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

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Human influences during the previous century increased mineral inputs to the Florida Everglades by changing the sources and chemistry of surface inflows. Biogeochemical responses to this enrichment include changes in the availability of key limiting nutrients such as P, the potential for increased turnover of nutrient pools due to accelerated plant decomposition, and increased rates of mercury methylation associated with sulfate enrichment. Mineral enrichment has also been linked to the loss of sensitive macrophyte species, although dominant Everglades species appear tolerant of a broad range of mineral chemistry. Shifts in periphyton community composition and function provide an especially sensitive indicator of mineral enrichment. Understanding the influence of mineral chemistry on Everglades processes and biota may improve predictions of ecosystem responses to ongoing hydrologic restoration efforts and provide guidelines for protecting remaining mineral-poor areas of this peatland.

KEYWORDS: conductivity, Everglades, hydrology, minerotrophy, peatlands, periphyton, vegetation, wetlands

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INTRODUCTION

The Florida Everglades (Figure 1) 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).

FIGURE 1. Map of the Everglades showing (a) the major ecological units of the predrainage Everglades overlain in grey by modern boundaries of the Water Conservation Areas (WCAs) and Everglades Agricultural Area (EAA). For contrast the map in (b) illustrates the major hydrologic and land-management units of the present managed Everglades, including levee-canal systems (black lines) and hydraulic pump stations (white circles) that supply water to the Everglades. Shown in medium grey shading are the WCAs that now comprise the bulk of the remaining central Everglades. In dark shading are the areas of former Everglades that were converted in the early twentieth century to the EAA. Adjacent to the EAA is WCA-1 (Loxahatchee National Wildlife Refuge), used to illustrate mineral-ecological relationships in this paper. As a general spatial reference, several major roads that cross the Everglades are named and shown as dashed lines.
and more abundant minerals such as calcium (Ca). Water management actions over more than a century have reduced the relative influence of direct rainfall as a water source to much of the remaining Everglades by creating a new water source in the form of 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 human activity), and groundwater 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.

Everglades restoration efforts are focused primarily on increasing water deliveries in a manner that restores patterns of water flow, depths, and hydroperiods within this peatland. With the exception of P, for which a numeric criterion for the Everglades presently exists, the chemical suitability or quality of these deliveries has been evaluated largely with respect to statewide water-quality criteria (e.g., Weaver et al., 2008) rather than actual environmental responses within this peatland. In particular, potential ecological effects of increasing mineral concentrations have yet to be assessed in the Everglades. Minerotrophy represents one of three 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 northern and temperate peatlands (Bridgham et al., 1996; Heikkinä, 1987; Malmer, 1986; Økland et al., 2001; Wheeler and Proctor, 2000; Wheeler and Shaw, 1995). These and numerous other studies have documented the pronounced effect that local and regional differences in mineral chemistry have on the biogeochemistry and biota of these ecosystems. By contrast, the influence of mineral chemistry on the ecology of subtropical peatlands such as the Everglades remains largely unexplored.

Our objective in this paper is to synthesize what is known about the historic mineral chemistry of the Everglades and the effects that changes in water sources have had on the chemistry and ecology of the present-day managed ecosystem. We first summarize previous research on the evolution and hydrology of the predrainage ecosystem to argue that much of the Everglades existed in a mineral-poor state prior to regional hydrologic and land-use changes begun in the late 1800s. We then describe present chemical and ecological conditions in one of the few remaining rainfall-fed, softwater areas of the remnant Everglades, the Loxahatchee National Wildlife Refuge, and discuss the results of ongoing research investigating the ecological effects caused by the intrusion of mineral-rich waters into this northernmost impoundment of the remnant Everglades. The goal of our presentation is to elicit greater recognition of the potential importance of mineral chemistry as an environmental driver of ecological conditions in the predrainage Everglades and the implications for ecosystem restoration and other conservation efforts in this wetland.
Evolution and Mineral Chemistry of the Everglades Peatland

