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ORIGINAL PAPER

The Everglades: North America's subtropical wetland

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Abstract The Everglades is the largest subtropical wetland in the United States. Because of its size, floral and faunal diversity, geological history and hydrological functions on the Florida landscape, the remaining Everglades are considered to be the crown jewel of U.S. wetlands. It is also called a "sentinel wetland" to test our society's resolve for ecosystem restoration. Originally called Pa-hay-okee ("grassy lake") by the American Indians, it was later popularized as the "river of grass" by Marjory Stoneman Douglas. This metaphor unfortunately has led to a simplistic view of the complexities of the Everglades ecosystem and how it functions on the landscape. Often incorrectly referred to as the "marsh" or "swamp," the Everglades is a fen peatland or alkaline mire. These are important distinctions when one considers how different marshes and swamps are from peatlands in terms of their hydrologic controls, biogeochemistry, rate of peat development, plant and animal communities and-importantly-succession patterns. This paper provides a brief review of the geological processes that led to the development of the Everglades, compares historic and current hydrologic flow patterns, assesses nutrient conditions, presents information on vegetation communities and succession patterns, and provides a new peatland classification of the Everglades system, which may help in the development of a more appropriate restoration management framework.

Keywords Peatland · Wetland · Classification · Hydrology · Phosphorus · Biogeochemistry · Fire · Plant communities · Ecosystem management

Introduction

The name Everglades may have come from the term "Never Glades" as first used by Vignoles (1823). It was an almost impenetrable wall of sawgrass "plains" and reptile-infested waters according to the early Spanish and American explorers (Ives 1856; Lodge 2005; Richardson 2008). Originally called Pa-hay-okee ("grassy lake") by the resident Native Americans, the Everglades was later popularized and put forward as a threatened environment that needed federal protection by Marjory Stoneman Douglas's seminal volume (1947). Her book helped establish the Everglades National Park (ENP) and saved the Everglades from total destruction, even though vast areas of it have been destroyed over the past 100 years. Currently, 30% of the original 1,036,000-ha Everglades has been converted to agricultural and urban development, and 350,000 ha of the original area is

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now under state ownership as Water Conservation Areas (WCAs) 1, 2, and 3 for "flood protection, water supply, and allied purposes of navigation and fish and wildlife protection," as mandated by the 1948 U.S. Congressional Flood Control Act (Fig. 1). The remaining 565,000 ha comprise the ENP. The park is the largest Federally owned peatland in the lower 48 states and is the only subtropical wetland ecosystem in the U.S. that is enrolled in the Ramsar Convention of Wetlands of International Importance. The Everglades peatland-like a number of low-gradient wetlands found in the Okavango Delta in Botswana (Gumbricht et al. 2004), boreal peatlands in Canada and the northern USA (Glaser et al. 1981), as well as Costa Rica's Tempisque lower basin (Osland 2009)—have a distinct vegetation pattern related to flow regimes and groundwater interactions (Harvey and McCormick 2009). Because of its size, floral and faunal diversity, geological history and hydrological functions on the Florida landscape, the Everglades is considered by many ecologists and conservationists to be the "sentinel wetland ecosystem" for testing our society's resolve to restore and maintain this magnificent ecosystem as it comes under ever-increasing urban land development pressures, and highly regulated and constantly changing water management regimes (US Army Corps of Engineers 2005; Richardson 2008; Stokstad 2008).

The Everglades, with its mosaic of wetland communities, is often referred to as a marsh or swamp by writers, biologists, and engineers; however, it is correctly identified as a fen peatland or mire by wetland ecologists (Richardson 2000; Rydin and Jeglum 2006; Grunwald 2006; Richardson 2008). "Peatland" is a more generic term used to define a terrain covered by peat, usually to a minimum depth of 30 to 40 cm, while "mire" is a wet terrain dominated by living, peat-forming plants (Sjors 1948; Rydin and Jeglum 2006). The Everglades is not classified as a swamp because it is not a forest-dominated wetland, and it is not technically a marsh because marshes are characterized by standing or slow-moving water with submerged, floating-leaved, or emergent plant cover rooted primarily in mineral soil with nutrient-rich overlying waters (Rydin and Jeglum 2006). That is not to say that the Everglades did not start out nearly 5,000 years ago as a marsh or that some areas today have marsh habitats or tree islands. However, the overall wetland complex is dominated by peat-based soils that historically formed under natural peatland hydrodynamics not present in many areas today due to extensive canal and dike systems. The correct classification of the Everglades is important when one considers how different marshes and swamps are from mires in terms of their hydrologic controls, biogeochemistry, rates of peat accretion, plant and animal communities, and successional and geomorphologic development. Unfortunately, the terms "Everglades mire" or "peatland" by themselves do not reveal the vital and multifaceted hydrologic connections and nutrient sources that historically existed between the Everglades and surface water runoff coming from Lake Okeechobee via the Kissimmee River (Fig. 1), the close connections of groundwater and surface waters in the region due to the karst limestone underlying the wetlands, and most importantly the seasonal influence of the key water source—rainfall (Parker et al. 1955; Richardson 2008; Harvey and McCormick 2009).

However, to do a complete review of the complex interactions of geologic features, hydrologic regimes, and plant and animal communities as well as current restoration plans for the Everglades is beyond the scope of this paper. The reader is referred to a number of comprehensive books on the Everglades by Davis and Ogden (1994), Porter and Porter (2002), Sklar and van der Valk (2002) and Richardson (2008) and to recent papers concerning spatial community complexity and hydrogeological factors controlling water flow in the Everglades (Wu et al. 2006; Givnish et al. 2008; Wetzel et al. 2005; Harvey and McCormick 2009; Harvey et al. 2009). In this paper I briefly (1) provide background on the geologic formation of the Everglades, it soils, and climatic conditions (2) compare and contrast historic and current hydrogeologic and landscape conditions that created the Everglades with an emphasis on the importance of how major shifts in hydrologic regimes and nutrients have altered the current Everglades, (3) describe the major plant communities and successional patterns found in the Everglades, (4) re-classify the Everglades in terms of peatland hydrodynamics systems used worldwide, and (5) give an overview of the current hydrologic restoration plans that are being considered to sustain the Everglades.

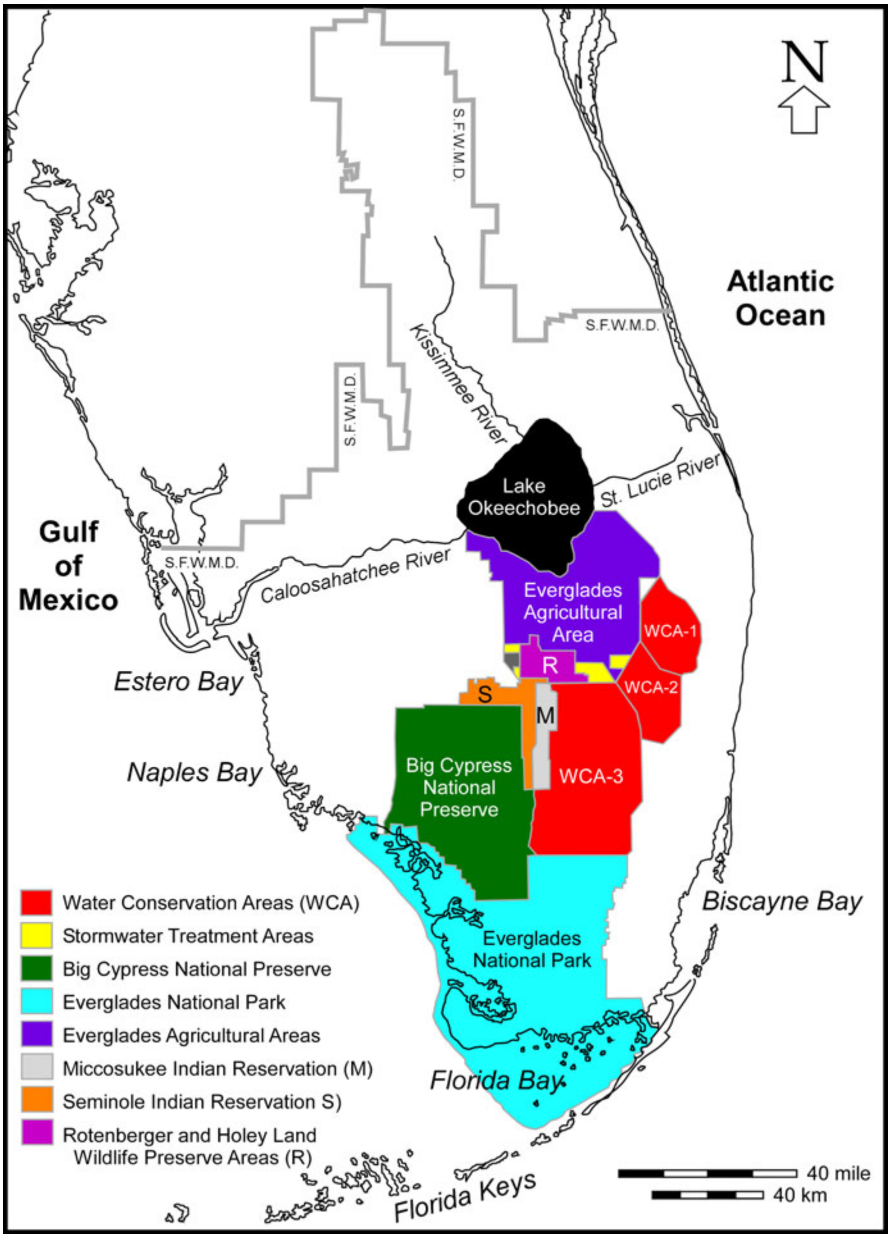


Fig. 1 A Map of the current boundaries of the South Florida Water Management District (SFWMD) that shows the Kissimmee River, Lake Okeechobee and Everglades land use complex. The Everglades is now divided into the state owned water conservation areas (WCAs), Stormwater treatment areas (STAs), the Everglades National Park and Everglades Agricultural Area (EAA). The surrounding areas are the Big Cypress National Preserve, Florida Bay and the developed crop and urban land, a large part of which was former Everglades. Two Indian Reservations are shown to be part of the current Everglades

The Everglades ecosystem

Geology and soils

The Everglades mineral substrate formed a large basin or trough during the Pleistocene, and shallow marine sediments were deposited, primarily during the Sangamon interglacial stage 125,000 YBP (Davis 1943; Parker and Cooke 1944; Gleason 1984). The retreat of the northern U.S. glaciers 18,000–16,000 YBP, blockage of drainage from the Everglades due to rising sea level, a change to a subtropical climate, and the concurrent increase in rainfall allowed for the development of the Everglades as we know it. Three limestone formations underlie the Everglades. The Miami Formation is found in the southern Everglades National Park region; the Anastasia Formation, comprised of sandy calcareous sandstone, is found in the northeast area; and the Fort Thompson Formation, which underlies the northern half to a depth of 50 m, is mostly marine and freshwater marls, limestone, and sandstone (Enos and Perkins 1977).

