chemistry conditions that were only mildly acidic.

Reconstruction of the predrainage mineral chemistry of the Everglades is hampered by a lack of information on the water chemistry of predrainage inflows from the Kissimmee-Okeechobee watershed and the chemistry of bulk atmospheric deposition prior to significant human development in south Florida. However, based on the above analysis, current mineral levels in portions of the Everglades interior that are most isolated from canal flows may provide the best available approximation of the historic rainfall-driven chemistry of the northern and central Everglades.

Loxahatchee Refuge: Case Study of a Rainfall-Driven Everglades Peatland

The area known today as the Arthur R. Marshall Loxahatchee National Wildlife Refuge occupies the northernmost 600 km² of the remaining Everglades (Fig. 1). The Refuge is among the oldest parts of the Everglades based on radiocarbon dating of basal peats (Gleason and others, 1974). Peat depths of 2-3 m are common across much of the Refuge and provide a record that can be used to infer past vegetation and water chemistry conditions. As with much of the Everglades, the Refuge developed on top of limestone bedrock, which would have strongly influenced the mineral chemistry of this peatland early in its history. This has been confirmed by deep peat cores showing a basal layer of marl, indicating that this system began as a shorter-hydroperiod calcareous wetland (Gleason & Stone, 1994). Increased hydroperiods allowed for the initiation of peat formation, a process that gradually isolated the wetland surface from bedrock influences on water chemistry. Bedrock elevations (Jones, 1948) show that the Refuge

developed in a shallow trough running southeast from Lake Okeechobee, indicating a historical flow path from the Lake. Models such as NSM also predict a surface flow path prior to drainage. However, peats in the Refuge are mineral poor (Gleason & Stone, 1994), indicating a strong influence of rainfall on both the hydrology and chemistry.

Today, the Refuge interior represents one of the last remaining low-mineral areas of the Everglades. The persistence of this condition in the Refuge is a consequence of its relative isolation from mineral-rich canal waters that have converted areas farther south (e.g., WCA 2A) into hard-water fens with distinct ecological features, including some that occur naturally in portions of the southern Everglades (e.g., the presence of an abundant calcareous periphyton assemblage) and others that are a consequence of human alterations (e.g., the influence of elevated sulfate loading on sediment microbial and geochemical processes). By contrast, the low-conductivity waters in the Refuge interior, which are derived largely from rainfall, support a characteristic soft-water periphyton community, wetland plant species that also may be adapted to low mineral environments, lower rates of key ecosystem processes such as decomposition, and a near absence of canal-borne contaminants such as sulfate.

Effects of canal-water intrusion on Refuge water chemistry

Water-quality-monitoring data collected by the SFWMD show that surface-water specific conductance in the Refuge interior averages near 100 $\mu\text{S}/\text{cm}$ and is among the lowest recorded in the managed Everglades. This level is an order of magnitude lower than that in the L-7 canal, which conveys canal water discharges along the western side of the Refuge. Specific conductance in the eastern (L-40) rim canal (mean value of approx. 600 $\mu\text{S}/\text{cm}$) currently is lower than on the west side, but is still much higher than in the interior. The variable topography of the Refuge (Desmond, 2004) and vegetative resistance to flow undoubtedly have helped to limit intrusion of water from these canals into the interior.

While the interior of the Refuge remains largely rainfall-driven, intrusion of canal water maintains mineral gradients closer to the perimeter. The chemical nature of these gradients is illustrated for a set of 11 sampling stations monitored by the SFWMD between 1996 and 2005 (Fig. 9). Conditions at these stations do not capture the full spatial extent of canal-water intrusion as specific conductance at all stations exceeds that farther into the interior. Mean specific conductance ranged from >900 $\mu\text{S}/\text{cm}$ at stations closest to the canal to near 300 $\mu\text{S}/\text{cm}$ at the most interior stations.

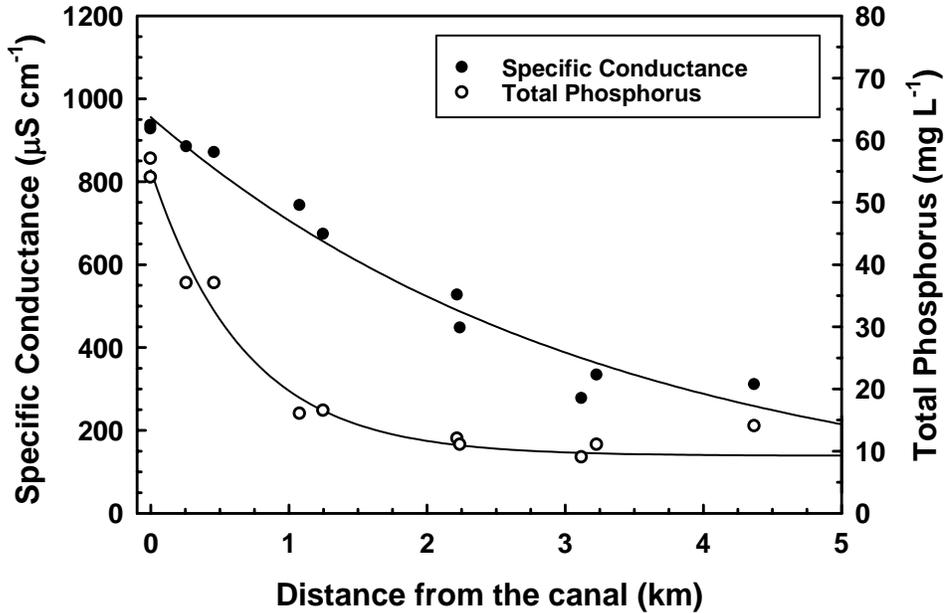


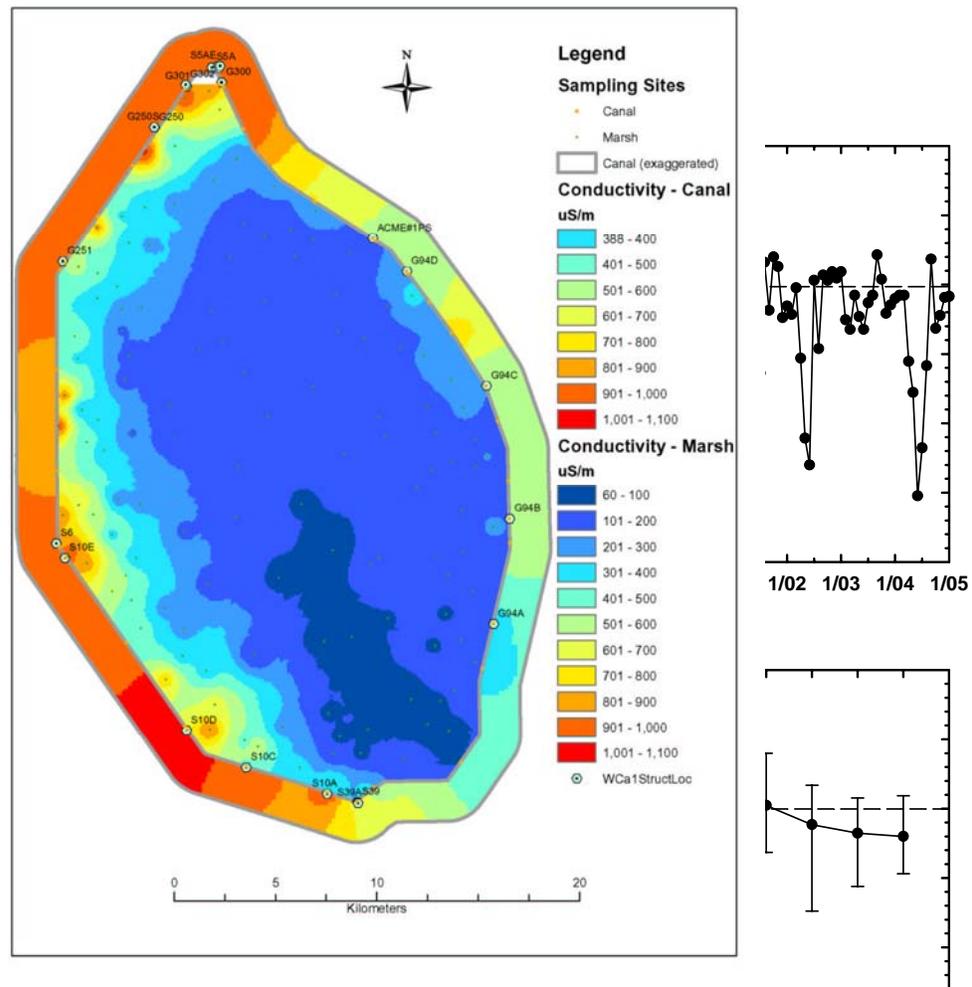
Figure 9. Surface-water specific conductance and total phosphorus across transects monitored by the SFWMD in the southwest corner of the Refuge. Points are means of data collected monthly between April 1996 and October 2005. Curves show best fit to an asymptotic decay equation. See Appendix A for transect locations.

Figure 10. Spatial patterns for surface-water specific conductance across the Refuge and adjacent rim canals. Specific conductance was measured during February 2004 at 130 wetland microbes and plants given its status as a limiting nutrient in the Everglades. Two zones of canal locations (black dots on the map) and 39 canal locations. Kriging was used to map the distribution of 11 specific conductance categories for the wetland and 8 categories for canals.

Specific conductance was correlated strongly with concentrations of all major ions but was less strongly related to P, which also enters the Refuge in canal water but is rapidly sequestered by influence can thus be discerned within the Refuge: 1) a relatively narrow zone of high P-high conductivity water; 2) a much larger zone of low P-high conductivity water. This spatial pattern is consistent with those documented at several other locations around the perimeter of the Refuge (Pope 1991).

A Refuge-wide survey of surface-water conductivity was performed jointly by the SFWMD, USGS, and U.S. Fish and Wildlife Service (USFWS) in February 2004 to better understand spatial patterns of canal-water intrusion. Predictably, locations in the Refuge interior had lower specific conductance than those near the rim canals (Fig. 10). An extensive area of elevated conductivity was documented across the western Refuge, whereas intrusion was limited along the eastern side. A similar pattern was found when this survey was repeated by the SFWMD in September 2004 (Susan Newman, SFWMD, pers. comm.). These results are consistent with the lower peat surface elevations along portions of the western perimeter and water management operations that historically have directed most canal flows down the western rim canal. Both of these conditions increase the potential for canal-water intrusion into this part of the Refuge.

Several factors including local variation in topographic and vegetative resistance to flow affect the intrusion of canal water into different parts of Refuge. However, a simple predictor of the timing and magnitude of canal-water intrusion across the Refuge is the difference in water-surface elevations between the rim canals and Refuge interior. Water management operations and natural forces such as droughts that result in canal stages above those in the Refuge promote the movement of canal water into the Refuge, whereas higher stages in the interior cause water to



drain off the Refuge. Water stage in the center of the Refuge often is higher than that in the rim canal, but canal stages periodically exceed those in the Refuge during most years, sometimes for several months (Fig. 11A). There is some seasonal periodicity to these stage differences, with the greatest possibility that canal stages will exceed those in the interior late in the wet season (September) (Fig. 11B). However, canal stages in excess of that in the interior can occur during almost any month of the year.