This peatland developed in a shallow trough on top of a sandy limestone surface comprising the surficial groundwater aquifer in this area of southern Florida (Gleason and 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 et al., 1974). Marl sediments are indicative of wetlands that are inundated with water of moderate to high mineral content, such as the marl prairies that presently occur in the southern Everglades, including portions of Everglades National Park (Davis et al., 2005). The shift toward a wetter climate roughly 5000 YBP initiated widespread peat accretion across south Florida, which in turn progressively increased the spatial extent and water surface elevation of the Everglades (Gleason and Stone, 1994). The accumulating peat increasingly isolated the wetland surface from bedrock and groundwater mineral influences and increased the influence of rainfall on surface-water chemistry. This same process is responsible for the evolution of temperate and northern peatlands toward a mineral-poor state (Moore and Bellamy, 1974). Although the potential for groundwater–surface water interactions still exists even in the presence of thick peat accumulations (Siegel and Glaser, 1987), the development of the Everglades toward a low-mineral state is evidenced by peat deposits 1–3 m deep without significant intervening marl layers across much of the wetland north of Tamiami Trail (see Figure 1). Available paleoecological data provides further evidence of a mineral-poor chemistry in these areas prior to drainage and development (Slate and Stevenson, 2000; Winkler et al., 2001). By contrast, peat accumulations in the southern Everglades generally were <1 m thick and contained abundant calcite layers (Gleason and Stone, 1994; Renken et al., 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 et al., 2001).

Water Sources to the Predrainage Everglades

The present understanding of historic water sources also supports the thesis that the predrainage Everglades peatland was a relatively mineral-poor ecosystem. Information about water sources to the predrainage Everglades comes from a recent synthesis (Harvey and McCormick, 2009) based on the South Florida Water Management District’s (SFWMD) efforts to simulate water flow in both the present day and predrainage ecosystem. The water budget for the predrainage system uses the results of the Natural Systems Model (NSM; Version 4.5), which encompasses the breadth of the historic
Everglades from the southern rim of Lake Okeechobee southward to the present-day location of Tamiami Trail (South Florida Water Management District [SFWMD], 2006). According to this model, direct rainfall provided on average 81% of annual water inputs to the predrainage system. 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 (SFWMD, 2009), the median specific conductance of rainfall in the northern Everglades is <20 \( \mu S/cm \) and median concentrations of all major ions except for \( \text{Cl}^- \) (median value = 1.5 mg/L) are <1 mg/L. Contemporary measurements of atmospheric deposition may overestimate historical mineral inputs from this source due to contamination from local (e.g., locally generated dust, trapped insects, other debris) and regional (e.g., farming, urban, industrial pollution) sources. Still, available data clearly illustrate that, in the absence of significant water sources other than precipitation, surface waters in peat-building portions of the Everglades would have a depleted mineral chemistry.

Based on the NSM model, surface runoff and Lake Okeechobee overflows are estimated to have contributed 10% and 8% of the total water input to the predrainage Everglades, respectively. Upland soils in the northern Everglades are mostly acidic sands with low ionic content and thus were not a significant mineral source. The mineral-depleted nature of these soils in south Florida is evidenced by the soft-water chemistry of tributaries to Lake Okeechobee (Table 1), as measured by Parker et al. (1955) during the period of 1939–1941, which was prior to much of the land-use conversion that has since altered these water bodies. Overflows from Lake Okeechobee entered the northern end of the Everglades primarily during the summer wet season. With a present specific conductance of approximately 400–500 \( \mu S/cm \), and relatively high proportional contributions of \( \text{Mg}^{2+} \), \( \text{SO}_4^{2-} \), \( \text{Ca}^{2+} \), and alkalinity (\( \text{HCO}_3^- \)) to its ionic balance, Lake Okeechobee’s mineral content presently is substantially higher than that of rainfall and therefore can be viewed as a significant source of minerals to the predrainage northern Everglades. However, the lake has been exposed to mineralized canal discharges from surrounding agricultural lands for many decades (Joyner, 1960).