A geological study of the bedrock that underlies the Everglades shows a differentiation in permeability from north to south. Low-permeability limestone underlies the northern portion of the Everglades basin around Lake Okeechobee and extends into the northern half of WCA-3A and into the western portions of WCA-2A (Gleason 1974; Perkins 1977). In the southern section of WCA-3A and the southeastern section of WCA-2B, there is an abrupt shift to highly permeable limestone (Perkins 1977; Harvey and McCormick 2009). This has important ramifications for the movement and storage of water, peat development, and the establishment of plant communities. According to Gleason (1974), bedrock configuration established the drainage directions prior to peat deposition in the Everglades. For example, Lake Okeechobee flowed through a channel eastward to the area now known as WCA-1, and a deep depression bisected the lower Everglades and created a southwest flow gradient toward Florida Bay (Fig. 2). Gleason (1974) also noted that tree island orientation is correlated with drainage directions expected from bedrock topography. Wu et al. (2006) further suggest it is impossible to understand the spatial complexity or patterns of the tree islands or the ridge and slough communities (note: sloughs are shallow depressions and ridges topographic highs) on the landscape in the Everglades without understanding how water flow patterns affects microtopography.

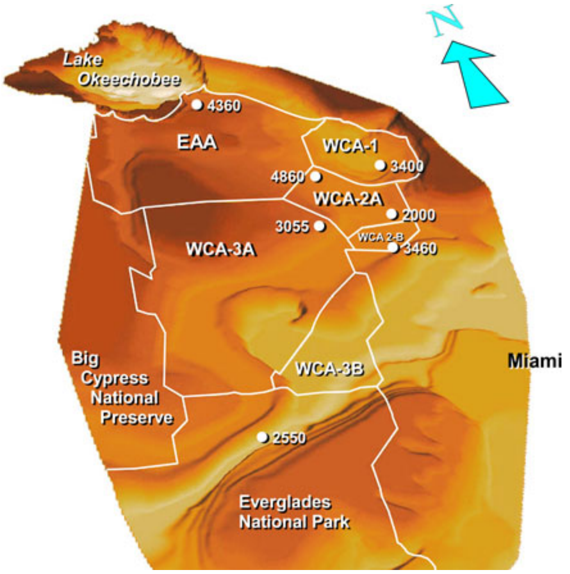


Fig. 2 Bedrock map of the Everglades prior to peat development based on kriging of USGS depth measurements and isopleths maps (Parker et al. 1955; Parker and Cooke 1944). *Darker shades* represent higher regions (bedrock plateau south of Lake Okeechobee, etc.) and *lighter shades* represent depressions or troughs in the bedrock (e.g., in WCA-1 and in lower WCA-3A, WCA-3B, and in the northern portion of the ENP where Taylor slough is now found). Also shown are basal dates of peat from ^{14}C measurements (McDowell et al. 1969; Gleason 1974; Craft and Richardson 1998)

Blocked drainage in the Everglades mire complex was caused by development of limestone substrata of various porosities overlain on a flat basement rock and confined by sandy ridges that developed from sea level rise and fall (Gleason and Stone 1994). Peat buildup from undecomposed plant material then further restricted water flow, resulting in the buildup of highly saturated peat soils. Peat formation in the Everglades began around 5,000 years before present (YBP) in the northern Everglades and around 2,000–3,000 YBP further south (Gleason and Stone 1994). These dates are verified by ^{14}C dating of basal peats in numerous peat cores (Fig. 2). The rate of peat accumulation from north to south has always been of interest to scientists concerned with the formation of the Everglades, and peat cores collected from various sites indicate several interesting trends. First, the Everglades is geologically a relatively young ecosystem. Second, accelerated mass spectrometry ^{14}C dates for samples from depths between 30 and 50 cm indicate that there has been more peat accumulation in the north. For instance, the date estimated for the 36–38 cm depth from a core in ENP was about 2,400 YBP (Richardson and Huvane 2008). However, for the core collected from WCA-2 the date estimated for the interval 33–48 cm was only about 800 YBP. This suggests different patterns of peat initiation and much higher rates of accretion in the northern Everglades compared to the southern. Another indication of this north-to-south trend was an analysis of peat depths in WCA-2, WCA-3 and the ENP (Fig. 1). Depth probes to bedrock taken during grid soil surveys in 2001 throughout WCA-2A averaged 145 ± 37 cm in depth and a range from 62 to 252 cm (Richardson and Huvane 2008). Peat was generally deeper in the northern than the southern part of WCA-2A. Peat depth probes taken in 2000–2003 throughout WCA-3 averaged only 80 ± 36 cm in depth, with a range from 16 to 180 cm. Peat depths were shallowest in the northern part of WCA-3 compared to the southeast corner of WCA-3 (Richardson and Huvane 2008). Severe fires in the north along with dry, peat-oxidizing conditions may have contributed to the shallower peat depths in the northern part of WCA-3. Peat depths taken in 1993 in the ENP are even shallower, with an average depth being less than 27 ± 14 cm (Richardson, unpublished data). Thus, peat depths in the more northern area are deeper where WCA-2 depths were 1.8 and 5.3 times those found in the southern Everglades in WCA-3 and the ENP respectively. The decreasing peat depth data in the south and older basal radiometric dating in the northern Everglades clearly supports a north to south trend in increased peat accumulation and older peat over the past 5,000 years (Fig. 2).

The soils of the Everglades are recent Holocene Histosols and Inceptisols (Gunderson and Loftus 1993). The soils are primarily peats and mucks that had accumulated to a depth of nearly 4 m in the north but are often less than 20 cm deep in portions of the ENP (Stephens and Johnson 1951; Craft and Richardson 2008). As noted earlier, historic northern peat accumulation rates are nearly twice what are currently found. The deepest peats in the southern Everglades are found in depressions and major water flows, such as the Shark River slough. Gleason (1974) dated the basal peats and found that peat deposition began as early as 5,490 ± 90 YBP, but most peats date from 2,000 to 4,500 YBP (Fig. 2). However, the tree islands are more recent formations and date only from 1,300 YBP (Gleason and Stone 1994; Craft and Richardson 1998). The other dominant and oldest soil type is a calcitic mud, an Inceptisol, formed by cyanobacteria (blue–green algae) that reprecipitate calcium carbonate or marl ($CaCO_3$) originally derived from the limestone substrate (Browder et al. 1994). It is found underlying most of the peatlands and has been dated at 6,470 YBP (Gleason and Stone 1994). It is also sometimes found in layers within the peat, indicating periods of short seasonal hydroperiod as compared to the longer period of flooding required for peat formation by macrophytes.

Climate

The subtropical climate of south Florida has hot humid summers, mild winters, and a distinct wet season with 80% of the rainfall falling from mid-May through October (MacVicar and Lin 1984). Harvey and McCormick (2009) report that 81% of the predrainage water budget for the Everglades was from rainfall, with 8% coming from lake overflow, 10% from marginal runoff, and only 1% coming from groundwater. The Everglades has more in common with tropical climates in that a wet/dry season is probably more important to vegetation composition than winter/summer differences in temperature. Daily temperatures average above 27°C from April through October in the northern part of the Everglades and from March to November in the south. Average daily temperatures are above 10°C even in winter, but freezing temperatures do occasionally occur. The key component of climate's control over vegetation patterns and succession is the amount of precipitation. A 110-year weighted average analysis of annual rainfall over south Florida (1895–2005) shows distinct drought and heavy rainfall periods when compared to the long-term average annual rainfall of 1,320 mm per year (Fig. 3). The Everglades underwent distinct periods of drought beginning in the early 1900s lasting through the mid-1920s. There was a similar drought period during the 1970s and 1980s up until about 1990. A long-term wet period began in the 1940s and lasted through the 1960s, broken only briefly in the 1950s. The highest period of rainfall, totaling 1,450 mm, was seen in 1995. Importantly, the Everglades Agricultural Area (EAA), which drains partially into WCA-2, WCA-3 and the Everglades National Park (ENP), the southern most remnant of the original everglades (Fig. 1), have received annual rainfall consistently below the historical rainfall for southern Florida. During the period 1970–1985, the EAA and ENP received less rainfall 80 and 67% of the time, respectively (South Florida Water Management District 1992). Since the 1990s the Everglades have experienced dramatic increases in rainfall, with highest levels occurring in the mid-1990s, often during hurricane events (Fig. 3). These data indicate that the Everglades have experienced both reduced rainfall for extended periods followed by significant rainfall periods that dramatically altered the plant-growing environment (Richardson et al. 2008). These rainfall patterns, when combined with effects of dikes and canal drainage, have resulted in severe drying and flooding of portions of the Everglades with a resultant shift in plant communities. Annual rainfall is the main driver of hydrology, but hurricanes (sustained winds of 120 km h^{-1}) are an important reoccurring event (≅every 3 years) in south Florida. Hurricanes can produce great wind damage and significant increases in annual rainfall and storm surges (Gunderson and Loftus 1993). Thus, extreme hydrologic events like hurricanes and droughts have had significant effects on the water budgets for south Florida and the Everglades. A severe drought occurs on average every 10 years (Abtew et al. 2006). El Niño weather patterns result in greater than average rainfall in Central and South Florida, while La Niña patterns have the opposite effect (Abtew et al. 2006). These shifts in rainfall patterns have also influenced the yearly nutrient loadings and concentrations (especially P) entering the WCAs (South Florida Water Management District 2004, 2005, 2006).

Evapotranspiration (ET) is also an extremely important component of Everglades water patterns. It has been estimated that 70–100% of rainfall exits the Everglades this way (Dohrenwend 1977; Fennema et al. 1994). ET varies across South Florida where lakes, impoundments, and flooded wetlands evaporation losses equal potential ET (Abtew et al. 2006). Higher ET occurs in the southern part of the Everglades compared to areas north of Lake Okeechobee (Richardson and Huvane 2008). However, the temporal variation in ET varies little in South Florida compared to annual rainfall variations (Abtew et al. 2003). The combination of severe variation in rainfall, droughts and hurricanes along with water management plans had a great impact on the hydrologic flow of water in the Everglades landscape.