This simple relationship between canal and Refuge stages provides at least a partial explanation for the occurrence of periods of elevated specific conductance within the Refuge as illustrated using data from a long-term SFWMD monitoring station (LOX10) located approximately 2.5 km from the western rim canal (Fig. 12). Specific conductance values at this site are correlated positively with the difference in canal and interior stages. While this relationship does not explain all variation in conductivity at this site, it does reveal that high conductivity events during the past 11 years are associated with periods where canal stage approaches or exceeds that in the interior. Two exceptions to this pattern occurred during May 1996 and for a longer period beginning in July 2001. During the 1996 event, canal water stage exceeded that in the interior for a brief period of time following the sampling event that measured specific conductance. During the late summer of 2001, the stage differential between the canal and the Refuge interior reversed repeatedly and may have contributed to the lack of a clear canal-water signal at LOX10. In contrast to conductivity patterns at LOX10, those at LOX8 show a marginally significant negative relationship with canal-wetland stage differences, indicating that canal waters do not exert a strong influence on this site in the center of the Refuge. As discussed earlier, seasonal variation in water depth as influenced by rainfall, which dilutes minerals, and ET, which concentrates minerals, provides a better explanation of surface-water mineral concentrations in the center of the Refuge.

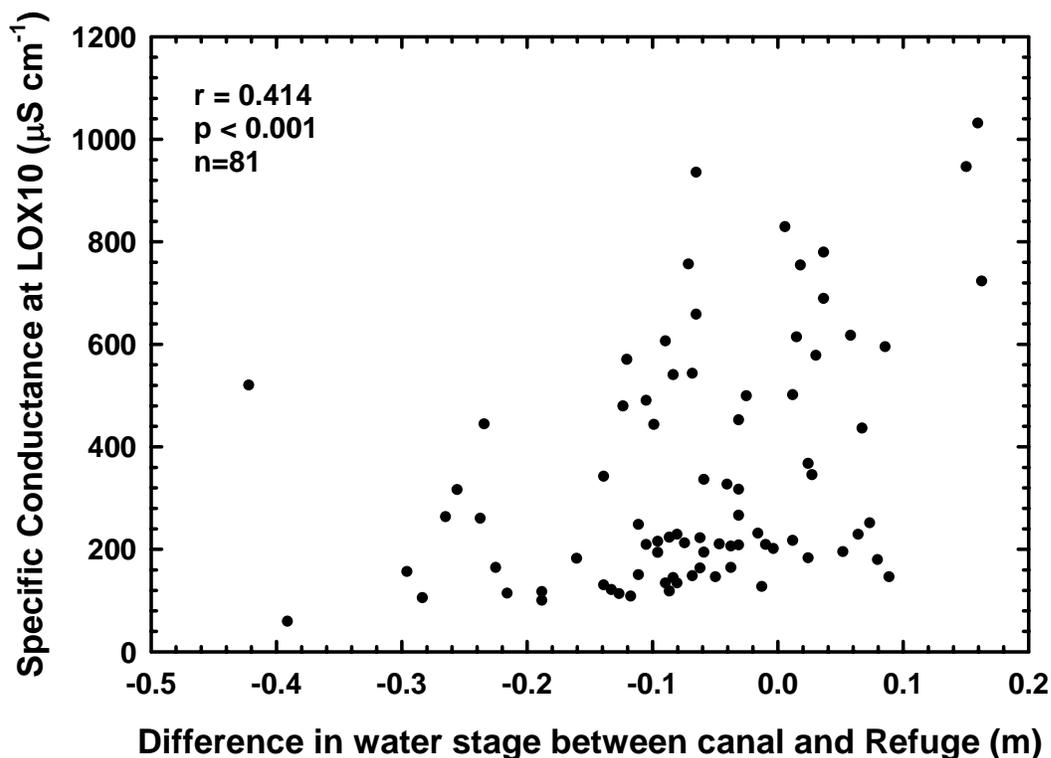


Figure 12. Relationship (with Spearman Rank correlation) between specific conductance at a canal-influenced monitoring station (LOX10) in the Refuge and the stage difference between the western rim canal (S10Dh gage) and the Refuge interior (LOX8), which indicates the potential for canal-water movement into the Refuge. See Appendix A for site locations. Specific conductance data collected by the Refuge and the SFWMD and stage data collected by the USGS between 1994 and 2005.

The above analysis illustrates the importance of canal flows in determining spatial and temporal patterns of surface-water mineral concentrations in the Refuge. While seasonal fluctuations in water levels resulting from rainfall and ET produce modest fluctuations in specific conductance in the interior of the Refuge, more pronounced changes closer to the perimeter of the Refuge are associated with canal intrusion. This intrusion is influenced in part by differences in stage between the canal and the Refuge. Natural events such as droughts may affect conductivity patterns within the Refuge by exacerbating these stage differences. Hydrologic modeling efforts and more spatially intensive water-quality monitoring currently being performed in the Refuge by USFWS staff and their contractors should provide greater insight into the influence that these and other factors have on canal-water intrusion.

Effects of canal-water intrusion on Refuge soil chemistry

Intrusion of mineral-rich canal waters into the Refuge has produced chemical gradients in soils and plant tissue as well as in the surface waters.

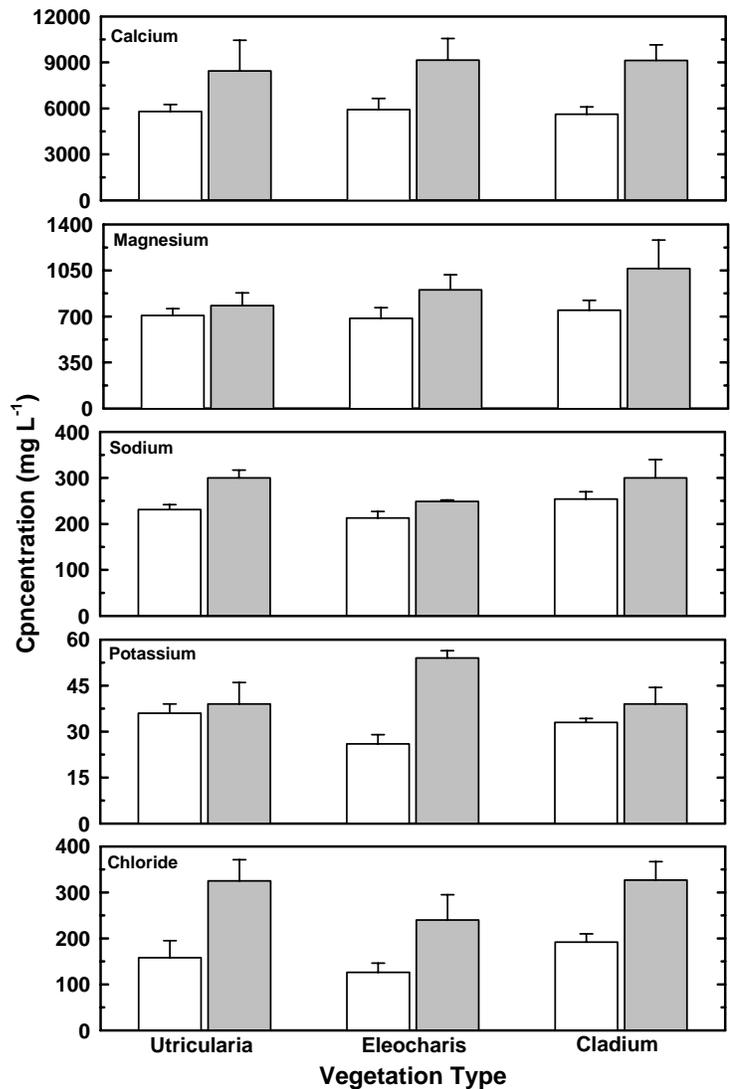


Figure 13. Changes in available soil mineral concentrations (as estimated by Mehlich-1 extractions) in the 0-30 cm depth increment in three vegetation types in the Refuge interior (open bars) and near the Refuge perimeter (shaded bars). Bars are means of measurements from multiple locations + 1 SE. Data source: Pope, 1991.

Pope (1991) compared soil chemistry in major vegetative habitats across different hydrologic zones within the Refuge that corresponded with different degrees of canal influence. Concentrations of extractable minerals were higher across habitats sampled near the canal than in the interior (Fig. 13). Average soil Ca concentrations increased by approximately 50% while Cl concentrations were twice as high in some habitats. Concentrations of Mg, Na, and K typically exhibited much smaller increases. These estimates of the effect of canal-water intrusion on soil mineral levels are conservative because they are based on soil cores taken to a depth of 30 cm, which includes a large amount of peat accumulated long before any human influences on water chemistry.

Patterns of soil and plant chemistry related to increasing canal influence were investigated by USGS in 2004 in conjunction with conductivity mapping efforts described earlier. Grab samples of surface soils corresponding roughly to the 0-5 cm depth layer were collected from 130 sites across the Refuge and analyzed for total C, N, P, and a suite of other elements including Ca, Mg, Na, K, and S. Samples of live sawgrass (*Cladium jamaicense* Crantz.) also were collected at sites where this species was present and analyzed for C, N, P, and S. Strong correlations were found between surface-water specific conductance and soil concentrations of several elements, including Ca and P (Fig. 14). Sawgrass tissue S concentrations also were correlated positively with specific conductance (Fig. 15). Accumulation of some elements (e.g., sawgrass S) was linearly related to conductance while others (e.g., soil Ca) exhibited more complex relationships.

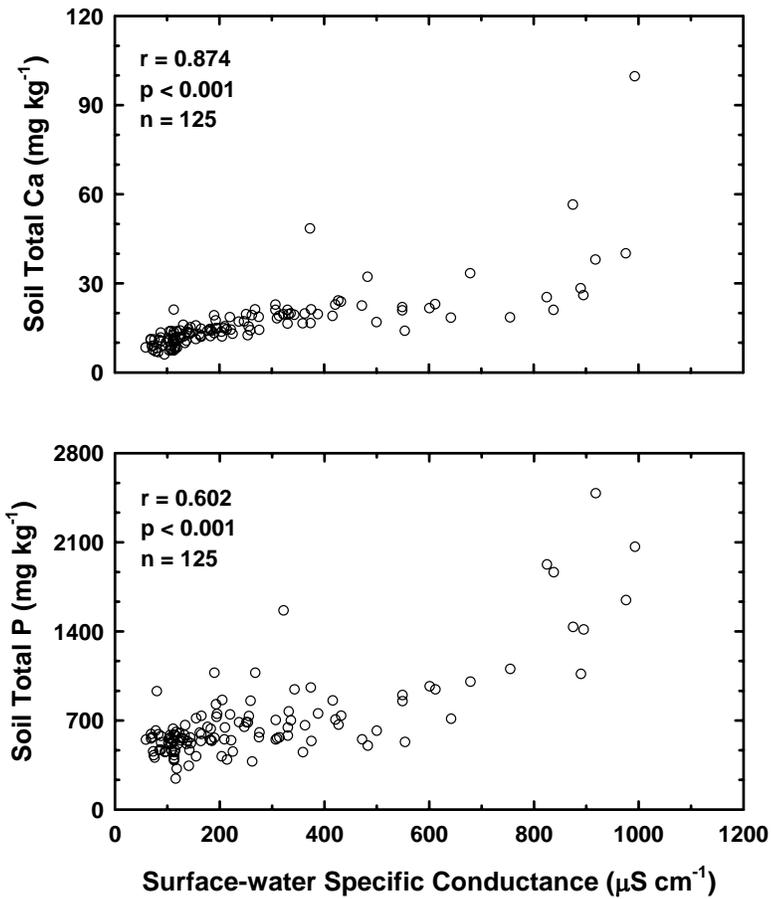


Figure 14. Relationships between surface-water specific conductance and total Ca and P in the surface-soil-litter layer of sawgrass stands measured by USGS across the Refuge during February 2004. Spearman Rank correlation coefficients provided in upper left-hand corner.