<table>
<thead>
<tr>
<th>Tributary</th>
<th>( n )</th>
<th>SC (( \mu S ) cm(^{-1} ))</th>
<th>( M ) concentration (mg L(^{-1} ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kissimmee River</td>
<td>36</td>
<td>81</td>
<td>5.6  1.7  8.5  14  5.9  12</td>
</tr>
<tr>
<td>Fisheating Creek</td>
<td>3</td>
<td>76</td>
<td>3.0  1.5  7.0  8   1.4  16</td>
</tr>
<tr>
<td>Taylor Creek</td>
<td>1</td>
<td>72</td>
<td>7.0  1.2  6.0  22  2.9  10</td>
</tr>
</tbody>
</table>

Note. SC = specific conductance.
Everglades Mineral Chemistry

1971; Parker et al., 1955), and the mineral-depleted chemistry of the lake’s tributaries (presented previously) suggest that the mineral content of the predrainage lake was lower than that measured in recent years.

The mineral chemistry of surface waters in the Everglades was influenced only minimally by interactions with mineral-rich groundwater from the underlying aquifer, which accounted for only 1% of total inflows to the predrainage system as predicted by the NSM. Shallow groundwater in south Florida acquires Ca$^{2+}$, Mg$^{2+}$, and HCO$_3^-$ from the dissolution of limestone bedrock and Na$^+$ and Cl$^-$ by vertical mixing with ancient seawater trapped deeper in the aquifer (Harvey and McCormick, 2009). Groundwater influences in the southern Everglades may be substantially higher than that in the central and northern Everglades due to thinner peats and greater transmissivity in the underlying aquifer (Harvey et al., 2006). The greater interactions between surface water and groundwater in the southern Everglades may have contributed to a more mineral-rich historical condition compared to the central and northern Everglades (Price and Swart, 2006).

Water Sources to the Managed Everglades

Water management across south Florida has increased the extent of interactions between surface water and groundwater in the Everglades, beginning with the first efforts to drain the wetland by dredging canals in the early 1900s. Drainage efforts through the 1950s led to oxidation and peat subsidence in the northern Everglades, which fundamentally changed the general direction of horizontal groundwater flow and increased the vertical component of this flow (Harvey et al., 2002; Miller, 1988). These effects have been particularly pronounced along the boundaries of the remaining Everglades and in the large area of wetlands that was drained and then developed for agriculture in what is now known as the Everglades Agricultural Area (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 et al., 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 groundwaters (Harvey et al., 2002). Other water management practices that contribute to increased groundwater discharge include the storage of water behind levees within the Everglades, which produces abrupt water-level differences that produce the driving force for relatively deep vertical exchange of groundwater, and pumping operations, which increase local vertical driving forces beneath the canal bottoms that cause discharge of deeper groundwater (Krupa et al., 2002; Miller, 1988). These changes in hydrologic interactions from the predrainage state are illustrated in Figure 2.
FIGURE 2. North-south cross-section of the predrainage and managed Everglades illustrating schematically the hydrogeologic transect shown in Figure 1b. Note the vertical exaggeration of the $x$-axis relative to the $y$-axis to emphasize the topographic changes brought about by water management, the drainage and subsidence that occurred in the Everglades Agricultural Area (EAA) and the effects of levees and canals on hydrologic connectivity. Also depicted are the accompanying reductions in thickness of Everglades peat in the northern Everglades, as well as the dredging of canals that directly penetrated the underlying surficial aquifer. All of these topographic and soil disturbances have contributed to increased groundwater–surface water exchange (black arrows) in the managed Everglades.

Water management actions and the environmental consequences just described have significantly altered the water budget for the present-day managed Everglades. The extent of this change is apparent from a synthesis of the SFWMD South Florida Water Management Model runs (SFWMM; SFWMD, 1999). Although direct rainfall still remains the primary source of water (61% of total water input), canal discharges containing drainage waters from former wetlands converted to agriculture represents a new and significant (18%) input. The importance of runoff from marginal areas increased slightly (from 8 to 12%), the percentage of inputs from Lake Okeechobee decreased slightly (from 8 to 4%), whereas groundwater discharges in the wetland interior remained about the same (1% of inputs).
The most significant sources of water to the main conveyance canals flowing into the Everglades (the Palm Beach, Hillsboro, North New River, and Miami canals shown in Figure 1) include water releases from Lake Okeechobee, runoff of rainfall and soil water from agricultural fields in the EAA, and groundwater discharge to canals within the EAA (Harvey et al., 2002; Miller, 1988). The median specific conductance of surface waters in the main canals ranges between 700–1100 µS/cm (Figure 3), more than 50-fold higher than that of rainfall and twice that of present levels in Lake Okeechobee, which also is exposed to elevated mineral loads from human sources. Sources of minerals to EAA canals include mineral additives applied with fertilizer to EAA farm fields in addition to minerals naturally present in EAA groundwater and the oxidizing peat soils in this drained wetland area. Specific conductance decreases from north to south across the Everglades canal network (Figure 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. Canal waters are released into the Everglades as point discharges through water-control structures and their influence on wetland surface water conductance declines predictably with