Hydrology

In 1898 Willoughby reported in his book *Across the Everglades: A Canoe Journey of Exploration* that there were vast amounts of standing water, high dense sawgrass, and numerous upwelling of water from shallow pools in the bedrock. He stated, "All this moving water cannot be accounted for by the rain alone, and the water is too hard for rainwater, so that in all probability more comes from below than above" (Willoughby 1898). This, coupled with the documentation of waterfalls pouring out of the Everglades, upwellings from numerous springs at the edge of the Everglades, and freshwater bubbling up in Biscayne Bay in the early 1900s clearly indicates an Everglades that maintained a large hydrologic freshwater head on the landscape and originally relied heavily on base flow, a much different hydrology than the one we see today. The role Lake Okeechobee played in supplying water to the Everglades was also not well understood (Fig. 1). Historically, lake levels in excess of 20 ft (6 m) were measured in the lake in the 1850s and as late as the early 1900s, and it was reported that when lake levels exceed 22 ft (approximately 20.6 ft NGVD) water would spill over the soil bank on the southern part of the lake into the Everglades (Steinman et al. 2002). Before major alterations and the building of Hoover Dike around the southern part of the lake, Ives (1856) reported in a military survey that at least eight rivers ran directly into the Everglades for 2 or 3 miles (3.2–4.8 km) and disappeared (McCally 1999). Thus, some believed that the periodic overflow of Lake

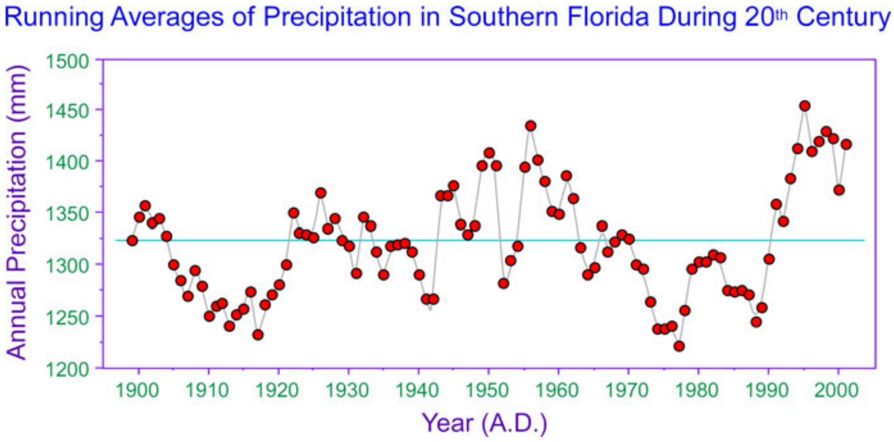


Fig. 3 Annual precipitation (9 point smoothing was used to better show trends) in the Florida Everglades based on data from 1895 to 2005. The average rainfall from 1895 to 2005 is shown with a horizontal line. Data source used was from NOAA for the Florida Everglades and SW Division at (http://www.ncdc.noaa.gov/onlineprod/drought/xmgr.html)

Okeechobee was not the source of water that maintained sheet flow, but rather the rivers that according to early surveys continually supplied the northern Everglades. The more recent evidence does not support true rivers but supports the idea of overflow arms of the lake extending into the dense sawgrass communities found south of the lake. These discrepancies clearly indicate how poorly we understood the hydrologic relationship of the Kissimmee-Lake Okeechobee-Everglades complex. Moreover, the importance of surface and ground water interactions in the Everglades was not really appreciated until the USGS report by Parker et al. (1955), who detailed studies on surface and groundwater flows and storage. Parker clearly showed for the first time the complexities of the hydrologic system that controlled the Everglades and that the extensive canal and dike system installed since the early 1900s (Hofmockel et al. 2008; Romanowicz and Richardson 2008) had significantly altered water storage, surface and groundwater interactions, flow of water, and water depths throughout the Everglades.

The shallow elevation gradient of 1.57–3.16 cm km^{-1} (US Army Corps of Engineers 1994), coupled with deep overlying peat, allows for storage of water during wet periods and a slow release of excess water during dry periods. Recent hydrologic studies in the Everglades have shown that flow across this low-gradient peatland is very slow, with values falling between 0.10 and 0.59 cm s^{-1} in WCA-3 (Harvey et al. 2009) and averaging 0.25 cm s^{-1} in WCA-2 (Romanowicz and Richardson 2008). Importantly, a considerable difference exists in the flow rate and amount water passing through the ridge and slough communities. The flow rate in the ridge community with deeper peat and denser vegetation averaged 0.28 cm s^{-1}, while the shallow sloughs flowed at 0.36 cm s^{-1}, a 29% difference (Harvey et al. 2009). The higher flow rate coupled with the 67% landscape coverage by sloughs in WCA-3 resulted in 86% of the water in WCA-3 flowing through sloughs when tested by Harvey et al. (2009). The importance of this flow difference is not simply the volume of water, since earlier studies by Leonard et al. (2006) and Larsen et al. (2007) demonstrated the importance of this flow in creating higher rates of particulate matter in the water column, which is transported more in sloughs than ridges. These findings suggested a possible theory of ridge buildup from particulate matter in the water column moved from sloughs to ridges during storms and high flow. Most striking in an earlier study was the finding that surface water and subsurface water often flow in different directions. For example, water was measured flowing northeast in the direction of the prevailing wind at rates of 0.4 cm s^{-1} in WCA-2, but subsurface flow followed the hydraulic slope gradient south at 0.2 cm s^{-1} at the bottom depths (Romanowicz and Richardson 2008). When analyzed together these studies show that water flow in the WCAs is now controlled by a combination of surface water and gradient slope, wind at the surface, and opening and closing of water control structures. Importantly the structures create surface water gradients and pulse water events. This suggests that future water management should carefully take into account not only water depth but also frequency and duration of water release inputs.

The effects of dramatic shifts in the water flow at the landscape scale due to development of canals and ditches can be easily appreciated by comparing flows under natural conditions and current water management plans using a Minard-type diagram of the historic surface and groundwater flows based on predictions from the Natural System Model (South Florida Water Management District 1998). In the diagram, the width of the lines shows the amount of water flowing along key points; the direction of flow is shown as well (Tufte 1983). The historical NSM model was run with no canals and dikes in place and then compared with flows measured in the mid 1990s with dikes and flow pumps and gates in operation (Fig. 4; Larsen 1994). Under historic conditions, a balanced and similar annual volume ($\sim$1,481 $\times$ 10^6 m^3) of water was found leaving the Kissimmee Basin flowing into the Everglades National Park (ENP) via the Tamiami Trail. Historically on average only 503 $\times$ 10^6 m^3 of water left Lake Okeechobee annually because of high ET rates in the lake coupled with restricted flow south due to a natural soil berm, dense sawgrass, and no direct outlets to the Caloosahatchee or St. Lucie Rivers. The central Everglades had approximately 1.49 $\times$ 10^6 m^3 of water, of which approximately half or 814 $\times$ 10^6 m^3 exited the Everglades to the Lower East Coast (LEC) yearly (Fig. 4). The historical total discharge for the LEC to the Atlantic was estimated by the NSM to be 1987 $\times$ 10^6 m^3 per year.

By 1994 the annual Everglades water budget was highly regulated, and LEC flows dramatically increased from 1987 $\times$ 10^6 m^3 to 4,579 $\times$ 10^6 m^3

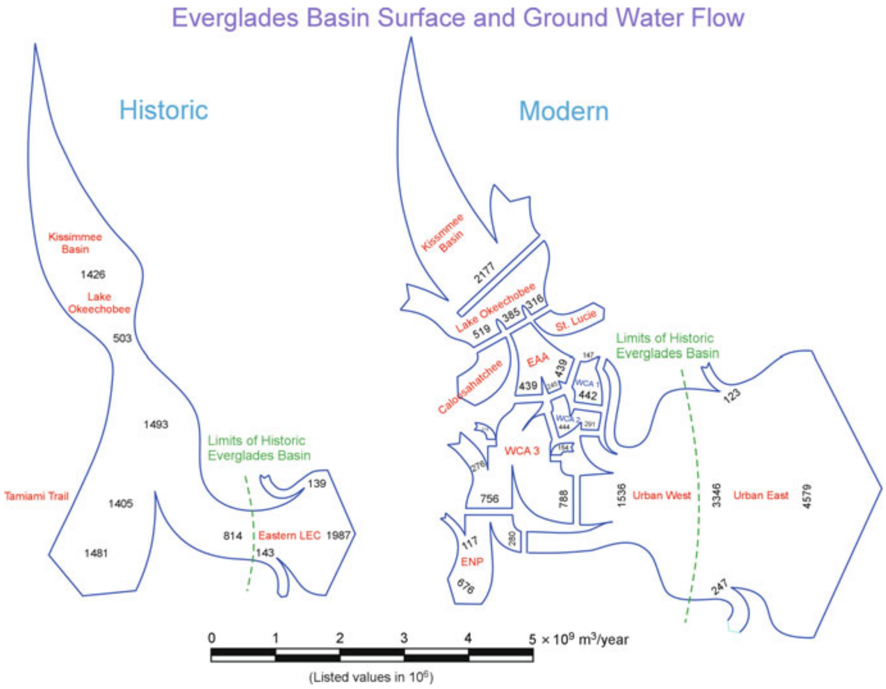


Fig. 4 Minard-type graphic of the historic (before 1880) and modern average annual water flows (based on 1993 SFWMD LEC Report data and Larsen 1994). The line widths are proportional to the volume of the water flows. Values are given as 10^6 m^3 per year (from Richardson and Huvane 2008)

as fresh water was being transported to the Atlantic Ocean via a complex series of canals and pumping stations at the expense of flows into the ENP (Fig. 4). Importantly, water inputs into the ENP were less than half of historic inputs, and flows shifted east to the LEC had more than doubled. The transportation of fresh water to the Atlantic Ocean was orchestrated through directives from the Corps and SFWMD to keep the urban LEC from flooding.

Other important components that affect Everglades hydrology are natural disturbances, which include hurricanes, storms, drought, flood, fire, and freezes. Individual disturbances mutually influence each other (Gunderson 1994). For example, hurricanes and storms have a strong influence on the annual water input and may prohibit the other forms of disturbance such as fire. In the absence of hurricanes or major storms, other disturbances (e.g., drought or fire) may thrive. Fire may be promoted by freezing conditions that kill native species and augment fuel loading (Richardson et al. 2008). Drought periods (low water) and fire also increase nutrient concentrations, especially phosphorus in the Everglades waters (Richardson et al. 1997, Richardson 2008). Moreover, it has been shown that water column TP and TN concentrations are inversely related to water depth (Vaithiyanathan and Richardson 1998). Each storm disturbance and drought represents an important component of the natural system hydrology and nutrient cycles. Although a hydrologic disturbance regime is an unpredictable event, it is a critical ingredient to the persistence and integrity of the Everglades.