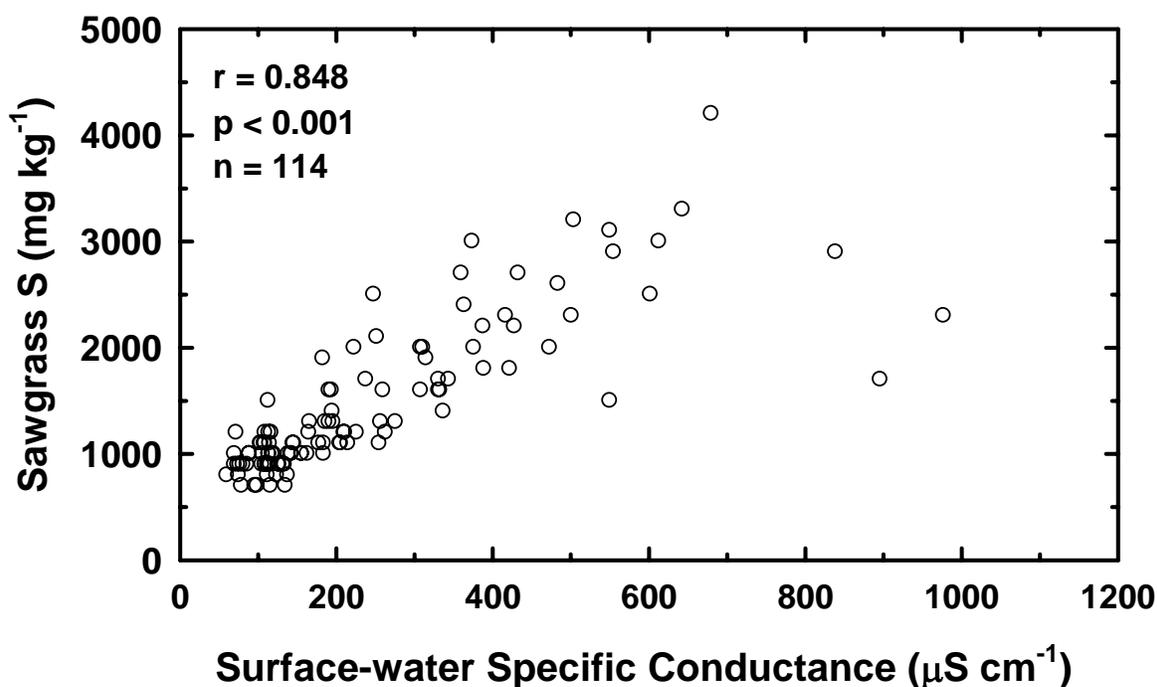


Figure 15. Relationship between surface-water specific conductance and the sulfur content of live sawgrass measured by USGS across the Refuge during February 2004. Spearman Rank correlation coefficients provided in upper left-hand corner.

Analysis of water- and soil-chemistry data collected by USGS and Refuge staff since 2005 along an east-west transect across the Refuge indicates an extensive zone of S enrichment associated with episodic canal-water intrusion. Surface-water chemistry has been monitored monthly at several of these sites for more than a decade and at other sites for more than a year. Soil S (0-10 cm depth increment) was measured during the summer of 2006 and compared with mean surface-water sulfate concentrations for the previous year (Fig. 16). Both surface-water sulfate and soil S concentrations increased predictably with decreasing distance from the canal and were elevated above background concentrations (< 1 mg/L sulfate and < 1% soil S) at sites within approximately 5 km of the western and eastern rim canals.

Ecological effects of mineral enrichment in the Refuge

Biogeochemical Processes

Increased concentrations of Ca^{2+} and other major ions in Refuge waters may affect the availability of P, a key limiting nutrient, and perhaps N by mechanisms similar to those documented in other peatlands as discussed earlier. Soil samples (0-20 cm depth increment) collected at 12 sites along an east-west transect across the Refuge in late summer 2004 showed shifts in P and N fractions with increasing distance from the rim canals (Fig. 17). Total P concentrations (mg/kg) were approximately twice as high at sites closest to the canal compared to the most interior locations. While sites were selected intentionally to be away from the

heavily P-enriched zone near the Refuge perimeter, increased soil TP at the sites closest to the canal likely reflect canal P loading. As in all peatlands, organic P comprised most of the soil P pool. Inorganic P increased from 2% or less at the most interior sites to 10% at sites closest to the canals due to increases in both plant-available (NaHCO_3 -extractable) and Ca-bound (HCl-extractable) pools. Plant-available (NaHCO_3 -extractable) organic P showed no strong pattern across the transect, while microbial P increased 50-100% with increasing proximity to the canals and more refractory forms of organic P showed a corresponding decline in importance. Increased Ca-bound P at sites near the canals likely is due to higher Ca availability and pH, both of which increase the potential for Ca-P coprecipitation. The significance of this increase in terms of P availability is unclear since the amount of P in this fraction was relatively small even at sites near the canals. By comparison, Ca-bound P comprises as much as 13% of the total P in surface soils in minerotrophic Everglades peatlands such as WCA 2A and likely plays a more important role in P storage in these areas (Qualls & Richardson, 1995). The size of the microbial P fraction suggests that microbial immobilization may be a more important process controlling P availability at all of these sites.

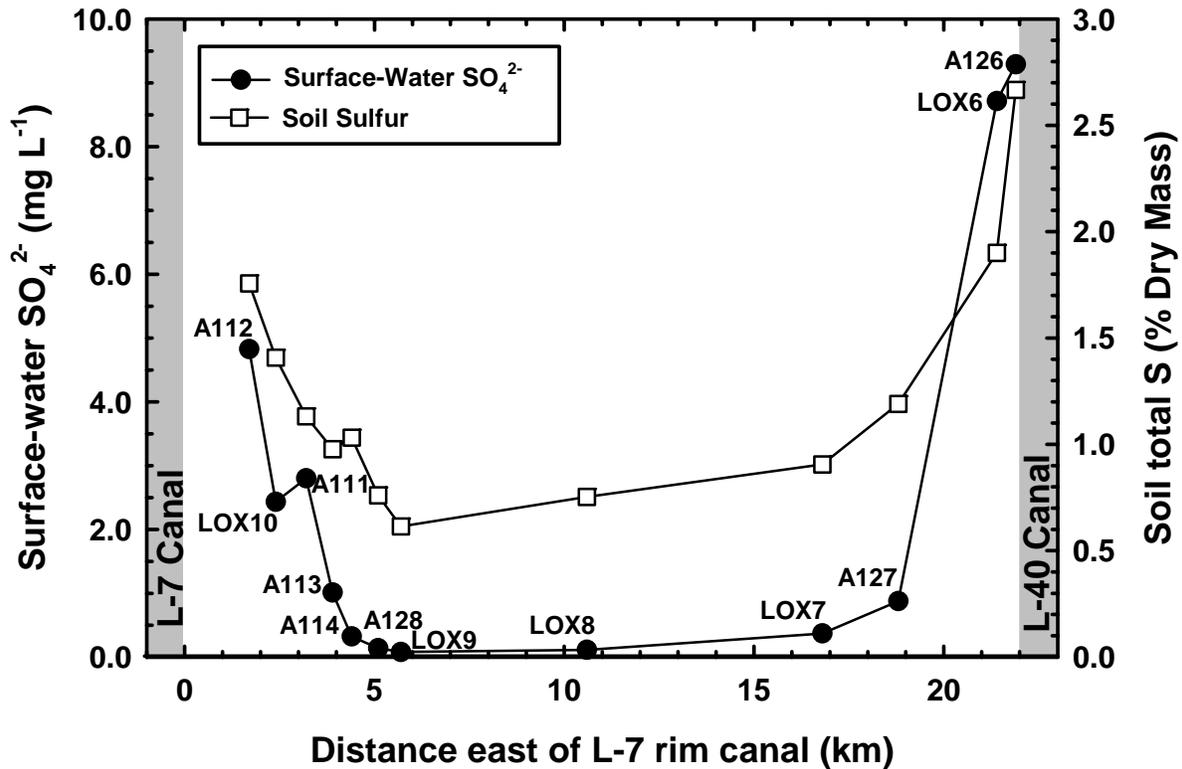


Figure 16. Surface-water sulfate and soil sulfur concentrations measured by USGS at 12 monitoring sites along a 22-km transect across the central Refuge. See Appendix A for site locations. Sulfate points are means of monthly data collected by the Refuge and the South Florida Water Management District during 2005. Soil sulfur points are single samples of the 0-10 cm soil depth increment collected during July 2006.

In contrast to soil P, soil TN was similar across much of the gradient, although the 2 sites at the western end (A112 and LOX10) had modestly (10-20%) lower concentrations than other sites (fig. 17). Plant-available N (exchangeable NH_4) was similar among sites. Microbial N was a minor fraction of organic N at interior locations, but was as much as 40-70 times higher and represented a major N pool at sites closest to the canal. As for P, these data indicate that microbial immobilization is an important process regulating N availability across canal gradients.