![Figure 3](image-url)  
**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, midline, 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 10–90th 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.
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 et al. (1998). Fifty locations were sampled during September 1993 and an additional 49 were sampled during September 1994. See Figure 1 for a more detailed regional map. This figure was modified from Stober et al. (1998) with permission.

distance from these discharge points. Areas strongly influenced by canal discharges typically have conductance values as high as 1000 µS/cm, whereas those that are predominantly rainfall-fed have values as low as 100 µS/cm or less.
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 (Figure 1). The Refuge is among the oldest parts of the Everglades based on radiocarbon dates of 4800 YBP for basal peats (Gleason et al., 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 and 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. Peats in the Refuge are mineral poor (Gleason and Stone, 1994), indicating a strong influence of rainfall on both the hydrology and chemistry.

At present, the Refuge interior represents one of the last remaining low-mineral areas of the Everglades and thus may provide clues as to some of the predrainage characteristics of peat-forming 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 other parts of the Everglades into hard-water fens with distinct ecological features. The Refuge is encircled by a rim canal that conveys EAA drainage water and Lake Okeechobee discharges southward through the Everglades and to urban areas along Florida’s southeastern coast. The variable topography of the Refuge (Desmond, 2004) combined with vegetative resistance to flow help to limit the intrusion of canal water into the interior and maintain a largely rainfall-fed chemistry. Water-quality-monitoring data collected by various investigators show that surface-water-specific conductance in the Refuge interior averages around 100 µS/cm, a level that is 5–10 times lower than in the rim canal and among the lowest recorded in the managed Everglades (Scheidt and Kalla, 2007; USFWS, 2009).

The following synthesis of available information on patterns of mineral chemistry and associated environmental responses in the Refuge includes both previously published findings as well as new data. Much of this information was collected at fixed sampling stations across the Refuge. The locations of these stations are shown in Figure 5.

Effects of Canal-Water Intrusion on Water Chemistry

Although 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-water intrusion. The major water-chemistry gradients created by this intrusion are illustrated for a set of nine stations located near the Refuge perimeter and monitored by the SFWMD between April 1996 and March 2000 (Figure 6; see McCormick et al. [2000] for site descriptions and data collection methods). Conditions at these stations do not capture the full spatial extent of intrusion as specific conductance at transect stations farthest from the canal were approximately twice that at a more distant monitoring station in the center of the Refuge (also shown for comparison in Figure 6).
Mean specific conductance ranges from near 900 µS/cm at stations closest to the canal to near 200 µS/cm at the farthest transect stations. Declines in specific conductance are best described as a linear function, suggesting that dilution with ion-poor Refuge water rather than biological uptake is the primary cause of the decline. Specific conductance is correlated strongly with concentrations of all major ions measured across this transect ($r > .930$, $p < .001$, Spearman rank correlation coefficient) but is less strongly related to P ($r = .565$, $p < .001$, Spearman rank correlation coefficient), which also enters the Refuge in canal water but is subject to rapid biological uptake and therefore is best described by an exponential decay function. Thus, two zones of canal influence can be discerned within the Refuge: (a) a relatively narrow zone of high P-high conductivity water; (b) 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, 1992).

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 (see Chang et al., 2009; Newman and Hagerthy, 2011). Predictably, locations in the Refuge interior had lower specific conductance than those near the rim canals. An extensive area of elevated conductivity caused by canal-water
intrusion was documented across the western Refuge, whereas intrusion was limited along the eastern side. 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.