Nutrients

In the past two decades over 100 papers have been written on the impacts of nutrient cycling and storage in the Everglades, and many of these are cited and summarized in the books by Davis and Ogden (1994), Porter and Porter (2002) and Richardson (2008). In this paper, I only highlight the main points of those findings. Historically, the Everglades was a P-limited ecosystem that survived on low levels of nutrients primarily from rainfall, limited surface flow, and recycling within the system, especially after fire (Davis 1943; Swift and Nicholas 1987; Richardson 2008). Rainfall input studies by Richardson and Huvane (2008) reported that geometric mean total P concentration in rainfall from 1993 to 1997 was 10.5 μg l^{-1}, almost identical values to those reported by Ahn (1997). Phosphorus deposition showed strong seasonal and interannual variations, which reflect inputs from local fires, large scale burning of sugarcane fields to the north, as well as seasonal and annual differences in rainfall patterns. Annual wet rainfall geometric mean P deposition from 1993 until 1997 was 23.6 mg m^2 $year^{-1}$, which was similar to values measured a various locations in south Florida and around the globe (Richardson and Huvane 2008). The Everglades, as a P-limited system, evolved plant and algal species that can survive under TP water concentrations as low as 5 µg/l (Koch and Reddy 1992; Richardson and Vaithiyanathan 1995; Richardson et al. 1999; Hagerthey et al. 2008). The exception to communities evolving under low P concentrations are tree islands and the vegetation around alligator holes (Davis 1943; Loveless 1959; Steward and Ornes 1975; Craft and Richardson 1993a; Sklar and van der Valk 2002) as well as plant communities adjacent to Lake Okeechobee with its high historical TP concentrations >30 µg l^{-1} (Walker 2000). Another factor maintaining P limitations in the Everglades, unlike northern mires or marshes, is the nitrogen-fixing blue-green algae community (periphyton) found in open-water sloughs. Because of the periphyton community's high rates of nitrogen-fixation, Everglades soils are exceptionally high in nitrogen (2–4% by weight, Craft and Richardson 2008); thus, very high N: P ratios (>100) exist, further driving the system to severe P limitations (Richardson et al. 1999).

Agricultural runoff from the Everglades Agricultural Area (EAA) and Lake Okeechobee (Fig. 1) significantly changed the nutrient inputs and balance in the Everglades after the 1970s, since both contributed water with much higher concentrations of N and P than is typically found in rainfall and historic runoff in the Everglades (Craft and Richardson 1993b; Davis and Ogden 1994; Walker 2000; Richardson and Huvane 2008). A landscape analysis of the P gradient for south Florida showed that the dairy and cattle regions northeast of Lake Okeechobee had by far the highest total P input concentrations between 1973 and 1999, and the P load averaged 498 MT per year. The lake P concentration increased from ~40 µg l^{-1} P in 1973 to ~100 µg l^{-1} P by 1999 (Walker 2000). The average P concentration in water leaving the EAA farmland in the early 1990s was 150 µg l^{-1} P, which was reduced to 115 µg l^{-1} P in the canals and edges of WCA-1 (South Florida Water Management District 1992). Water flowing out of WCA-2 into WCA-3 often contained 40 µg l^{-1} P. However, by the time surface waters reached the structures above the Everglades National Park, concentrations were 10 µg l^{-1} P or lower.

A trend analysis of inflow, interior, and outflow P concentrations over the past 27 years reveals interesting patterns of higher P inputs into the northern WCAs and much lower P inputs into the ENP (Fig. 5). Over 70 µg l^{-1} P flowed into WCA-1 and WCA-2 on average from 1978 until 2000, with some inputs reaching maximum concentrations over 1,400 µg l^{-1} P (South Florida Water Management District 2006). From 2001 until 2004, inflow P concentrations decreased significantly in both WCA-1 and WCA-2. In 2005, input concentrations increased in WCA-1 nearly back to values prior to any Best Management Practices (BMP) implementations. The SFWMD attributes this rise to excess rainfall and runoff due to high hurricane activity in late 2004 and 2005 (South Florida Water Management District 2006). Inputs of P into WCA-3 from1978 until 2000 averaged 36 µg l^{-1} P and had

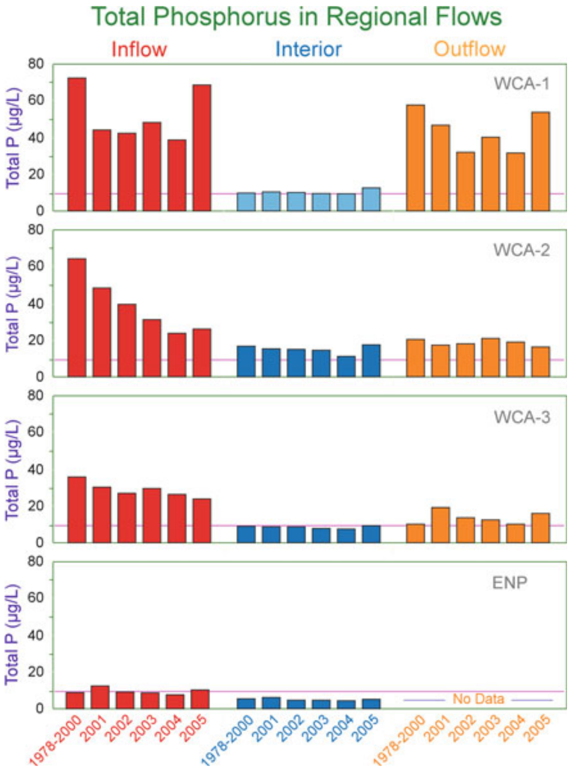


Fig. 5 A comparison of phosphorus input, interior and outflow concentrations from 1978 to 2005 for WCA-1A, WCA-2A, WCA-3A, and the ENP. All values are the annual geometric mean of total phosphorus. Data are from the South Florida Water Management District (2003, 2004, 2005, 2006)

dropped to 24 μg l^{-1} P by 2005. Low-level mean P inputs (8.9 μg l^{-1} P) into the ENP were recorded over the period 1978 to 2000, and values rose only slightly in 2005 to 9.1 μg l^{-1} P. Interior P values were lowest in WCA-3 and ENP throughout the study period, averaging around 10 μg l^{-1} P and 5 μg l^{-1} P, respectively. The SFWMD (2006) reported that interior P concentrations rose during low rainfall periods and droughts and were diluted during the wet season in all areas. WCA-1 had interior values that averaged 10 μg l^{-1} P from 1978 until 2000 and then rose in 2005 to 12.1 μg l^{-1} P. However, interior WCA-2 values were always the highest, averaging 17.1 μg l^{-1} P from 1978 to 2000 then rising slightly to 17.9 μg l^{-1} P in 2005. The rises in 2005 interior P values was attributed to periods of excessive rainfall and periods of soil P release during drought conditions (South Florida Water Management District 2006). However, the fact that WCA-2 interior site P concentrations have virtually remained the same even though inputs have been reduced by >50% may be due to the reflux of the large residual amount of resident P in soil at this site (Reddy and Rao 1983; Richardson 2008).

According to the 2006 SFWMD report, approximately 85% of the P samples collected in 2005 in the entire Everglades (all sites and areas) had values below 50 μg l^{-1} P, 51% were below 15 μg l^{-1} P, and 32% were at or below 10 μg l^{-1} P. These data indicate that the interior sites in the ENP and WCA-3 meet the USEPA criterion of less than or equal to 10 μg l^{-1} P (South Florida Water Management District 2006). However, current inflow P concentrations into WCA-1, WCA-2, and WCA-3 are still far in excess of the approved P criterion, and interior values of WCA-2A have not changed (Fig. 5). More troubling are the high concentrations of P that are still flowing out of the WCAs and toward the ENP. The northern WCAs release far higher P concentrations than WCA-3, but all values are well above the USEPA-approved P criterion even though farm BMPs have been in place for over a decade and Stormwater Treatment Areas (STAs) are now in operation.

Phosphorus loadings from the EAA have been implicated in the replacement of sawgrass by cattail in WCA-1 (Loxahatchee National Wildlife Refuge) and WCA-2 in the early 1980s (Toth 1987, 1988; Belanger et al. 1989; Urban et al. 1993). Belanger et al. (1989) asserted that additions of nutrient-enriched water to WCA-2 have contributed to the invasion of a monotypic cattail community. The high P levels in vegetation, soils, and surface waters of the cattail-dominated areas of WCA-2 suggest that P may be primarily responsible for the invasion of cattails in WCA-2 (Belanger et al. 1989; Richardson and Craft 1993; Craft and Richardson 1997; Richardson et al. 2008). Thus, the control of cattail expansion and community shifts will require an understanding of the effectiveness of the Everglades BMP regulatory P-reduction program since its implementation in 1996 (Fig. 6). Over 1,600 MT of P have been prevented from entering the EPA since 1996, and the predicted P load has been reduced from the baseline period (1978–1988, prior to any treatments or BMPs) average annual loading of 444 MT and P concentrations 173 μg l^{-1} P to 182 MT and 124 μg l^{-1} P by 2005 (South Florida Water Management District 2006). Of note is the sharp reduction in mass P loadings since full implementation of the BMPs in 1996, except for 2000 and 2005. These increases have been attributed to rainfall and weather events by the SFWMD, but they were far below the predicted loads of over 400 MT in those years. Thus the BMP program has had a dramatic effect on reductions of P going into the EPA, but loads are still variable from year to year and will be greatly influenced by the P removal effectiveness of the STAs.

The major hope for reducing P loads into the Everglades in the future was the use of STAs to treat EAA, upstream, and Lake Okeechobee waters prior to their release. The design criteria for these STAs was carefully planned and modeled to determine the correct sizing of the STAs by scientists at the SFWMD (Walker 1995; Walker and Kadlec 2006). To date 6 STAs covering over 16,564 ha have been built, the earliest in operation since 1994–1995 (Fig. 1). They were designed initially around a 1.3 to 1.5 $g.m^2$ $year^{-1}$ loading rate (Richardson 2008). Since their inception they have been estimated to reduced P loadings by 617 MT into the Everglades, and in 2005 all the STAs combined removed 189 MT of P, or 71% of the 268 MT of loadings (South Florida Water Management District 2006). The flow-weighted mean inflow ranged from 247 μg l^{-1} P in STA-1 W to 78 μg l^{-1} P in STA-6 in 2005. Overall mean inflow P averaged 147 μg l^{-1} P and outflow concentration 41 μg l^{-1} P in 2005. Unfortunately, the actual loading rates to some of the STAs during