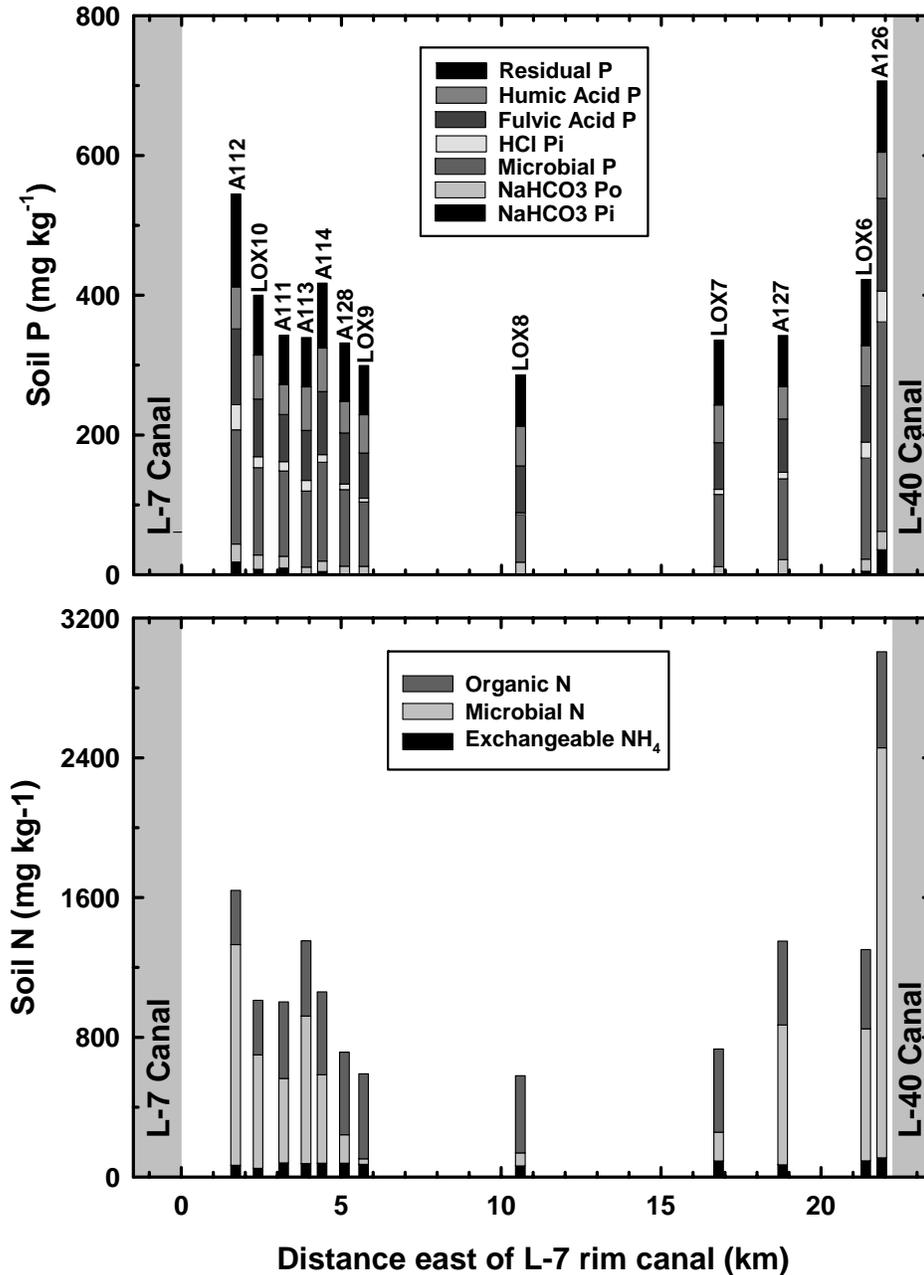


Figure 17. Phosphorus and nitrogen fractions in soil cores (0-20 cm depth increment) collected by USGS during August 2004 at 12 monitoring sites along a 22-km transect across the central Refuge. See Appendix A for site locations. Soil nutrient fractions are stacked in the same order in the legend and in the graph.

Changes in biogeochemical processes in response to canal-water intrusion also are indicated by pore-water chemistry changes documented along a gradient of canal influence in the southwest corner of the Refuge (Susan Newman, SFWMD, unpubl. data). Measurements of pore-water chemistry in the 2-12 cm depth increment in the late 1990s showed higher pore-water pH and higher concentrations of dissolved P and N as well as Mg^{2+} , Ca^{2+} , K^+ , Cl^- , S^{2-} , and sulfate at sampling sites closer to the canal. By contrast, pore-water redox levels and dissolved Fe concentrations were lowest at these sites. Increased exposure to P-rich canal waters undoubtedly contributed to higher P availability near the canal. However, recent evidence (Orem and others, 2006) indicates that increased sulfate loading also may contribute to increased pore-water P concentrations in areas of the Everglades downstream of canal discharges. Mechanisms underlying this relationship may include ion-exchange processes as well as the formation of insoluble FeS under low redox conditions, which reduces the capacity for Fe-P binding in aerobic soil layers. This latter mechanism is consistent with observed high S^{2-} and low dissolved Fe and redox in pore water at sites near the canal. While higher N, Mg, and Ca availability at locations closer to the canal likely were due in large part to increased loading of these elements, a controlled field experiment showed that P enrichment can increase pore-water concentrations of these elements, possibly by increasing rates of organic matter decomposition (Susan Newman, SFWMD, unpubl. data). Thus, there is increasing evidence that mineral and P loading from canals may directly and indirectly affect the bioavailability of many different elements in Everglades peat soils.

Organic matter decomposition is a key process controlling both soil formation and nutrient cycling in peatlands. Increased mineral loading may influence decomposition rates in the Refuge through: 1) effects on organic matter quality either through increases in litter mineral content or shifts in plant species composition; 2) increased availability of electron acceptors such as sulfate that are used in anaerobic microbial respiration; and, 3) increased availability of elements such as Ca that serve as co-factors regulating enzyme activity. Sawgrass and cattail litter collected and incubated in the Refuge interior decayed up to 30% more slowly than equivalent material incubated in the interior of WCA 2A, a minerotrophic peatland just to the south (Newman and others, 2004). While not suggesting a specific mechanistic explanation, these findings indicated that intrusion of mineral-rich canal water promoted faster rates of decomposition. Rates of sawgrass decomposition were measured by the USGS during 2004-2005 at 12 sites that spanned gradients of canal influence in the Refuge. Standing-dead litter was collected from each site, dried and weighed, returned to the site in fine-mesh (2-mm mesh size) bags, and incubated just above the soil-water interface. Additional bags from selected sites near the canal were transferred to a site in the center of the Refuge (LOX8) that is minimally impacted by canal-water intrusion. Decomposition rates were measured as loss of dry mass after 12 months of incubation. Litter decomposition rates during the first year were 50% higher at sites exposed to canal-water intrusion along the western side of the Refuge compared to sites in the rainfall-driven interior. A similar pattern was observed along the eastern side of the Refuge, with the exception of low decomposition rates at a long hydroperiod site closest to the eastern perimeter (Fig. 18A). Litter mineral and P concentrations generally increased with increasing exposure to canal-water intrusion, and this enriching effect might be one cause of these decomposition patterns. Litter collected from sites closer to the canal decomposed more slowly when transferred to an interior site (Fig. 18B), suggesting that site-specific factors including surface-water chemistry also may play a role.

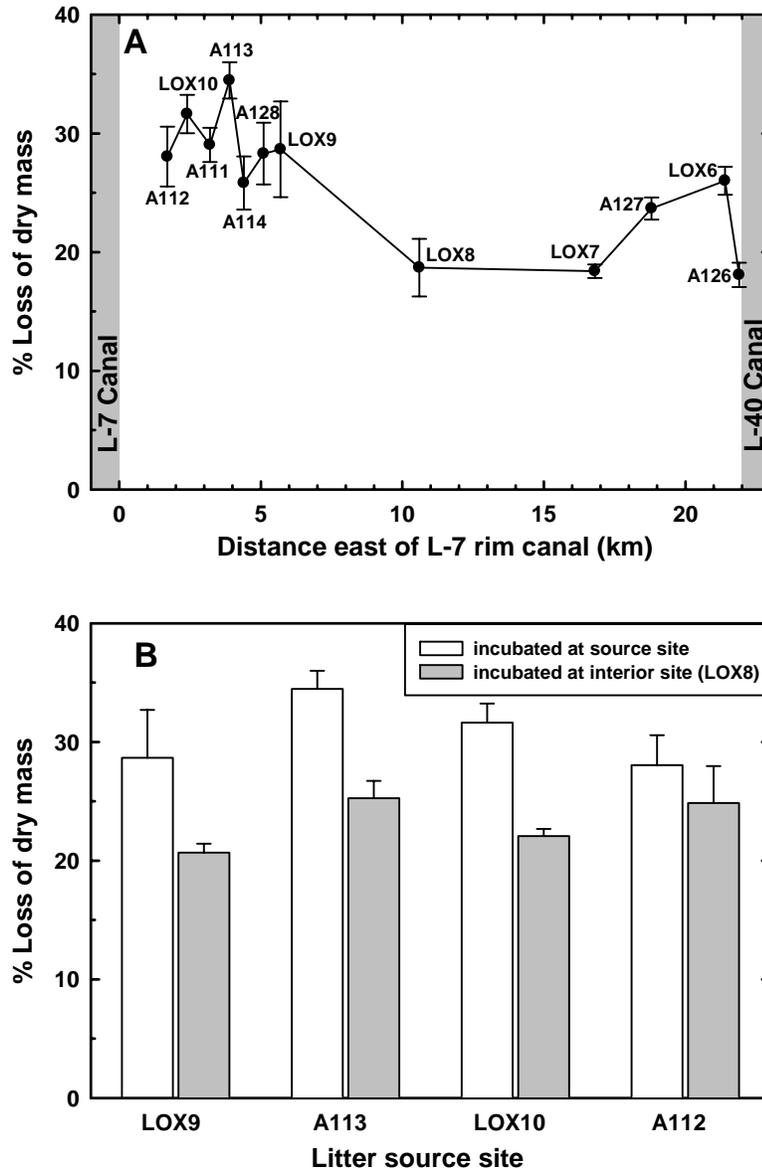


Figure 18. Decomposition of sawgrass litter incubated for 12 months at 12 USGS monitoring sites along a 22-km transect across the central Refuge. Plate A shows decomposition of litter collected from each site and returned to the same (source) site. Plate B compares decomposition of litter collected from selected sites and either returned to the source site or to an interior site (LOX8) that is minimally impacted by canal-water intrusion. Points and bars are mean decomposition values for three litter bags and error bars are one standard error of the mean. See Appendix A for site locations.

Special importance is attached to sulfate in the Everglades because of its effects on the cycling and bioavailability of Hg, a contaminant that enters the Everglades via atmospheric deposition

and is converted to its bioavailable form (methyl-Hg) primarily through microbial pathways (Benoit and others, 2003). Elevated sulfate concentrations also can affect vegetation patterns due to the inhibitory effects of hydrogen sulfide — an end product of sulfate reduction — on plant growth. Sulfate is a significant component of the mineral composition of canal water, and has been identified as one of the most widespread contaminants in the Everglades (Bates and others, 2001). While atmospheric deposition and ground water are likely sources of some of the sulfate entering the Everglades, agricultural drainage water entering the wetland in canal discharges has been identified as the primary source of this ion. As already discussed, areas of the Refuge subject to canal-water intrusion exhibit both higher sulfate concentrations in the surface water as well as elevated S concentrations in the soil and plants, indicating the accumulation of a pool of S that is potentially available as sulfate via organic matter mineralization. A mesocosm experiment conducted in the Refuge interior (Gilmour and others, 2004) showed enhanced rates of Hg methylation in response to sulfate additions to the surface water, indicating that elevated sulfate levels may increase the risk of Hg bioaccumulation in fish and wildlife. Evidence for other ecological effects of sulfate enrichment at levels found in the Refuge is lacking. However, ongoing experimental work in the central Everglades (Orem and others, 2006) examining the effects of controlled sulfate loading on biogeochemical processes and plant and invertebrate communities should provide additional insight into its potential impacts in the Refuge.

Responses of Everglades Vegetation

Wetland habitats across the Everglades contain many native plant species in addition to a few ubiquitous and commonly recognized taxa such as sawgrass (*Cladium jamaicense*), fragrant water lily (*Nymphaea odorata*), and bladderwort (*Utricularia* spp.) (www.regionalconservation.org), and the floral diversity of the Everglades likely has been underestimated due to a lack of basic plant inventory work. Conceptual models (e.g., Ogden, 2005) and performance measures (www.evergladesplan.org) that serve as the basis for measuring the success of Everglades restoration have focused on the effects of water-quality changes on important landscape features and habitats but have ignored potential effects on plant-species richness and diversity. The broader wetlands literature suggests that changes in mineral levels could significantly affect the distribution and abundance of some species.