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 weather patterns 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. This simple relationship between canal and wetland stages provides at least a partial explanation for the occurrence of periods of elevated specific conductance within the Refuge as illustrated for a long-term SFWMD monitoring station (LOX10) located approximately 2.5 km from the western rim canal and shows that high conductivity events are associated with periods where canal stage approaches or exceeds that in the interior (Figure 7). By contrast, conductivity levels at a monitoring station farther into the interior (LOX8, 10.6 km) are unrelated to this stage differential and more strongly influenced by seasonal patterns in water depth as influenced by rainfall and evapotranspiration; periods of high rainfall result in greater water depths and a dilution of ionic activity, whereas evapotranspiration causes a decline in water depths and the concentration of dissolved minerals when conditions are dry.

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. Pope (1992) 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 (Figure 8). Average soil Ca concentrations increased by approximately 50% whereas Cl concentrations were twice as high in some habitats. Concentrations of Mg, Na, and K exhibited 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.

We documented patterns of soil and plant chemistry related to increasing canal influence in 2004 in conjunction with the conductivity mapping efforts described previously. Grab samples of surface soils corresponding roughly to the 0–5 cm depth layer were collected from 130 sites across the Refuge. Soils were dried at 105°C, ground with a mortar and pestle, and analyzed for total S
by combustion analysis and for total Ca and P by inductively coupled plasma spectroscopy. Samples of live sawgrass (*Cladium jamaicense* Crantz) also were collected at sites where this species was present. These samples were dried at 105°C, ground in a Wiley mill, and analyzed for the same elements as for soils. Strong correlations were found between surface-water specific conductance and soil concentrations of Ca and P (Figure 9). Sawgrass tissue S concentrations also were correlated positively with specific conductance (Figure 10).

Ecological Effects of Mineral Enrichment in the Refuge

**BIOGEOCHEMICAL PROCESSES**

Peatland mineral chemistry exerts strong control over biogeochemical processes that regulate nutrient cycling and productivity. With the exception of K, major minerals such as Ca rarely limit peatland primary production...
FIGURE 8. Changes in available soil mineral concentrations (as measured 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 (Pope, 1992).

(Bedford et al., 1999; Bridgham et al., 1996). However, mineral chemistry can affect peatland fertility through its influence on the availability of limiting macronutrients such as N and P as well as micronutrients such as iron (Fe). Although total soil nutrient concentrations in mineral-poor bogs are typically lower than those in minerotrophic fens due to lower external inputs, the relationship between total nutrients and nutrient availability is more

FIGURE 10. Relationship (with Spearman rank correlation coefficient) between surface-water-specific conductance and the sulfur content of live sawgrass measured across the Refuge during February 2004.
complex. High $Ca^{2+}$ and $Mg^{2+}$ concentrations and pH can reduce P availability in fens (Boyer and Wheeler, 1989; Verhoeven and Arts, 1987), whereas increased $SO_4^{2-}$ loading can increase P availability by various reactions (Beltman et al., 2000; Lamers et al., 2001). Forms of plant-available N also vary across pH gradients (Kinzel, 1983). Inhibition of bacterial growth may reduce microbial nutrient immobilization in ombrotrophic peatlands due to low pH (Wilson and Fitter, 1984). These biological and chemical processes may explain why concentrations of extractable and pore water P and N can be higher in bogs than in fens despite similar or lower total nutrient concentrations (e.g., Schwintzer and Tomberlin, 1982; Vitt et al., 1995; Waughman, 1980).

We collected soil samples (0–20 cm depth increment) at 12 sites along an east–west transect across the Refuge in late summer 2004 to document shifts in P and N fractions with increasing distance from the rim canals. Soils were kept at 4°C prior to be analyzed for soil P and N fractions using the methods described by Ivanoff et al. (1998) for P and White and Reddy (2000) for N. Total P concentrations (mg/kg) were approximately twice as high at sites closest to the canal compared to the most interior locations as a result of intrusion of P-rich canal water (Figure 11). 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, whereas 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. This fraction comprises as much as 13% of the total P in surface soils in minerotrophic Everglades peatlands and plays a more important role in P storage in these areas (Qualls and Richardson, 1995). The size of the microbial P fraction suggests that microbial immobilization may be a more important process controlling P availability at canal-influenced sites.