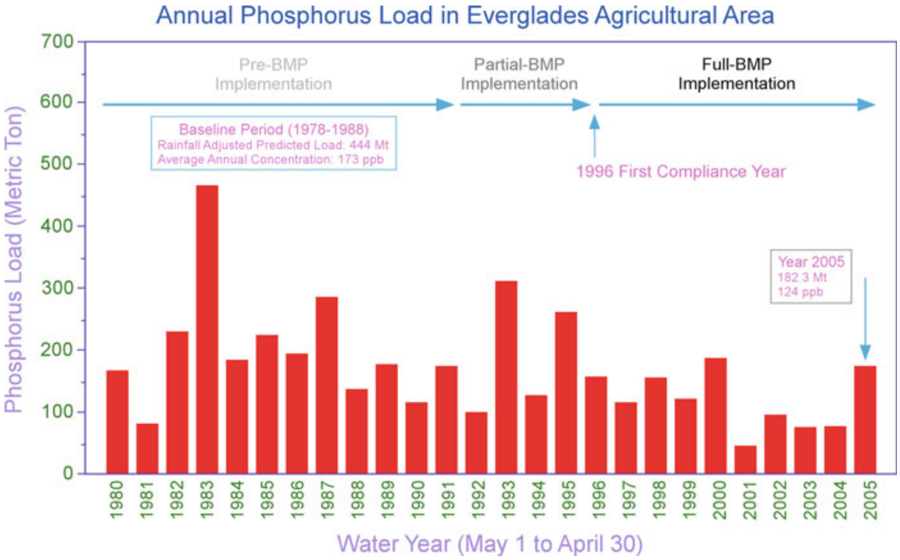


Fig. 6 Total phosphorus loads from the Everglades Agricultural Area (EAA) to the Everglades Protection Area (EPA) from 1980 until 2005. Best management practices (BMP) are denoted as well as the first compliance year. Data from South Florida Water Management District (2006)

operation have greatly exceeded their design loading criteria by more than a factor of two, and outflow P concentrations have also greatly exceeded desired levels (Richardson and Huvane 2008). In fact, in 2005 and 2006 four of the STAs exceeded 50 μg l^{-1} P, and several had output values over 100 μg l^{-1} P. Importantly, only three of the STAs (STA-2, STA-34, and STA-6) were loaded with P near their design criteria, and only these sites came close to outflow concentrations of 20 μg l^{-1} P over the entire period. Moreover, two STAs (STA-2 and STA-6) doubled their concentration output in 2005, which was again attributed to high rainfall and runoff inputs (Richardson 2008).

In terms of P reductions, both the BMPs and the STAs have resulted in a significant decrease of P to the Everglades. However, EAA outflow P concentrations continue to remain high, and STA reductions have not consistently reached the low concentrations 10–15 μg l^{-1} P that had been hoped for by many scientists. While P mass loadings are significantly reduced by more than 50% for the EAA, even in wet years like 2005, P concentrations remain too high for major improvements in the receiving waters as noted in Fig. 5. If the present trend continues and no additional STAs are built, the Everglades will continue to receive unacceptable concentrations and loads of P for the foreseeable future. However, the recent purchase of 75,000 ha of farm land south of Lake Okeechobee provides a fantastic opportunity to provide further nutrient reductions to help meet the new USEPA criterion of 10 μg l^{-1} P for the Everglades by potentially creating a connecting natural water flow system south, expanding the size of the STAs and developing a series of reservoirs to help store water and remove pollutants (Stokstad 2008). This plan could have significant positive consequences for the native biota and ecosystem structure and function if the hydrologic regime is properly restored. However, recent findings have now suggested that sulfur releases from the EAA may be another major factor in plant and microbial community changes due to hydrogen-sulfide toxicity at the plant-soil interface, sulfate exchange releasing additional soil P into the water column as well as the increase in toxic methylmercury from sulfur-reducing bacterial processes (Richardson 2008; Lissner et al. 2003).

Vegetation and plant communities

The only detailed historic vegetation map of the Everglades came from early survey work of J.H. Davis (1943) and was based on his extensive field observations in the late 1930s (Fig. 7). (I was later a student of Dr. Davis at University of Florida, where he first introduced me to the wonders and complexities of the Everglades.) Although, the mapping was done prior to any massive increase in farming in the EAA (Everglades Agriculture Area), many of the large canals had been dug and peat subsidence had started according to his field notes. His map provided distributions of all the major plant communities,

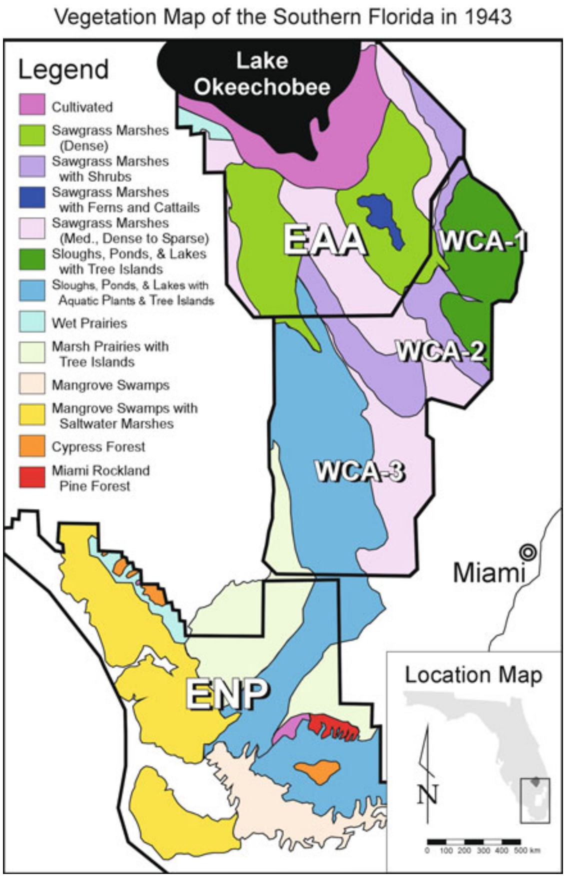


Fig. 7 Historic map of the vegetation communities in the Everglades based on the map of J.H. Davis (1943). The map has been redrawn and simplified from the original map, and the boundaries of the current water conservation areas (WCA-1, WCA-2, WCA-3), the Everglades National Park (ENP), and the Everglades Agricultural Areas have been added

indicated that higher densities of sawgrass stands existed in the northern Everglades, and clearly showed wet prairies and ombrotrophic (rainfall-driven) areas in WCA-1. The map also demarks slough and ponds areas, mangrove swamps, and vast areas of tree islands as well as pointing out a large stand of ferns and cattails (>8,000 ha) in what is now the EAA. The reason for the prevalence of cattails, which are commonly found in P-enriched areas, is unknown because farming had not started to any extent; however, Davis (1943) suggested it may have been related to fires occurring shortly before the mapping, which would have released P from the burned peat (Richardson 2008). Wetzel et al. (2005) have recently shown a large understory population density of ferns on tree islands, areas also with elevated soil P concentrations and a possible source of fern spores for repopulation after a fire.

A complete listing of the plant species characteristic of each vegetation community in the Everglades is shown on Table 1. The dominant species for each community are noted, as well as their growth form. An abbreviated summary of the key ecological components of the major plant community types found in the Everglades fen is presented in the following sections. The common local names for the community types or habitats are used for comparative purposes. These habitats and their spatial distribution make the Everglades one of the more diverse peatland ecosystems in the world (Fig. 7). An aerial overview of tree islands and related communities in the southern Everglades is shown in Fig. 8.

Sawgrass

Sawgrass (*Cladium jamaicense*) is the dominant vegetation community found throughout the freshwater Everglades peatland (Fig. 7). Sawgrass is a sedge that grows to 2–3 m in height on deep peat but only 0.5 m on shallow peat. It was earlier thought that it prefers sites with a fairly constant water depth of 10–20 cm (Toth 1987; Gunderson 1990) but more recent studies show that it grows best in areas with low water to moderate levels and survives nicely under drought conditions (Lissner et al. 2003; Richardson 2008). Its presence in the Everglades is due to its ability to survive fire, low soil nutrient content and occasional freezing (Stewart and Ornes 1975). Sawgrass does not survive well in highly variable deep (>30 cm) water regimes (Toth 1987). The current diking and flooding in portions of WCA-2 as well as in other parts of the Everglades has resulted in the loss of this community due to deep and fluctuating water levels. Sawgrass occurs either in almost pure stands or mixed with a wide variety of other plants, e.g., bulltongue (*Sagittaria lancifolia*), maidencane (*Panicum hemitomon*), pickerelweed (*Pontederia cordata* (Muhl.) Torr.), or cattail (*Typha* spp.) (Loveless 1959). Estimates of the extent of mixed sawgrass areas range from 65 to 70 percent of the remaining Everglades fen (Kushlan 1987; Loveless 1959; Schomer and Drew 1982; Steward and Ornes 1975; Davis 1994). Davis et al. (1994) estimated that pure sawgrass-dominated areas make up only 38% of 417,000 ha of historic sawgrass-dominated areas.

Table 1 Characteristic plant taxa in the vegetation communities of the Everglades ecosystem

Community	Species	Common name	Growth form	
Ponds, slough	(D)	*Nymphaea odorata* Ait.	White water-lily	FL
	(D)	*Nymphoides aquatica* (S.G. Gmel.) Kuntze	Floating hearts	FL
		Nuphar lutea (L.) Sibth. & J.E. Smith	Spatterdock	FL
		Sagittaria lancifolia L.	Lance-leaf arrowhead	E
		Pontederia cordata L.	Pickerelweed	E
		Bacopa caroliniana (Walt.) Robins	Water hyssop	S
		Utricularia foliosa L.	Leafy bladderwort	S
		Utricularia purpurea Walt.	Purple bladderwort	S
Sawgrass “prairie”				
Tall stature	(D)	*Cladium jamaicense* Crantz.	Sawgrass	E
		Justicia angusta (Chapm.) Small	Pineland water-willow	E
		Eleocharis cellulosa Torr.	Gulfcoast spikerush	E
		Typha domingensis Pers.	Southern cattail	E
Intermediate stature	(D)	*Cladium jamaicense* Crantz.	Sawgrass	E
		Crinum americanum L.	Southern swamp-lily	E
		Peltandra virginica (L.) Schott & Endl	Green arum	E
		Hymenocallis latifolia (Herb.) M. Roem.	Mangrove spider-lily	E
		Aeschynomene pratensis Small	Netted shy-leaf	E
		Ipomea sagittata Poir.	Arrow-leaf morning-glory	V
Wet prairies (peat soil)				
Eleocharis marshes	(D)	*Eleocharis cellulosa* Torr.	Coastal spikerush	E
	(D)	*Eleocharis elongata* Champ.	Water spikerush	E
Rhynchospora flats	(D)	*Rhynchospora tracyi* Britt.	Tracy′s beakrush	E
		Rhynchospora inundata (Oakes) Fern.	Horned beakrush	E
Panicum flats	(D)	*Panicum hemitomon* Schult.	Maidencane	E
		Paspalidium geminatum (Forssk.) Stapf	Water panicum	E
		Crinum americanum L.	Southern swamp-lily	E
		Bacopa caroliniana (Walt.) Robins	Water hyssop	S
		Sagittaria lancifolia L.	Lance-leaf arrowhead	E
		Oxypolis filiformis (Walt.) Britt	Water dropwort	E
Wet prairies (marl soil)	(D)	*Cladium jamaicense* Crantz.	Sawgrass	E
	(D)	*Muhlenbergia filipes*	Muhly grass	E
		Schizachyrium rhizomatum (Swallen) Gould	South Florida bluestem	E
		Dichromena colorata (L.) Hitchc.	White-top sedge	E
		Schoenus nigricans L.	Black sedge	E
		Aristida purpurascens Poir. in Lam.	Arrowfeather grass	E
		Panicum tenerum Beyr.	Bluejoint panicum	E
		Rhynchospora divergens Champ. ex M.A.Curtis	Spreading beakrush	E
		Rhynchospora microcarpa Balw. ex Gray	Southern beakrush	E
Tree Island types				
Bayhead	(D)	*Persea borbonia* (L.) Spreng.	Red bay	T
Swamp forest	(D)	*Magnolia virginiana* L.	Sweet bay	T
	(D)	*Ilex cassine* L.	Dahoon holly	T
	(D)	*Salix caroliniana* Michx.	Carolina willow	T