Few studies have examined spatial patterns of vegetation in the Refuge, but available data show a relationship between species composition and canal-water mineral gradients. These patterns are illustrated based on the species composition of slough-wet prairie (SWP) plant communities at 12 stations along an east-west transect across the central Refuge (Fig. 19). The presence and abundance rank of common Refuge plant species at each site was determined based on quarterly surveys conducted by the USGS during 2005 and 2006. Timed (10 min) surveys were conducted by airboat within an approximate radius of 0.1 km around fixed sampling locations at each site and the abundance of each species was scored using the following scale:

- 0 - not detected;
- 1 – rarely detected and in small numbers (< 5 specimens)
- 2 – always detected but not abundant (5-20 specimens)
- 3 – always detected in larger numbers (>20 specimens)
- 4 – among the most abundant species at the site

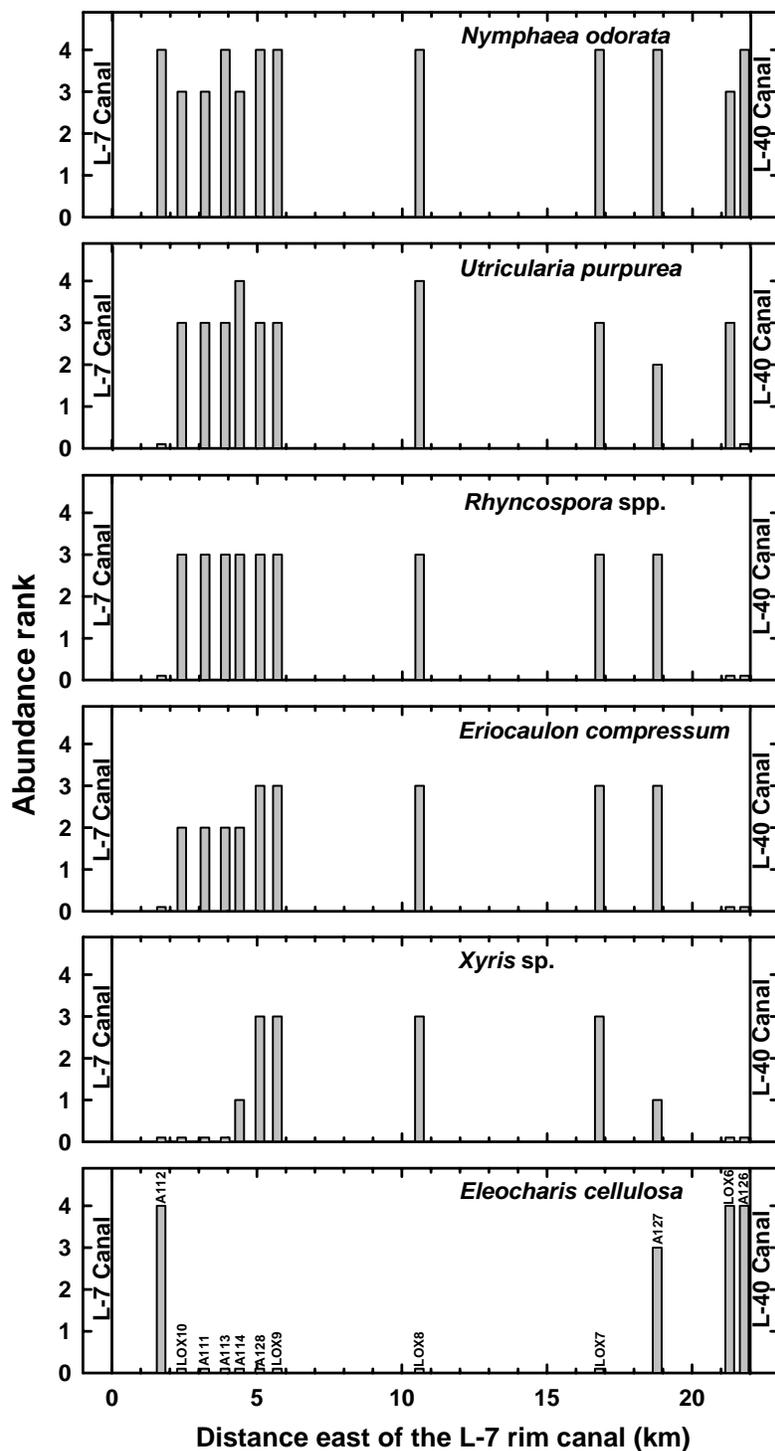


Figure 19. Abundance of common interior slough-wet prairie macrophyte taxa measured by USGS during 2005 at 12 monitoring sites along a 22-km transect across the central Refuge. Site names are shown on the bottom plate. See Appendix A for site locations. See text for abundance rank category definitions.

Results indicate that interior SWP taxa differ greatly in their tolerance to canal-water intrusion and generally can be classified into those that are: 1) found throughout the Refuge regardless of the level of canal influence; 2) restricted to perimeter locations with substantial canal influence; and, 3) restricted to interior locations with less canal influence. Taxa such as *Nymphaea odorata* and *Utricularia* spp. were present at all sites and also occur throughout the Everglades, including areas with some of the highest mineral concentrations such as WCA 2A. Previous studies also have found these taxa to be indifferent to surface-water mineral concentrations (Moyle, 1945; Walker & Coupland, 1968). One species, *Eleocharis cellulosa*, occurred only at sites closest to the canals. The distribution of *Eriocaulon compressum* and species of the genus *Xyris* were restricted to interior locations with background or only slightly elevated specific conductance. Two other common species of the genus *Rhynchospora*, *R. inundata* and *R. tracyii*, appeared less sensitive to canal influences and were absent only from sites closest to the perimeter. Most species of *Xyris* and *Eriocaulon* are indicative of oligotrophic, acidic conditions and are found along the margins of soft-water lakes and in poor fens and even bogs (Keddy & Reznicek, 1982; Wilson & Keddy, 1986; Glaser, 1992). A plant community similar to that found in the Refuge interior, including *X. smalliana*, *E. compressum*, and *R. inundata*, is common in wet prairie habitats in the Okefenokee Swamp, an ombrotrophic peatland in southeastern Georgia (Gerritsen & Greening, 1989).

Relationships between species distributions and canal-water gradients are correlated with several environmental changes and, thus, do not provide conclusive proof that increased mineral inputs are the cause of observed vegetation shifts. Canal waters have high P concentrations, and this factor alone can cause pronounced shifts in Everglades vegetation (McCormick and others, 2001). While sampling sites used to illustrate the above vegetation shifts were intentionally located away from the zone of heaviest P influence near the perimeter of the Refuge, soil P concentrations were higher at sites closest to the canal. Thus, soil mineral gradients caused by canal-water intrusion are partially confounded by a limiting-nutrient gradient (Fig. 20). Canal

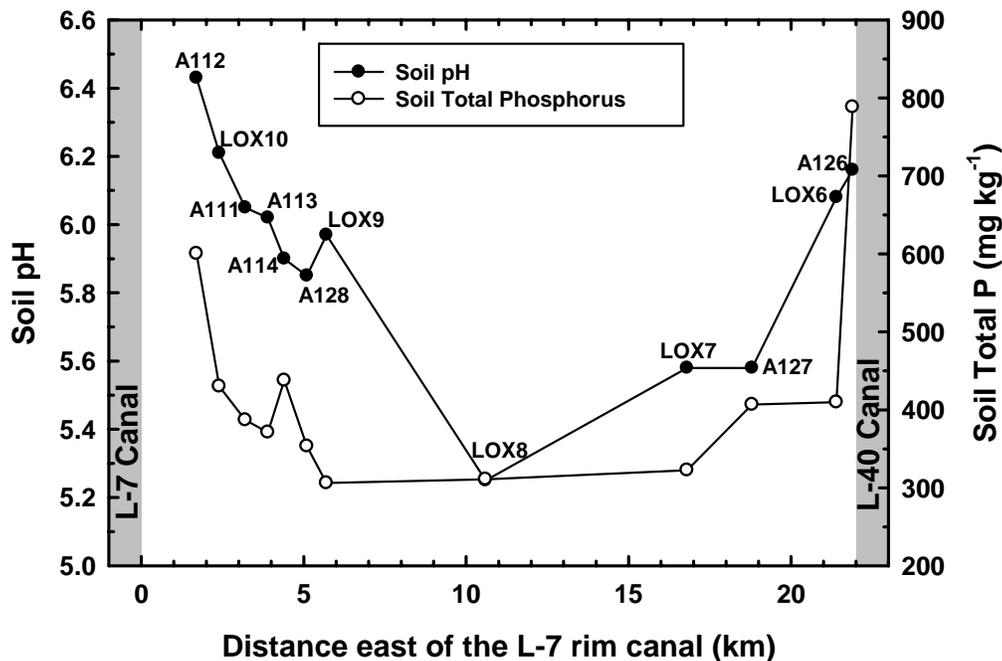
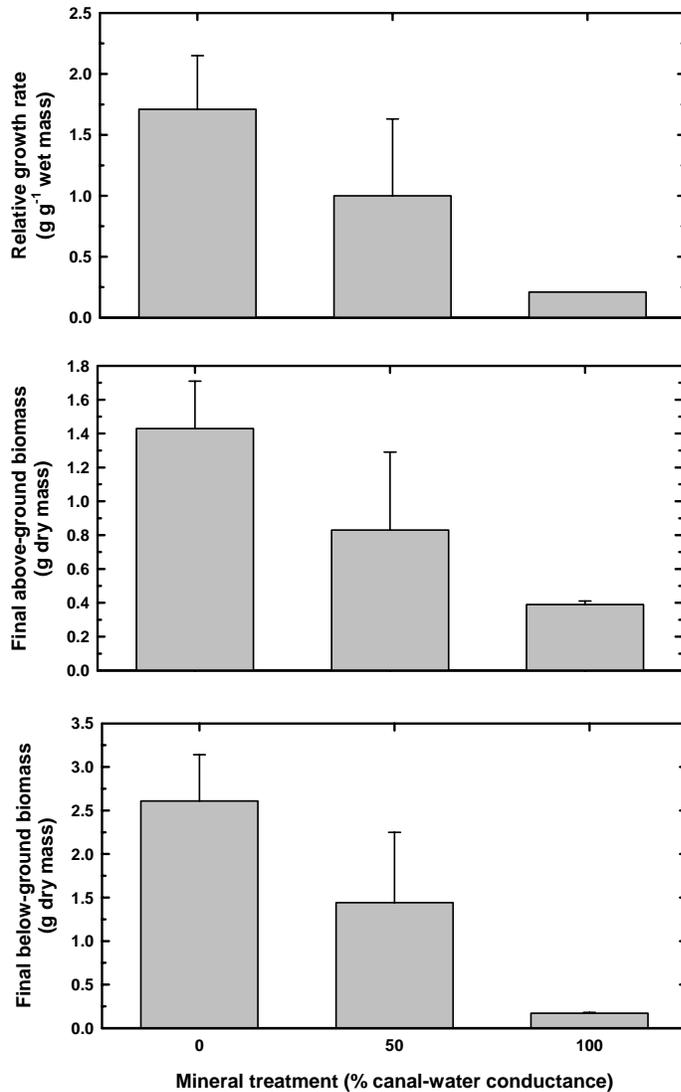


Figure 20. Soil pH and TP measured by USGS across the same transect of 12 monitoring sites surveyed for slough-wet prairie vegetation (see fig. 18). See Appendix A for site locations.



pulses into the Refuge produce a less stable hydrology with more extreme fluctuations in water depth. Water depths also tend to be greatest near the perimeter in some parts of the Refuge. Deeper and less stable water depths near the rim canals may favor SWP taxa such as *E. cellulosa* over those such as *Rhynchospora*.