In contrast to soil P, soil TN concentrations showed no strong pattern with distance from the canals, ranging between 31 and 39 g kg$^{-1}$. Labile N pools accounted for only 1.5% of TN at interior sites and approximately 2% at sites closest to the canal. Two of these fractions, labile organic N and plant-available N (exchangeable NH$_4$) were similar among sites (Figure 11). By contrast, microbial N was a minor fraction of organic N at interior locations, but was as much as 40–70 times higher and represented the major labile N pool at sites closest to the canal. As with P, these data indicate that microbial immobilization is an important process regulating N availability at canal-influenced sites.
FIGURE 11. 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 Refuge. See Figure 5 for site locations. Soil nutrient fractions are stacked in the same order in the legend and in the graph.

Measurements of soil pore water chemistry suggest that nutrient loading rather than mineral chemistry is the primary factor influencing nutrient availability across canal gradients in the Refuge. Pore water (2–12 cm depth increment) at canal-influenced sites had a higher pH and higher concentrations of both major ions (Mg$^{2+}$, Ca$^{2+}$, K$^{+}$, Cl$^{-}$, S$^{2-}$, and sulfate), but also had higher dissolved N and P than interior locations (McCormick et al., 2000). 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. A controlled field experiment showed that P enrichment can increase pore water concentrations of N as well, possibly by increasing rates of organic matter decomposition (Newman and Hagerthy, 2011). Recent evidence (Orem et al., 2006) has indicated that the high sulfate loads in canal water also may elevate pore water P concentrations due to competitive binding and the formation of insoluble FeS under low redox, thereby limiting Fe-P binding in aerobic soil layers.

Organic matter decomposition is a key process controlling both soil formation and nutrient cycling in peatlands. Among peatlands, litter decomposition rates are typically lower in bogs than in fens. 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 and Grigal, 1988; Verhoeven et al., 1990), indicating that environmental factors such as low pH also may limit decomposition.

Increased mineral loading may influence decomposition rates in the Refuge through (a) effects on organic matter quality either through increases in litter mineral content or shifts in plant species composition, (b) increased availability of electron acceptors such as sulfate that are used in anaerobic microbial respiration, and (c) increased availability of elements such as Ca that serve as cofactors 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 oligotrophic interior of a minerotrophic peatland just to the south (Newman and Hagerthy, 2011). Although not suggesting a specific mechanistic explanation, these findings indicated that intrusion of mineral-rich canal water promoted faster rates of decomposition.

We also investigated the response of litter decomposition rates at several locations across a canal mineral gradient in the Refuge. Standing dead sawgrass was collected from each site and allowed to air dry in the laboratory for 1 week. The material was then cut into approximately 7.5-cm pieces, weighed, and sealed in mesh bags constructed from nylon window screen. Additional air-dried material was weighed, dried for 72 hr at 70°C, and then reweighed to calculate a conversion factor between air-dried and oven-dried material. Bags were returned to the sites where the material was collected and incubated at the soil-water interface for 12 months. Bags were then returned to the laboratory where the material was removed, gently rinsed with deionized water, dried for 72 hr at 70°C, and weighed to determine decomposition rates as the percent loss of dry mass during the incubation period. Decomposition rates declined with increasing distance from the canal and, thus, were positively related with site conductivity (Figure 12). This result provided further evidence for the stimulation of organic matter decomposition with mineral enrichment.
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 et al., 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 (Orem et al., 1997). Although atmospheric deposition and groundwater are likely sources of some of the sulfate entering the Everglades, agricultural drainage water entering the wetland in canal discharges has been identified as another important source of this ion (Bates et al., 2001).

Water- and soil-chemistry data collected since 2005 along an east-west transect across the Refuge show 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 (USFWS, 2009). We augmented these water-chemistry data by collecting soil samples (0–10 cm depth increment) at these sites during the summer of 2006 and assaying them for total S by combustion analysis. Soil S concentrations were compared with mean surface-water sulfate concentrations for the previous year (Figure 13). 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. A similar pattern exists for plant-tissue S (see Figure 10).

A mesocosm experiment conducted in the Refuge interior (Gilmour et al., 2003) 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 et al., 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.