Table 1 continued

Community	Species	Common name	Growth form	
	(D)	*Myrica cerifera* L.	Wax myrtle	T
		Chrysobalanus icaco L.	Coco plum	SH
		Blechnum serrulatum L.C.Richard	Swamp fern	F
		Acrostichum danaeifolium Langsd. & Fisch.	Leather fern	F
		Acer rubrum L.	Red maple (north)	T
		Rhizophora mangle L.	Red mangrove (south)	T
Pond apple forest	(D)	*Annona glabra* L.	Pond apple	T
		Fraxinus caroliniana Mill.	Pop ash	T
		Commelina gigas Small	Climbing day-flower	V
		Cucurbita okeechobeensis (Small) Bailey	Okeechobee gourd	V
		Sambucus simpsonii Rehd. ex Sarg.	Common elderberry	T
		Ficus aurea Nutt.	Florida strangler fig	T
		Baccharis halimifolia L.	Saltbush	SH
		Tillandsia spp.	Air plants	EP
			Orchids	EP
Willow heads	(D)	*Salix caroliniana* Michx.	Carolina willow	T
		Myrica cerifera L.	Wax myrtle	T
		Cephalanthus occidentalis L.	Buttonbush	SH
		Cladium jamaicense Crantz.	Sawgrass	E
Cypress forests		*Taxodium ascendens* Brongn.	Pond cypress	T
		Cladium jamaicense Crantz.	Sawgrass	E
		Schizachyrium rhizomatum (Swallen) Gould	South Florida bluestem	E
		Dichromena colorata (L.) Hitchc.	White-top sedge	G
Hardwood hammock	(D)	*Ficus aurea* Nutt.	Florida strangler fig	T
	(D)	*Bursera simarubra* (L.) Sarg.	Gumbo-limbo	T
	(D)	*Quercus virginiana* P.Mill.	Live oak	T
	(D)	*Lysiloma litisiliquum*	Wild tamarind	T
		Sabal palmetto (Walt.) Lodd.	Cabbage palm	T
		Celtis laevigata Willd.	Hackberry, Sugarberry	T
		Morus rubra L.	Red mulberry	T
		Citrus spp.	Citrus	T
		Diospyros virginiana L.	Common persimmon	T
		Swietenia mahogani (L.) Jacq	West Indian mahogany	T
		Acoelorraphe wrightii (Griseb. & Wendl.)	Paurotis palm	T
		Roystonea regia (Kunth) O.F.Cook	Florida royal palm	T
Successional shrub		*Trema micranthum* (L.) Blume	Jamaican nettletree	T
		Baccharis halimifolia L.	Saltbush	SH
		Myrica cerifera L.	Wax myrtle	T
		Pteridium aquilinum	Bracken fern	F

Dominant species are indicated by (D). Nomenclature follows Long and Lakela (1971), Avery and Loope (1980), and Tobe et al. (1998)

Common regional names are used to describe the community types found in the Everglades fen. Modified from Gunderson and Loftus (1993)

E emergent, *EP* epiphyte, *F* fern, *FL* floating-leaved, *G* grass, *S* submergent, *SH* shrub, *T* tree, *V* vine

Fig. 8 Aerial view of tree islands in the southern Everglades. Note the surrounding sloughs and sawgrass stands with ponds (small circular deep water areas) scattered throughout and often created by fire and maintained by alligator activity. (Photo by Curtis J. Richardson)

Wet prairies

Wet prairies are among the common vegetation types in the northern Everglades. Often referred to as "flats," these freshwater communities are characterized by low stature and emergent plant species, and they are found in the northern and central Everglades in conjunction with tree islands (Goodrick 1984; Gunderson and Loftus 1993). Wet prairies exist on both peat and marl soil. Variation in species composition is shown on Table 1. The wet prairies in the south found on calcitic mud or marl occur on higher and drier sites but are wet 3 to 7 months of the year (Davis 1943; Gunderson and Loftus 1993). The water depth of these areas is generally less than sloughs but deeper than sawgrass; thus, the vegetation seldom burns. Loveless (1959) described three well defined wet prairie associations in the northern Everglades: (1) *Rhynchospora* flats, (2) *Panicum* flats and (3) *Eleocharis* flats. These plant associations are composed primarily of Tracey's horned rush (*Rhynchospora tracyi*), gulfcoast spikerush (*Eleocharis cellulosa*)—both sedges—and maidencane (*Panicum hemitomon*), a wetland panic grass. However, many other plant species may also be present on these flats, depending upon hydrological conditions, the season of the year, and soil type. Wet prairies usually dry out on an annual basis and are transition zone between sawgrass areas and sloughs (Goodrick 1984). Wet prairies require seasonal inundation with standing water present for 6 to 10 months of the year (Schomer and Drew 1982). Seasonal drying of the moist soil conditions in these communities is required for seed germination and establishment of new seedlings (Dineen 1972).

Sloughs

Sloughs are open water marshy type areas, found primarily in the northeast and south-central Everglades, which are dominated by floating-leaved aquatic plants with some emergent plants of low stature (Davis 1943; Loveless 1959). Sloughs are among the most widespread community types in the Everglades. Aquatic sloughs represent the lowest elevation of the Everglades ecosystem, except for ponds. They have deep water levels averaging 30 cm annually and longer inundation periods than other Everglades wetland communities (Gunderson and Loftus 1993). Sloughs occur throughout the Everglades, with the largest pond-slough systems occurring in the Everglades National Park (Shark River and Taylor Sloughs) and portions of the northern Everglades (McPherson et al. 1976; Fig. 7). Sloughs are narrow drainage channels that are water-filled, or at least wet, most of the year. The "valleys" of these channels average only a few cm to 60 cm below the elevation of adjacent sawgrass areas. Not as extensive as they once were, some sloughs apparently have been replaced by either sawgrass or wax myrtle and willow stands. Cattail has also filled many of the sloughs in the enriched areas of the northern Everglades (Rader and Richardson 1992; Urban et al. 1993; Craft and Richardson 1997; Richardson et al. 2008). Further reduction in slough areas has been due to artificial drainage and the increase in sawgrass in the southern Everglades (Loveless 1959; Davis et al. 1994). Sloughs are easily recognized by their water drainage patterns and by characteristic plant species, such as white waterlily (*Nymphaea odorata*), floating hearts (*Nymphoides peltata*), bladderworts (*Utricularia* spp.), spikerushes (*Eleocharis* spp.), spatterdock (*Nuphar lutea*), or water hyssop (*Bacopa caroliniana*) (Davis 1943; Loveless 1959; Van Meter-Kasanof 1973; Gunderson and Loftus 1993; Table 1).

Sloughs and wet prairies are ecologically important in the Everglades landscape. During the dry season, sloughs serve as important feeding areas and habitats for Everglades wildlife. As the higher elevation wet prairies dry out, sloughs provide refuge for aquatic invertebrates and fish. This high concentration of aquatic life, in turn, makes sloughs important feeding areas for Everglades wading bird populations. When the fen is re-flooded, the animals that have survived in the sloughs repopulate the fen as water level rises (Loveless 1959). The slough/wet prairie sawgrass mosaic covers 271,000 ha (44%) of the remaining 618,000 ha area of the Everglades (Davis et al. 1994). The plant species diversity tends to be higher in sloughs and wet prairie communities than in pure sawgrass and cattail communities (South Florida Water Management District 1992; Craft et al. 1995). The abundance of macroinvertebrates, fish, and wading birds is also higher in sloughs than in sawgrass and cattail communities (South Florida Water Management District 1992; Rader and Richardson 1992, 1994; Davis and Ogden 1994).

Ponds

Ponds are small, open water areas that are scattered throughout most of the Everglades and represent the deepest water regime. They occur in bedrock depressions where fire has burned away the peat (Loveless 1959). Alligator activity often maintains open water in the ponds, which the locals call “alligator holes” for this reason. Ponds are wet except in the driest years; thus, they are important habitats for animals, especially birds. These holes have borders of water lilies *(Nymphaea* spp.), spatterdock (*Nuphar* spp.), pickerelweed (*Pontederia cordata*), and woody species such as Carolina willow (*Salix caroliniana*) or water primrose (*Ludwigia peruviana* (L.) Hara) (Gunderson and Loftus 1993).

Tree islands (bayhead/swamp forests)

Everglades broadleaf, hardwood forests are locally called tree islands. The term refers to a variety of tree clusters that stand above a matrix of shorter vegetation (Craighead 1984). They cover less than 5% of the Everglades but number in the thousands, ranging in size from 10 m^2 to >70 ha, with elevations ranging from 0.2 m to 1.5 m above the sloughs (Sklar and van der Valk 2002). Tree islands occur throughout the entire Everglades but are most abundant in the central part of WCA-1 (Loveless 1959). Tree islands may be either bayhead (swamp forests) or hammocks (upland forest), or a combination of the two (Davis 1943; Gunderson and Loftus 1993; Wetzel et al. 2005). The dominant species in each type of forest is shown on Table 1. Red bay (*Persea borbonia*), swamp bay (*Magnolia virginiana*), dahoon holly (*Ilex cassine*), Carolina willow (*Salix caroliniana*), and wax myrtle (*Myrica cerifera*) dominate the swamp forests (Pinion et al. 2008). The large tree islands have a teardrop shape with the main axis paralleling the flow of water. The small islands ($\cong$100 m^2) are usually round. The forests are found on the highest sites in the Everglades on a peat classified as Gandy peat (Davis 1943; Loveless 1959). The sites are wet 2 to 6 months/year, but in drought conditions these systems are very susceptible to burning (Gunderson and Loftus 1993; Wetzel et al. 2005). The soil P nutrient content of tree islands is usually much higher (>1,000 mg kg^{-1} vs 500 mg kg^{-1} of P) than the surrounding landscape (Wetzel et al. 2005; Richardson 2008).