Controlled experiments are being used to isolate the ecological effects of individual environmental factors that vary along canal gradients. The effects of limiting nutrients such as P and major mineral ions on plant growth was investigated by the USGS in a series of experiments using the plant species *Xyris* sp., which is limited in its distribution within the Refuge to interior SWP habitats. Plants were collected from the Refuge interior and grown in the laboratory under controlled light, temperature, and hydrologic regimes. Selective enrichment with N, P, and K alone or in combination for three months elicited no strong growth response from this species. However, enrichment with a mineral solution that approximated the concentration of major mineral ions in canal waters significantly reduced growth rates during this same time

period compared to plants grown with water from the Refuge interior (Fig. 21). Germination and initial seedling growth of this species also declined with increasing mineral levels. The negative response of this species to mineral enrichment may explain its absence from areas of elevated conductivity near the Refuge perimeter.

Shifts in vegetation habitats across the Refuge also are correlated with canal mineral

Figure 21. Growth response of *Xyris ambigua* to increased mineral loading measured in the laboratory by USGS. Plants were grown in interior slough soil and watered for three months with interior slough water amended with minerals to achieve different specific conductance levels relative to those in the western rim canal. Bars are means of three replicate plants + 1 SE.

gradients. Higher specific conductance near the eastern and western perimeter is associated with a decline in the coverage of SWP habitats and an increase in sawgrass cover. This pattern is illustrated in Fig. 22 across the same transect used to examine changes in SWP plant communities. However, this spatial

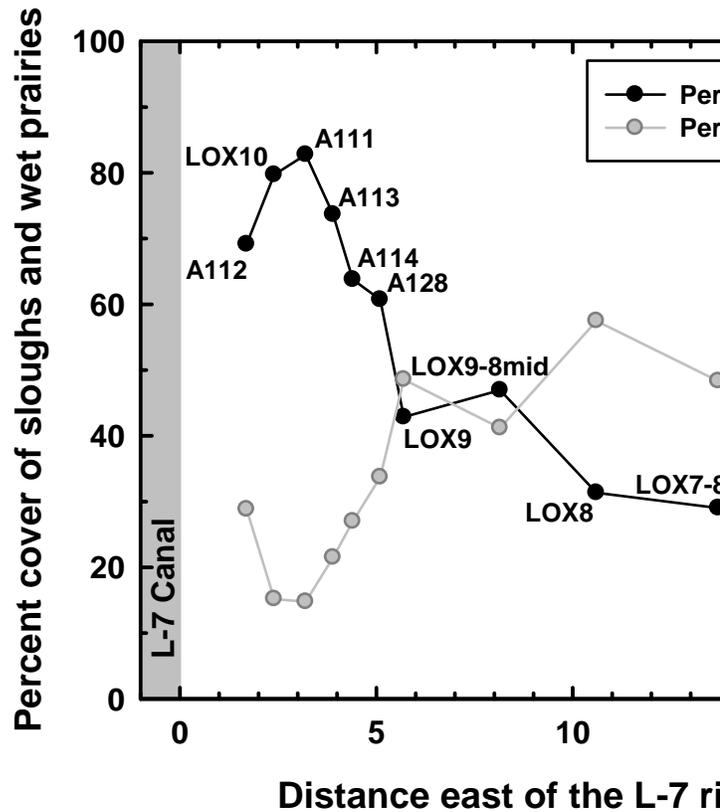


Figure 22. Percent cover of slough-wet prairie and sawgrass habitats calculated by USGS for 14 sites along a 22-km transect across the central Refuge. Habitat cover was determined in a radius of 0.2 km around the GPS coordinates for each site using aerial photography (0.6 m resolution) collected by Palm Beach County in 2004. See Appendix A for site locations.

relationship between sawgrass cover and canal influences such as mineral enrichment may be confounded by predrainage vegetation patterns such as those described by the survey work of Davis (1943). While aerial photography collected in 1940 and used by Davis in his mapping efforts showed all of the present-day Refuge to be part of the larger ridge-and-slough landscape, this imagery also indicated a shift in vegetative composition towards increasing dominance by sawgrass near the western boundary of the Refuge. Therefore, the current distribution of

sawgrass across the western Refuge does not by itself provide firm evidence for the effects of canal influences on this species.

Relatively little is known about the autecology of *C. jamaicense* with respect to mineral content. Steward & Ornes (1975) noted that this species has a very low mineral content and concluded that it had very low requirements for most macronutrients including major mineral elements such as Ca. However, their studies were located in a hard-water portion of the Everglades (WCA 3B) and no studies have been conducted to examine the response of this species to increased mineral concentrations in soft-water areas. The calcicole habitat of related temperate species of *Cladium*, including *C. mariscus* and *C. mariscoides* is well recognized. For example, dominance of *C. mariscus* is indicative of high mineral levels in peatlands across Europe (Wheeler & Proctor, 2000), although it has also been found in poor fens and even bogs in coastal areas where atmospheric mineral inputs are higher and acidity is less extreme (Tansley, 1939). *Cladium mariscoides* also is restricted to extremely rich fens in northern peatlands in North America (Glaser 1983, Glaser and others 1990). Experimental liming (CaCO_3) of wetland plots surrounding an acidified lake in the Adirondacks of New York produced nearly a 3-fold increase in the cover of *C. mariscoides* after 2 years, although it still represented a minor vegetative component (Mackun and others, 1994).

A laboratory experiment was conducted by the USGS to determine the potential influence of peat mineral concentrations on sawgrass growth in the Refuge. Sawgrass seeds from a common source were germinated and then transplanted into soils from three different locations (interior slough, interior sawgrass stand, perimeter slough). Interior soils, which had a low mineral content, were left untreated or enriched with either moderate or high concentrations of major mineral ions (Ca^{2+} , Mg^{2+} , Na^+ , K^+ , HCO_3^- , sulfate, and Cl^-) corresponding to soil concentrations documented across canal mineral gradients in the field. Seedling growth was measured over a 3-month period as an increase in plant height and final above-ground dry biomass. Seedlings in untreated interior sawgrass and perimeter slough soils grew four times faster than those in interior slough soils (Fig. 23). Slower growth in interior slough soil was attributed to the lower soil P concentration, which was half that in the other soil types. Growth rates in both sawgrass and slough soils enriched with high concentrations of minerals were twice those in untreated soils. These findings indicate that both increased P and mineral concentrations may increase the growth of sawgrass in Refuge soils.

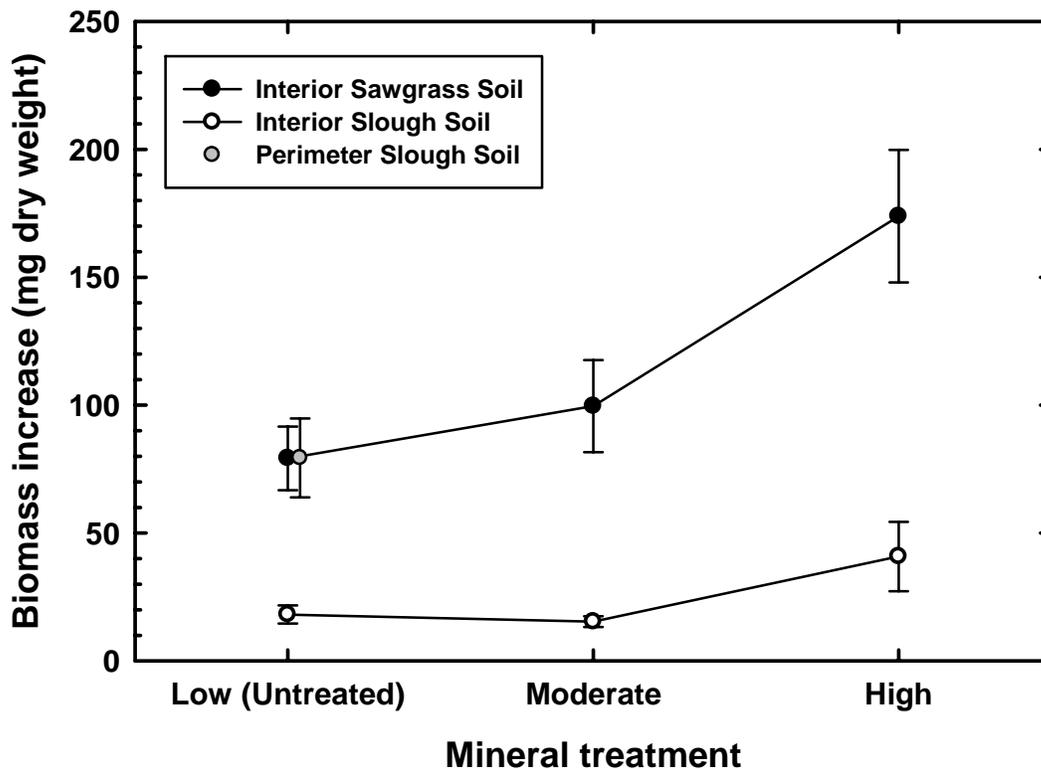


Figure 23. Biomass increase of sawgrass seedlings grown in the laboratory by USGS for three months in different soil types amended with different mineral concentrations. See text for details of experimental design. Points for each treatment are means of ten replicate plants \pm 1 SE.

In his analysis of aquatic vegetation patterns related to conductivity, Moyle (1945) noted that “The natural separation between hard and soft waters seems to be at a total alkalinity of about 40 [mg/L], 30 [mg/L] being the lower limit of toleration of the more typical hard-water species, and 50 [mg/L] the upper limit of toleration of the more characteristic soft-water species” (p. 404). While current information from the Everglades is insufficient to indicate mineral levels that might impact soft-water SWP plant communities, preliminary transect data already discussed for the Refuge are broadly consistent with the patterns in this earlier study. Alkalinity levels in the Refuge interior average near 10 mg/L, while those at sites where soft-water taxa are either rare or absent generally range between 30-50 mg/L. Sites where none of these taxa have been found have an alkalinity between 40-60 mg/L with periodic alkalinity spikes above 100 mg/L.

Response of Everglades Periphyton

Periphyton is a significant component of SWP habitats throughout the Everglades. Floating and attached periphyton mats provide both habitat and a food source for aquatic invertebrates (Williams & Trexler, 2006) and likely play a key role in maintaining aerobic conditions in the water column in oligotrophic areas where periphyton is most abundant

(McCormick & Laing, 2003). The restoration and maintenance of the spatial distribution and taxonomic composition of native periphyton communities is an important performance measure for CERP (Ogden, 2005). Periphyton communities are extremely sensitive to changes in water chemistry, which explains their widespread use as indicators of water quality in the Everglades and other aquatic ecosystems.