**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., Malmer, 1986; Sjörs, 1950; Vitt et al., 1990; Waughman, 1980; Wheeler and Shaw, 1995), and plant communities have been used to classify fens according to their mineral
status in many regions. Wetland plant species differ considerably in their tolerance to mineral concentrations and can be loosely grouped into 3 general categories: (a) those restricted to mineral-poor waters, (b) those restricted to mineral-rich waters, and (c) those that appear indifferent to mineral concentrations. Species responses across mineral gradients are the product of multiple effects of both mineral concentration (e.g., Ca\(^{2+}\), alkalinity) and pH on plant physiology and competitive ability. Bridgham et al. (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 because it depletes local and regional floristic diversity.

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 (Figure 14). The presence and abundance rank of common Refuge plant species at each site was determined based on quarterly surveys conducted by USGS personnel 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

Results indicate that interior SWP taxa differ greatly in their tolerance to canal-water intrusion and generally can be classified into those that are (a) found throughout the Refuge regardless of the level of canal influence, (b) restricted to perimeter locations with substantial canal influence, and (c) 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. Previous studies also have found these taxa to be indifferent to surface-water mineral concentrations (Moyle, 1945; Walker and Coupland, 1968). One species, Eleocharis cellulosa, occurred only at sites closest to the canals. The distribution of Eriocaulon compressum and Xyris smalliana were restricted to interior locations with background or only slightly elevated specific conductance. Two other common species of the genus Rhyncospora, 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
FIGURE 14. 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 Refuge. Site names are shown on the bottom graph. See Figure 5 for site locations. See text for abundance rank category definitions.
conditions and are found along the margins of soft-water lakes and in poor fens and even bogs (Glaser, 1992; Keddy and Reznicek, 1982; Wilson and Keddy, 1986). 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 and Greening, 1989).

Relationships between species distributions and canal-water gradients are correlated with several environmental changes and thus do not by themselves provide proof that 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 et al., 2002). Although sampling sites used to illustrate the 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. The perimeter of the Refuge also experiences greater water depth fluctuations compared to the interior (Pope, 1992), a condition that may favor SWP taxa such as *E. cellulosa* over others such as *Rhyncospora*. Therefore, some changes in SWP vegetation across these gradients may be due to factors other than mineral chemistry.

We investigated the effects of limiting nutrients such as P and major mineral ions on plant growth in a series of experiments using the plant species *X. smalliana*, which occurs in the Refuge interior but not near the perimeter. Plants were collected from the Refuge interior, planted in pots containing 300 g of field wet soil from the collection site, and grown in the laboratory under controlled light, temperature, and hydrologic regimes that mimicked conditions in the Refuge at the time of collection. Plant growth was measured as the production of dry-weight biomass over a 12-week period. Watering three times each week with solutions of N (200 µg L⁻¹ as NaNO₃ and NH₄Cl), P (50 µg L⁻¹ P as NaH₂PO₄), and K (100 µg L⁻¹ K as KCl) alone or in combination for three months elicited no measurable growth response from this species. However, a similar duration of enrichment with a mineral solution that approximated the concentration of the seven major mineral ions (Ca²⁺, Mg²⁺, Na⁺, K⁺, HCO₃⁻, sulfate, and Cl⁻) in canal waters significantly reduced growth rates during this same time period compared to plants grown with water from the Refuge interior (Figure 15). 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 chemistry gradients. We documented spatial shifts in vegetation composition associated with canal-water intrusion using aerial photographs with a 0.6-m resolution that were collected in 2006 at 14 USFWS-USGS sampling stations along an east-west transect across the Refuge (see Figure 5).
Coverages of SWP and sawgrass habitats were estimated for a 0.25 km² area centered on each sampling station. Canal-water intrusion near the eastern and western perimeter was associated with a decline in the coverage of SWP habitats and an increase in sawgrass cover (Figure 16). However, this spatial 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). 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, but this imagery also indicated a shift in vegetative composition toward increasing dominance by sawgrass near the western boundary of the Refuge. Therefore, the present 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 and 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 mineral-rich part of the Everglades 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. mariscoideus* is well recognized. For example, dominance of *C. mariscus* is indicative of high mineral levels in peatlands across Europe (Wheeler and
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 et al., 1990). Experimental liming (CaCO₃) of wetland plots surrounding an acidified lake in the Adirondacks of New York produced nearly a threefold increase in the cover of *C. mariscoides* after two years, although it still represented a minor vegetative component (Mackun et al., 1994).