Willow heads, cypress forests, pond apple forests, and hardwood upland hammocks

These forest types comprise only a small area of the Everglades. They include interesting communities with distinct species (Table 1). The pond apple forest (*Annona glabra*) existed primarily south of Lake Okeechobee in a band 5 km wide (Davis 1943). The land has been totally developed for agriculture and now the species only exists in small, scattered stands. Willow heads exist throughout the Everglades in monotypic stands (Loveless 1959). They exist in fire-disturbed areas, as well as around alligator holes. The upland hardwood hammocks are dominated by broadleaf hardwood trees of both temperate and tropical origin (Table 1). Dominant trees include live oak (*Quercus virginiana*), gumbo limbo (*Bursera simaruba*), sabal palm (*Sabal palmetto*), and strangler fig (*Ficus aurea*). The cypress forests are found only in the southwestern Everglades and are dominant in the adjacent Big Cypress National Preserve. Pond cypress (*Taxodium ascendens*) are very short and occur as widely scattered individuals displaying very stunted growth. They are often called dwarf or hat rack cypress and seldom reach heights over 3–5 m.

Periphyton

Periphyton and algal mats are seldom thought of as “valuable” ecological resources or even listed among vegetation community species. Several authors, however, have pointed out an important role of the calcareous periphyton and algal mats characteristic of sloughs and wet prairies in the Everglades (Pan et al. 2000). Components of the periphyton/algal mat (especially diatoms) are high-quality food for some animals (Browder et al. 1981; Browder et al. 1994). Photosynthesis by the algae in sloughs can raise daytime dissolved oxygen concentrations and pH much higher (7.5 to >10) than in adjacent sawgrass stands (Belanger et al. 1989; Rader and Richardson 1992, Richardson 2008). Also, the calcareous periphyton deposits marl (calcitic mud), the second most common soil sediment type (190,000 ha) in the Everglades (Gleason and Spackman 1974; Davis et al. 1994).

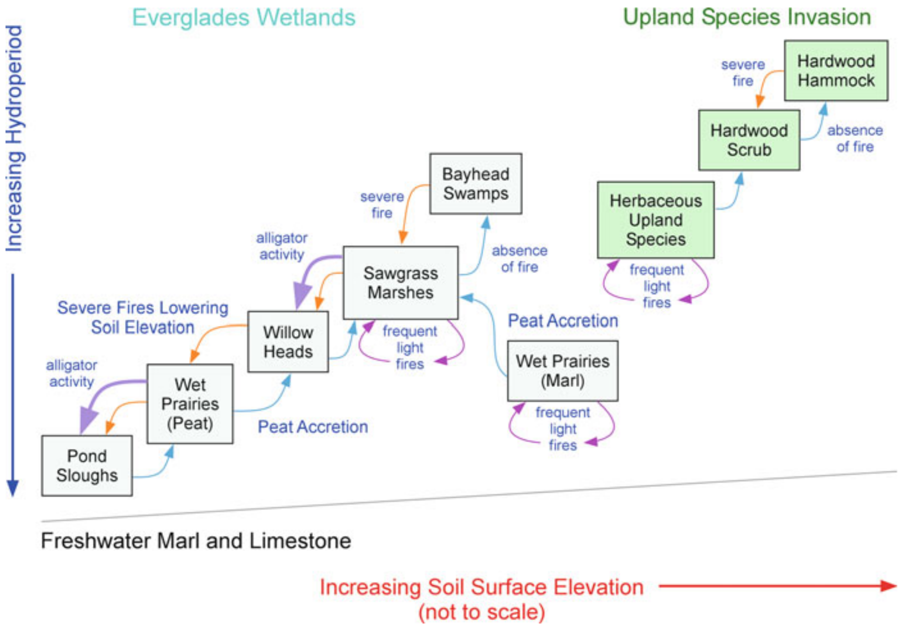
Three types of calcareous periphyton are known in the southern Everglades: calcareous blue-green, calcareous diatom-rich, and calcareous green (Browder et al. 1994). A defining feature of all calcareous periphyton is their high inorganic component, no less than 49% by mass (Browder et al. 1981, 1982; Vymazal and Richardson 1995). Periphyton is abundant in areas of the Everglades that retain the historic oligotrophic conditions of the marsh. In these areas periphyton biomass on an areal basis can reach values that are comparable to or higher than that of macrophytes. Gleason and Spackman (1974) reported total periphyton biomass (excluding the epipelon) in WCA-1 in the range of 40 to 225 g AFDM m^{-2} and up to 447 g DM m^{-2}. Van Meter (1965) reported DM up to 351 g m^{-2} from Taylor and Shark River sloughs in Everglades National Park (ENP). Also Browder et al. (1982) reported up to 2,682 g DM m^{-2} and 526 g AFDM m^{-2} from open water areas of southern Everglades ENP. The highest rates of periphyton productivity in the Everglades usually occur in sloughs and *Eleocharis* stands. McCormick et al. (1998) found areal periphyton biomass in the range of 100 to 1,600 g AFDM m^{-2} in oligotrophic sloughs and in stands of *Eleocharis*, but periphyton biomass was low in adjacent sawgrass (*Cladium jamaicense*) stands (7–52 g AFDM m^{-2}). Periphyton is also not found in *Typha and Utricularia foliosa* dominated communities. Also Vymazal and Richardson (Richardson et al. 2008) found periphyton biomass in southern WCA-2 sloughs up to 3,300 g DM m^{-2} and 1,340 g AFDM m^{-2}.

Everglades succession

Historically, the primary factor controlling long-term development of Everglades plant communities was climate (Richardson and Huvane 2008). The amount and seasonal distribution of rainfall from year to year controlled the hydrologic dynamics (flow rates, water depth and evaporation) of the fen system. The hydrologic conditions in turn controlled the fire patterns. The native seed bank was responsible for the regeneration of endemic plant communities once they were disturbed or altered (van der Valk and Rosburg 1997). This traditional view of natural succession in the Everglades was summarized by Gunderson and Loftus (1993), who suggest that the succession pattern of Everglades communities was influenced mostly by disturbance to the hydrology and, in turn, fire frequency and intensity. They developed a model of the plant communities along elevation gradients that translates directly into a hydrologic depth gradient, which controls fire intensity and frequency (Fig. 9). To some degree this model was based on an earlier model by Duever et al. (1976), who suggested that succession patterns and rates of vegetation change in southern Florida communities were influenced by hydroperiod and number of years since fire.

The gradual build-up of marl soil or peat via accretion (1–2 mm/year, Craft and Richardson 1993a) results in the gradual increase in elevation, which changes the hydroperiod for the species. In other areas limestone bedrock outcrops elevate the plant communities above the surrounding landscape, which is also dotted with peat- or marl- filled depressions or deeper holes in the karst topography. Ponds are the deepest and wettest sites, and soil accretion eventually allows them to develop into wet prairie communities, then willow heads and even sawgrass if not severely burned (Fig. 9). Frequent light fires have little effect on this successional sequence. Severe fires burn the peat soil and lower the sites, which results in a reversal of this sequence and moves the communities back to wetter habitats. The lack of fire due to drought or drainage allows for the invasion of upland macrophytes, scrub, and hardwood species, although dry conditions will increase the probability of severe fires.

Fig. 9 Succession patterns related to fire and hydroperiod in the Everglades. Modified from Richardson 2000



What is not incorporated into this model is how the influence of differential water flow rates, particulate transport, deposition through sloughs versus ridges, and the role that slower peat decomposition and net accumulation rates in wetter slough sites versus drier ridge sites might have on the development of the slough-ridge-tree island patterns seen in the Everglades (Ogden 2005; Wu et al. 2006; Givnish et al. 2008; Harvey et al. 2009). Other studies have revealed that tree islands are phosphorus “hot spots” on the landscape, i.e., they act as a reservoir of P on the landscape due to the transfer of P from low concentration surrounding areas by roosting birds and predators (Sklar and van der Valk 2002; Wetzel et al. 2005). The storage and release of high P concentrations from the tree islands has important effects on the ecological succession patterns of the Everglades, but they that are not well understood. We do know that the southern tail ends of tree islands are often areas of higher sawgrass productivity due to the release of P and that burning of tree islands also releases large amounts of P to downstream areas (Givnish et al. 2008; Richardson 2008). All these factors and several more were considered in a study by Givnish et al. (2008) that proposed a self assembly model with four major components explaining the patterned Everglades landscape found in WCA-3. The most important factors were local substrate height, woody plant invasion, subsequent P transport from nesting predators nesting on taller tree islands with ensuing downstream nutrient leakage, and water flow-induced feedback against total raised area. What was interesting in this study of numerous components controlling landscape pattern was the fact that water depth alone was the strong correlate with vegetation composition, thus supporting the earlier contention by Duever (1976) and Gunderson and Loftus (1993) that hydroperiod is a key driver of succession. However, similar communities are also found at very different water levels and hydroperiods (Givnish et al. 2008). This finding, along with a wide range of ridge and slough patterns, may be explained in part by the presence of both natural and deteriorating community states caused by dramatic anthropogenic alterations in hydrology and nutrient inputs (Newman et al. 1998; Wu et al. 2006; Hofmockel et al. 2008). This implies that disturbances have altered the normal successional dynamics of the Everglades and quantifying the process is now far more complex then originally thought.

The main difficulty for ecologists in determining future successional paths is in separating the influence of primary climate-driven factors like rainfall, hydroperiod, and fire from the secondary human factors of drainage and flooding, nutrient additions, site disturbance, and exotic species invasions. Moreover, the influence of anthropogenic inputs of nutrients and water varies greatly in each portion of the

Everglades, depending on proximity to canal input structures, mode of delivery (i.e., point or non-point source) and whether water delivery is seasonally pulsed or continuously released (Richardson 2008). In other regions like WCA-3, vast stands of exotic species, such as *Melaleuca quinquenervia* and *Schinus terebinthifolius* (Brazilian pepper) provide a seed source for the ever-increasing spread of these species, although intensive and expensive control measures are underway by state and Federal agencies.

In summary, these studies collectively suggest that restoration of the Everglades community landscape and the return to more normal succession patterns is dependent primarily on the creation of natural hydroperiods and hydropatterns that must include periods of drought, and fire. These conditions must be based on the ecological requirements of the dominant species of each community on the landscape. Of course, the reduction of P input and other ions to historic levels is critical to the restoration effort, as is the removal of the exotic species.

Hydrogeologic reclassification of the Everglades

To properly restore and manage this wetland complex a more comprehensive understanding of the original hydrologic and nutrient regimes that formed the Everglades is needed. One way to approach this is to use the historical plant communities (Fig. 7) to reestablish the peatland water classes (Fig. 10a) that existed prior to human development and use this information to provide insights into the sources and flow of water across the landscape and provide some indication of initial nutrient status and potential differences in these classes.