The Refuge interior contains a characteristic periphyton community dominated by desmid and diatom species indicative of soft-water conditions. Whereas periphyton mats across mineral-rich portions of the managed Everglades are dominated by calcium-precipitating (calcareous) cyanobacteria and have a high calcium carbonate content, those in the Refuge are largely organic (non-calcareous) in nature. Paleoecological evidence (Slate & Stevenson, 2000) indicates that the community currently found in the Refuge interior was more widespread across the pre-drainage Everglades when rainfall was the dominant source of water to this ecosystem. By contrast, calcareous communities historically were more abundant in the marl prairies of the southern Everglades, which support little or no peat accretion due to their short hydroperiods and thus have a water chemistry influenced more strongly by the limestone bedrock.

Surveys conducted by Swift & Nicholas (1987) established periphyton-conductivity relationships across the northern and central Everglades and clearly showed the unique character of the Refuge periphyton community in the managed system. Their analysis of species-environmental relationships found concentrations of major ions to be the most important factor explaining variation in periphyton taxonomic composition among the 3 WCAs (including the Refuge). Surface-water chemistry in the Refuge interior was associated with higher algal species diversity than in WCA 2A and WCA 3A due in large part to a species-rich desmid flora. Dominance of diatoms and filamentous chlorophytes known to be indicative of soft-water habitats also was greater. Periphyton nutrient content and production rates also were higher in the Refuge interior than in the more mineral-rich interior of other Everglades wetlands. These investigators hypothesized that the low Ca levels in Refuge waters reduced the potential for co-precipitation of P as hydroxylapatite, thereby increasing the availability of this limiting nutrient for algal uptake and growth. They concluded that significant alterations in the periphyton community could result from flows of mineral-rich canal water into the Refuge.

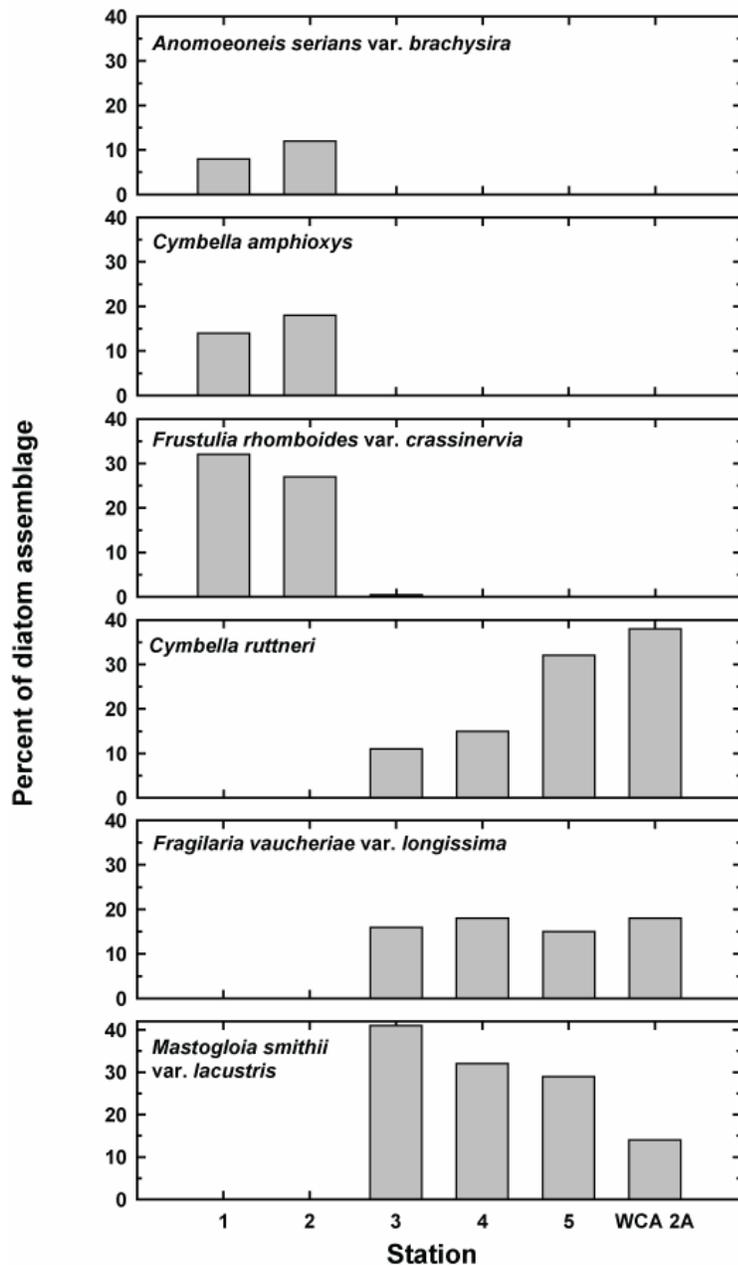


Figure 24. Relative abundance of dominant diatom species across a canal gradient (lowest specific conductance at site 1 to highest specific conductance at site 5 in the Refuge and at a location in the interior of WCA 2A, a minerotrophic peatland adjacent to the Refuge. See Appendix A for site locations. Data source: Gleason and others, 1975.

changes.

Changes in the Refuge periphyton community associated with canal-water intrusion were reported by Gleason and others (1975) based on data from five sites sampled along a mineral gradient during the dry season of 1974. All locations had phosphate concentrations below detection but differed greatly with respect to specific conductance, with average levels ranging from <100 to >900 $\mu\text{S}/\text{cm}$. Periphyton communities at the three most interior sites (specific conductance <400 $\mu\text{S}/\text{cm}$) were non-calcareous and dominated by a species-rich flora of desmids as well as other filamentous chlorophyte algae and diatoms indicative of soft-water, acidic conditions. The remaining two sites (>800 $\mu\text{S}/\text{cm}$) contained a community dominated by calcareous cyanobacteria and diatom species indicative of hard-water conditions and similar to that which presently occurs in the interior of WCA 2A, a hard-water wetland just to the south. Shifts in species composition with increasing specific conductance included a pronounced change in dominant diatom indicator species (Fig. 24). The high-conductivity periphyton community had a higher P content, suggesting increased P loading to these sites despite low surface-water phosphate. The nature of species shifts between these two groups of sites suggested that increasing calcium carbonate saturation and pH of the surface water at high-conductivity sites were important factors contributing to observed

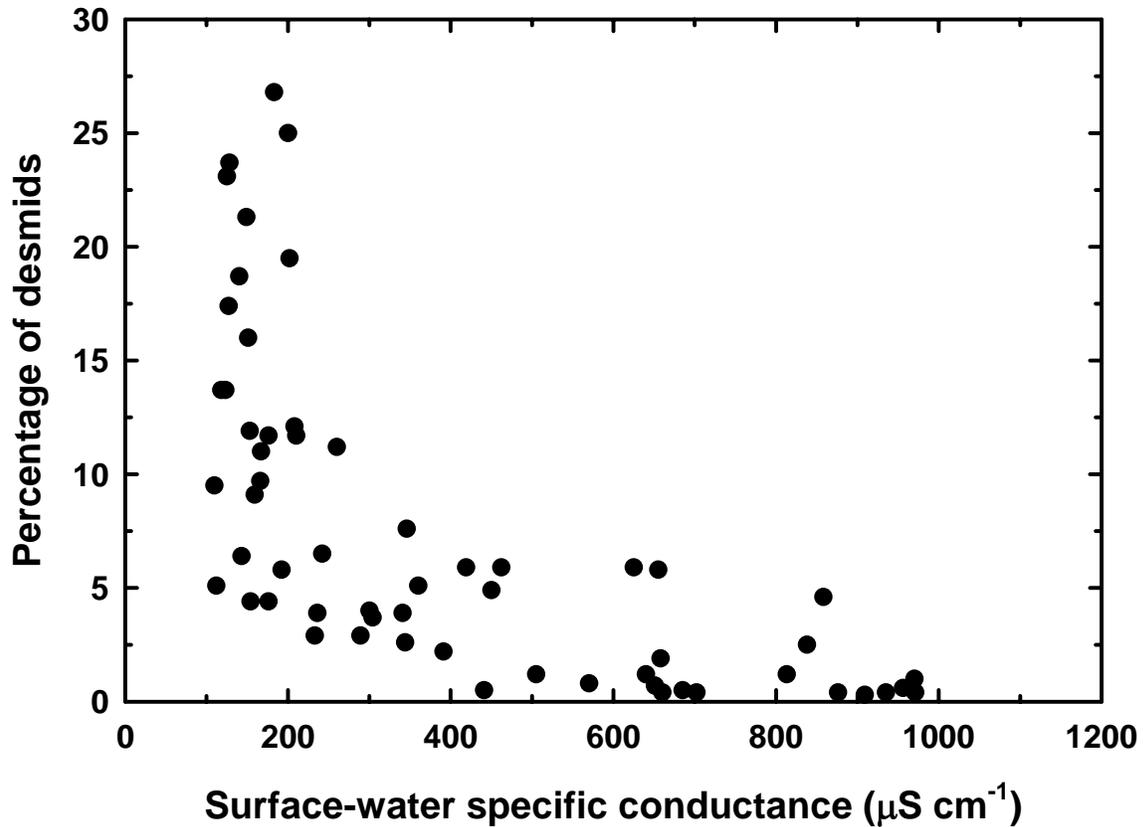


Figure 25. Changes in desmid dominance within the periphyton community at nine SFWMD monitoring stations across a water-chemistry gradient (see fig. 8) in the southwest corner of the Refuge. Samples were collected during eight sampling trips conducted by the SFWMD between 1996 and 1999. See Appendix A for transect locations.

Additional survey and monitoring studies have corroborated and expanded these initial findings. McCormick and others (2000) described patterns in periphyton composition on artificial substrates (glass slides suspended just below the water surface) at 9 monitoring sites across a water-chemistry gradient produced by intrusion of canal-water in the southwestern part of the Refuge. Phosphorus concentrations declined to background levels within 2 km of the canal, while the mineral gradient created by canal inputs spanned the entire 4.4-km transect. The major change in the taxonomic composition of the periphyton community across this broader mineral gradient was a decline in the proportion of desmids with increasing specific conductance (Fig. 25). This group comprised between 5-25% of the community at the most interior (lowest conductivity) sites compared to less than 5% at sites closer to the canal. Temporal variation in the importance of different taxa in periphyton communities is typical and is often seasonal in nature. Variability in desmid dominance among sampling dates at interior sites was not closely related to seasonality per se, although greatest dominance generally occurred during the summer. Patterns of desmid dominance across this gradient indicated a decline for this group as surface-water conductance increased above 200 $\mu\text{S/cm}$.

Controlled experimentation supports a cause-effect relationship between mineral concentrations and the composition of Everglades periphyton as just described. Periphyton mats collected from the Refuge interior were incubated under different conductivity regimes and near-natural light and temperature conditions in the laboratory (Sklar and others, 2004). Conductivity treatments were established and maintained using different mixtures of water from interior locations in the Refuge and in WCA 2A, a mineral-rich wetland just to the south. A sustained increase in specific conductance from background levels for the Refuge ($< 100 \mu\text{S}/\text{cm}$) to $> 200 \mu\text{S}/\text{cm}$ for 1 month resulted in a significant decline in desmids, diatoms, and cyanobacteria commonly found in the Refuge interior, and further increases to $>300 \mu\text{S}/\text{cm}$ resulted in a decline of other interior chlorophyte and cyanobacteria taxa.