We conducted a laboratory experiment 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, and perimeter slough). Interior soils, which had a low mineral content, were left untreated or enriched with different concentrations of the seven major mineral ions (see previous) to achieve moderate or high soil mineral concentrations as documented across canal gradients in the field. Seedling growth under light and temperature conditions similar to those in the Refuge 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 (Figure 17). 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

![Figure 16](image-url)
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.

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)

Present information from the Everglades is insufficient to indicate mineral levels that might impact soft-water SWP plant communities, but 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 are near 10 mg/L, whereas 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.

PERiphyton Responses

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 (noncalcareous) in nature. Paleoenecological evidence (Slate and Stevenson, 2000) indicates that the soft-water community presently found in the Refuge interior was more widespread across the predrainage Everglades. 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 more strongly influenced by the limestone bedrock.

Surveys conducted by Swift and 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 ecosystem. Their analysis of species–environment relationships found concentrations of major ions to be the most important factor explaining variation in periphyton taxonomic composition within the Everglades. Surface-water chemistry in the Refuge interior was associated with higher algal species diversity than in other areas due in large part to a species-rich desmid flora. Dominance of diatoms and filamentous chlorophyte algae 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. Swift and Nicholas hypothesized that the low Ca levels in Refuge waters reduced the potential for coprecipitation 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.

Changes in the Refuge periphyton community associated with canal-water intrusion were reported by Gleason et al. (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 µS/cm. Periphyton communities at the three most interior sites (specific conductance <400 µS/cm) were noncalcareous and dominated by a species-rich flora of desmids as well as other species of filamentous chlorophyte algae and diatoms indicative of soft-water, acidic conditions. The remaining two sites (>800 µS/cm) contained a community dominated by calcareous cyanobacteria and diatom species indicative of hard-water conditions. Shifts in species composition with increasing specific conductance included a pronounced change in dominant diatom indicator species (Figure 18). 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
FIGURE 18. 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 (Gleason et al., 1975). See Figure 5 for site locations.

surface water at high-conductivity sites were important factors contributing to observed changes.

Additional survey and monitoring studies have corroborated and expanded these initial findings. McCormick et al. (2000) described patterns in periphyton composition on artificial substrates (glass slides suspended just
below the water surface) at nine 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, whereas 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 (Figure 19). This group comprised between 5 and 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 $\mu$S/cm.

Controlled experimentation supports a cause-effect relationship between mineral concentrations and the composition of Everglades periphyton. Periphyton mats collected from the Refuge interior were incubated under different conductivity regimes and near-natural light and temperature conditions in the laboratory (Sklar et al., 2005). Conductivity treatments were established and maintained using different mixtures of water from interior locations in the Refuge and in a minerotrophic peatland just to the south.
A sustained increase in specific conductance from background levels for the Refuge (<100 µS/cm) to >200 µS/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 µS/cm resulted in a decline of other interior chlorophyte and cyanobacteria taxa.

CONCLUSIONS

Available information on historical water sources and water and soil chemistry indicate that mineral concentrations were lower across large areas of the predrainage Everglades than they are at present. Human alterations to regional hydrology and land use have increased mineral inputs to this ecosystem and converted historically mineral-poor areas of the Everglades into minerotrophic peatlands. Present spatial patterns of mineral chemistry across the Everglades are influenced strongly by inputs of canal water. Additional increases in mineral concentrations may occur in some areas following hydrologic restoration projects because available water sources for these efforts are also likely to be mineral rich.

Although anthropogenic changes in mineral chemistry in south Florida surface waters may be largely irreversible, an understanding of the sensitivity of the Everglades ecosystem to these changes will allow for improved predictions of environmental responses to hydrologic restoration and provide guidelines for protecting remaining mineral-poor portions of the peatland. Evidence presented here indicates that increased mineral loading can alter geochemical processes related to nutrient and contaminant availability as well as the species composition of plant and periphyton communities. Effects of surface-water conductivity on the distribution of fish and aquatic invertebrates have yet to be assessed. Studies that build on these initial data will provide a better foundation for understanding the nature and extent of ecological effects caused by the changing mineral chemistry of this peatland.

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