Potential Responses of Aquatic Fauna and Food Webs

Low mineral concentrations in aquatic environments may limit fish species distributions by exceeding their capacity to maintain internal osmotic balance (Dunson & Travis, 1991; Dunson and others, 1997). For example, sheepshead minnows (*Cyprinodon variegatus*) inhabit the southern freshwater Everglades but not the northern Everglades (Loftus & Kushlan, 2001; Trexler and others, 2001) for reasons probably linked to their osmotic requirements (Dunson and others, 1998). Similarly, several species of fishes are not found in Florida south of Lake Okeechobee (e.g., *Leptolucania ommata*), probably because they require low-conductivity habitats (Trexler, 1995). Additionally, species able to persist in soft water areas may have slower growth rates and reduced fecundity due to physiological stress. For example, *C. variegatus* is unable to reproduce, though it can survive, at low conductivity ($< 500 \mu\text{S}/\text{cm}$) (Dunson and others, 1998). In a more temperate location, Trippel (1993) found growth rate and fecundity were lower in low conductivity lakes than in high conductivity lakes. Fishes can substitute Ca^{2+} for Na^+ , permitting some marine species to inhabit Ca-rich freshwaters in karstic regions (Evans & Claiborne, 2006). The mineral content of water as indicated by conductivity also can affect the species composition of aquatic invertebrate communities (Paradise & Dunson, 1997; Baltzley and others, 1999).

Calcium is an important mineral for mollusk growth and shell development. Calcium levels must be above 5 mg/L to support many species of snails (Appleton, 1978; Lodge and others, 1987; Hury and others, 1995). Equally important in the success of snail populations is alkalinity as low pH can cause juvenile death and poor hatching in egg masses (Mackie & Flippance, 1983a; Hunter, 1990). The lowest levels of Ca^{2+} reported in the Refuge are 5 mg/L and thus may limit some snail species. Even if some species are not excluded, the low levels of Ca^{2+} may reduce the growth rate, shell strength, and fecundity of the snail populations. For example, Mackie & Flippance (1983b) found inter- and intraspecific variation in the Ca content of snails and bivalve shells and soft tissue.

Conclusions: Current Understanding and Information Gaps

Wetland degradation often is the product of cumulative impacts from multiple stressors (National Research Council, 1992). The success of wetland restoration efforts thus requires a clear understanding of the various causes of ecosystem decline to avoid unintended impacts from actions designed to achieve restoration objectives. The increasing importance of canal discharges as a source of water to the Everglades during the past century has altered many aspects of the hydrology, chemistry, and ecology of this wetland. One of the clearest contrasts

between canal-fed and rainfall-fed portions of the ecosystem is the elevated conductivity produced by high mineral loads in canal water. Consideration of the potential for significant ecosystem effects from this water-quality change seems warranted given the importance of mineral chemistry to peatland ecology,

Available information on historical water sources and ecosystem chemistry indicate that mineral concentrations in water and peat were lower across large areas of the predrainage Everglades than they are today. Human alterations to regional hydrology and land use have increased mineral inputs to this ecosystem and converted historically mineral-poor areas such as WCA 2A into minerotrophic peatlands. Hydrologic restoration efforts under CERP inevitably will increase the spread of high-conductivity water across the Everglades since these projects will rely on waters with a source and chemistry similar to those currently conveyed through the south Florida canal network. Much of the managed Everglades already has been exposed in varying degrees to these flows, but there is mounting evidence that remaining soft-water areas such as the Refuge increasingly may be exposed as well as new discharge structures (e.g., outflow pumps from a new stormwater treatment area, STA-1E, on the northeast side of the Refuge) become operational.

The broader peatlands literature provides a wealth of evidence for the importance of mineral chemistry to the ecology of temperate and northern peatlands. While environmental controls on the mineral chemistry of subtropical peatlands such as the Everglades may differ from those at higher latitudes, it is likely that many of the relationships between peatland mineral status and ecosystem properties are similar. In particular, recent investigations in the Everglades indicate possible effects of increased mineral loading on geochemical processes affecting nutrient and contaminant availability, the species composition of plant and periphyton communities, the balance between slough and sawgrass landscape features, and perhaps the distribution of fish and aquatic invertebrates. These findings suggest that the use of canal waters as the principal means for restoring hydrologic features could cause unintended changes in the ecology of some parts of the Everglades.

In contrast to extensive research on historic and current conditions in the Everglades with respect to hydrology and P, comparatively little attention has focused on the mineral chemistry of the predrainage ecosystem and the impacts of increased mineral loading on the managed ecosystem. Additional research on various aspects of this issue will allow for a more detailed assessment of the significance of this water chemistry feature. Major data gaps include the following.

The spatial extent and chemistry of the historic soft-water Everglades

Current understanding of predrainage hydrology, measurements of peat depths and chemistry, and a small amount of paleoecological data indicate that much of the interior of the northern and central Everglades was a soft-water wetland prior to drainage. More detailed chemical and paleoecological analyses of peat profiles in these areas could provide valuable information on the historical distribution, mineral chemistry, and ecology of this wetland type in the Everglades. Reconstruction of historic water chemistry based on geochemical analysis of mineral content may be feasible but is complicated by the mobility of major mineral elements in the peat profile (William Orem, USGS, pers. comm.). The reliability of various techniques for assessing historic water chemistry conditions from peat cores currently is being evaluated in the

Refuge by the USGS. Microfossils such as diatoms can provide highly reliable indicators of past water chemistry conditions for parameters such as pH and alkalinity. The utility of these indicators in the Everglades will be limited by the extent to which diatom frustules are preserved in the peat record.

A more detailed analysis of regional and local mineral sources, both prior to drainage and at present, would allow for a better understanding of historic and current mineral loads entering the Everglades. Such an analysis should include both surface-water and ground-water chemistry for the Everglades and surrounding areas such as Lake Okeechobee. A retrospective analysis could improve upon the water budget in Table 3 by expanding its scope to include a budget of mineral sources. More detailed water and mineral budgets for individual WCAs also would be helpful.

The relationship between canal flows and mineral concentrations in Everglades wetlands

The quantity and frequency of canal-water discharges varies across the Everglades. It is unclear how differences in exposure affect mineral concentrations in Everglades peat soils. For example, are there differences in long-term mineral accumulation rates in soils between areas exposed to similar mineral loads in the form of pulsed versus more continuous canal discharges? Does periodic exposure to low-conductivity rainwater have a flushing effect that counteracts this accumulation and, if so, to what extent? Multiple chemical and biological processes contribute to the accumulation of different elements such that the relationship between surface-water and soil concentrations is not a simple linear function. For example, Ca^{2+} accumulates on cation-exchange sites on the peat, which ultimately become saturated, and through periphyton-mediated precipitation reactions when water Ca^{2+} concentrations and pH are sufficiently high. These processes contribute to non-linear patterns of Ca accumulation with increasing conductivity and to soil Ca pools that are quite different in terms of their bioavailability. Additional information on the processes and environmental conditions affecting mineral accumulation and availability would allow for quantitative relationships between canal-water inputs and wetland mineral levels to be established.

Ecological effects of increased mineral loading

Available data from the Everglades and the broader wetlands literature indicate the effects of increased concentrations of individual elements such as Ca or S on biogeochemical cycles in the Everglades. Simultaneous enrichment with many different elements transported in canal water makes the prediction of such effects more difficult due to the potential for various antagonistic and synergistic interactions. Measurements of changes in soil nutrient availability and other soil properties (e.g., redox, pH, sulfide) across canal-water mineral gradients would provide a good starting point for determining the net effect of this complex mineral solution on Everglades nutrient cycles. Biological responses to canal discharges probably result from multiple stressors including both mineral and nutrient loading as well as associated hydrologic alterations. Sampling across canal-water gradients in the Everglades have been used to identify the cumulative impact of these discharges and may allow for mineral effects to be separated from those due to P enrichment since mineral gradients extend much farther from the discharge points

than do P gradients. Controlled experiments are needed to confirm patterns documented across these gradients and to further isolate effects attributable to individual stressors.

All research that helps improve our understanding of the specific causes of ecosystem changes in response to discharges of high conductivity water will be useful. Information that helps answer the question “Do specific constituents cause deleterious ecological effects or is degradation a more general response to increased ionic activity?” would be especially valuable. For example, learning that canal discharges from the EAA are a major source of S to the Everglades and that S cycling is closely tied to Hg methylation has been of great importance to our understanding of methyl-Hg production and bioaccumulation in the Everglades. Sulfur inputs to the Everglades might be controlled through best management practices to limit or change the timing of fertilizer applications or through manipulation of the fertilizer content itself, better control of saline ground-water discharge, and possibly through the use of S mitigation strategies. Undoubtedly, there are other relationships between water source, water quality, and ecological processes in the Everglades that need to be as well understood as those for S. Some constituents will not be as high a priority from a management standpoint, either because little can be done to reduce the source or because the ecological consequences are found to be not as great.

Hydrologic measurements and modeling of canal flows and mixing within the Everglades

Improved hydrologic measurements and models also are needed to identify water management strategies that minimize unnecessary canal-water intrusion into the Everglades interior. Studies that address the environmental costs and benefits of backfilling canals that are scheduled to be decommissioned as part of the Everglades restoration would be valuable. Determining how to limit inputs of canal waters into rainfall-driven areas such as the Refuge that are not scheduled for hydrologic restoration under CERP is of particular importance. Factors controlling the extent of canal-water intrusion into the Refuge are not clearly understood, but likely include both natural variation in water stage in the Refuge interior and water management actions by federal, state, and local agencies that control flow and stage in the rim canals surrounding the Refuge. Recent changes in the location and schedule of discharges into these canals may increase the frequency and extent of intrusion into the Refuge. The largest areas of intrusion currently exist along the western side of the Refuge where canal flows are greatest and peat surface elevations are low. The future operation of STA-1E, located on the northeastern perimeter of the Refuge, will increase canal flows along the eastern edge of the Refuge and may contribute to additional intrusion in this area. A better understanding of relationships between water management activities and canal-water intrusion will allow for more accurate predictions of the effects of current and proposed restoration projects and water-management operations on water quality in the Refuge.

Acknowledgements

This document was produced with support from the USGS Greater Everglades Priority Ecosystem Science Program. Joel Trexler (Florida International University) contributed the section *Aquatic Fauna and Food Webs*. Leslie MacGregor (A.R.M. Loxahatchee National Wildlife Refuge) provided GIS and graphics support and Bruce Taggart (USGS) assisted with document formatting. Nick Aumen (Everglades National Park), Laura Brandt (A.R.M.

Loxahatchee National Wildlife Refuge), and Joel Trexler reviewed an earlier draft of the document. A later draft was reviewed by Joffre Castro (Everglades National Park), Paul Glaser (University of Minnesota), Christopher McVoy (SFWMD), Martha Nungesser (SFWMD), Ed Pendleton (USGS), Bruce Taggart, and Michael Waldon (A.R.M. Loxahatchee National Wildlife Refuge).

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Appendix 1 - Locations of Refuge sampling sites referenced in report.