It has long been recognized that the origin of mire water is a major factor controlling peatland development (Du Rietz 1954). Complex environmental gradients caused by the geological substrate, hydrologic flows, and nutrient inputs were responsible for the distinct formation of the Everglades mire peat types and the north-to-south decrease in peat depths described earlier. These formation features help

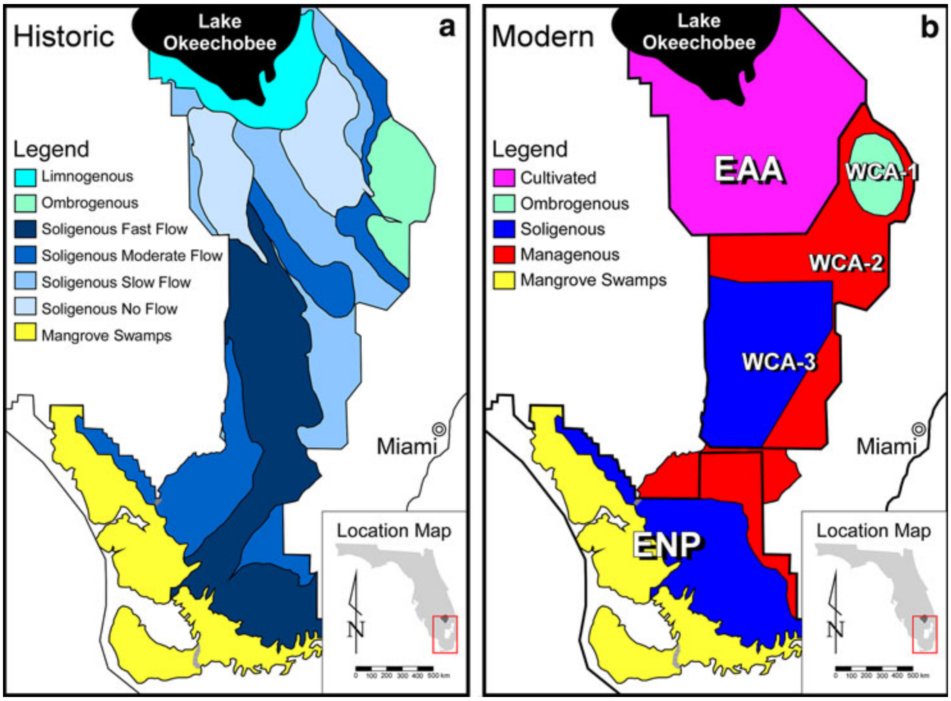


Fig. 10 **a** A comparison of hydrologic peatland classifications in the historic Everglades (1000 YBP) with **b** the present day (modern) Everglades water flow classes. Shown are the general categories of ombrotrophy and hydrologic flow, systems that control types of peatland formation

define its classification. The degree of wetness and aeration, along with gradients of calcium, salinity, pH, and nutrients, controlled the early development of the plant communities (Richardson 2008). For example, the Everglades is often described as a phosphorus limited rainfall-driven ecosystem, which would normally classify it as an ombrogenous peatland (nourished only by precipitation). To emphasize the chemical source driving productivity, wetland ecologists today refer to ombrogenous sites as ombrotrophic peatlands. However, due to the size and complexity of the Everglades it cannot be easily placed into a single classification. In the past thousand years before drainage ditches and peat oxidation took place, ombrotrophy may have been true for many portions of the Everglades, but it is relevant today only for the raised center portion of the Loxahatchee (WCA-1, Fig. 10b). Currently large portions of the Everglades are now nourished by waters that have passed over or through calcareous mineral parent soils and are then released through canal gate structures (Stephens and Johnson 1951; Romanowicz and Richardson 2008). Chemistry profiles and gradients found within the Everglades (Cooper et al. 2008; Richardson et al. 2008) make it clear that portions of the Everglades are currently nourished by calcium-laden mineral groundwater and should be referred to as minerogenous or in modern terms are minerotrophic systems (Richardson 1995; Vaithiyanathan and Richardson, 1997). Thus, the current Everglades ecosystem is not simply rainfall driven. Supporting this is a recent modeling study by Harvey and McCormick (2009), who report that after canals were in place rainfall dropped from 81 to 66% of the input water budget, while surface water flows increased from 18 to 33%. Importantly, they showed net recharge of groundwater increased after development from 1 to 16% to areas outside the Everglades.

To better categorize these changes I have further defined the peatland in terms of water flow regimes. The term minerogenous can be further divided into major hydrologic systems know as topogenous, soligenous or limnogenous peatlands (von Post and Granlund 1926; Sjors 1948). Topogenous peatlands have flat water tables located in basins with no outlet or a single outlet and inlet. Soligenous mires have a slope with directional water flow through the peat or surface. Limnogenous peatlands are located along lakes and streams and are flooded by these waters (Rydin and Jeglum 2006). To simplify terminology, many mire ecologists would follow the convention of using the term fen for minerogenous and bog for the ombrogenous types. Thus, historically the Everglades fen would have had several types of dominant hydrologic systems. For example, historically a limnogenous peatland was located along the southern edge of Lake Okeechobee, but it no longer exists due to the building of the Hoover dike in the 1930s and the conversion of the area to farmland (Fig. 10b). The main hydrologic system for the Everglades would have been classified as soligenous with a minor slope and water flowing generally south (Parker et al. 1955 Harvey and McCormick 2009). The center portions of WCA-1 would have originally (>5,000 YBP) been topogenous (known originally as the Loxahatchee trench), eventually evolving into the ombrotrophic system (domed peat system) it is today (Fig. 10b). Today most of the Everglades would be loosely classified as soligenous, but in reality it is almost a totally managed system and should be reclassified as managenous (managed water flow), the exceptions being the lower part of the ENP and maybe the center of WCA-1A (Fig. 10b).

The Everglades may also be further classified based on nutrient gradients. The terms oligotrophic, mesotrophic, and eutrophic have been adapted from limnology and used to further explain gradients of increasing productivity due to increasing nutrient availability, especially N and P. The oligotrophic class is somewhat broader than ombrotrophic and includes minerotrophic sites with low pH and underlain by nutrient poor sandy soils as found in pocosins in North Carolina (Bridgham and Richardson 1993). However, there are sites like the Everglades that would be classified as oligotrophic (low productivity) in minerotrophic conditions with very high pH and Ca content, because P has become limiting due to adsorption to Ca and high N-to-P ratios (Richardson and Vaithiyanathan 1995; Richardson et al. 1999; Richardson 2008).

These differences in water source and nutrient conditions for the Everglades peatland (Fig. 10ab) show that an understanding of the hydrologic equivalence concept proposed by Bedford (1996) along with an assessment of nutrient conditions will be essential to any restoration effort. The hydrologic equivalence concept proposes that hydrologic conditions similar to those of the original ecosystem type must be restored on the landscape to restore equivalent ecosystem functions. Thus, peatland hydrologic equivalence will have to be considered in the restoration of the modern Everglades if we ever hope to maintain the diversity of Everglades habitats and communities. For example, care must be taken to maintain the ombrogenous portions of the Everglades like WCA-1, reestablish limnogenous peatlands south of Lake Okeechobee, recreate conditions for soligenous peatlands where topographically possible, and reduce managenous water flow conditions (water pumping and release across narrow outlets) within portion of the Glades. Unfortunately, hydrologic equivalence concepts for peatlands were not been fully considered in the original restoration plans (US Army Corps of Engineers 1999). However, the previously mentioned purchase of farmland south of Lake Okeechobee to reconnect the lake and the Everglades provides a new opportunity for the restoration of peatland hydrologic and nutrient conditions. However, care must be taken since the farmland soil elevation has subsided below that of the remaining downstream Everglades, which presents significant hydrologic flow problems and the farmland soils are laden with nutrients, which will require significant increases in the size of storm water treatment area.

Future water management plans

To help overcome some of the major water management problems of past plans, the Central and Southern Florida Project Comprehensive Review Study (The Restudy) was undertaken by the Corps of Engineers under the Water Resource Development Acts of 1992 and 1996. The Corps was tasked with developing a comprehensive plan to restore and preserve the south Florida natural ecosystem while enhancing water supplies and maintaining flood protection. Restoration of the Everglades ecosystem was the key purpose of the plan, but as required by law the plan also provided for necessary water-related needs of the region, including urban and agricultural water supply and flood protection. The Restudy Plan emphasized four key problems: (1) the reduction in total area of the Everglades ecosystem by 50%, (2) the reduction of water flows to the Everglades by 70%, (3) the deterioration of water quality, and (4) the reduction and damage of natural habitats, such that 68 Everglades species were endangered. The plan was to be based on scientific research to correctly time the return of the right quantity and quality of water to each habitat and develop a flexible and adaptive approach that was multi-agency/multidisciplinary in nature. Key to the plan was the removal of 400 km of dikes and levees, the construction of new filter wetlands, and the use of hundreds of underground aquifer storage and recovery wells over a 20-year period. The benefits were that 80% of the “new or retrieved” water was to be sent to the ecosystem and 94% of pre-drainage flows returned to the ENP while maintaining flood control and water supply for a sustainable south Florida. The implementation plan was to achieve ecosystem restoration as soon as possible and to have more than 50% of the hydrologic restoration completed by 2010. The overall plan was to take over 30 years at an estimated cost of $7.8 billion, with costs to be shared by the State of Florida and the Federal Government. These costs have now ballooned to over $11 billion (Stokstad 2008).

The Comprehensive Everglades Restoration Plan (CERP 2005, Richardson 2008) to store, pump, and flow massive amounts of water into the Everglades and create 87,668 ha of storage reservoirs was designed to restore more historic natural flow to the Everglades complex, reduce current flow to the Atlantic Ocean and the Gulf of Mexico, and increase water volume to the ENP without drowning tree islands in the northern and central WCAs (Kloor 2000; Fig. 11). The plan proposed flows and allocations that would, when implemented, result in a 20% reduction per year of Lower East Coast (LEC) losses to the Atlantic Ocean with new environmental water allocated to the ENP. Flows of 2.025×10^6 m^3 per year into Lake Okeechobee were projected to be near 1994 levels, but outflows to the Caloosahatchee were doubled from 519×10^6 m^3 to $1{,}029 \times 10^6$ m^3 per year. EAA makeup water from the lake in the amount of 203×10^6 m^3 per year was also planned for additions to the WCAs. Almost immediately the plan was under attack from environmentalists and scientists who were concerned that too little water was being allocated to the ENP, although under the plan more water is allocated than in the past (Kloor 2000). Another key concern was that moving extra water to the park would come at the expense of the central

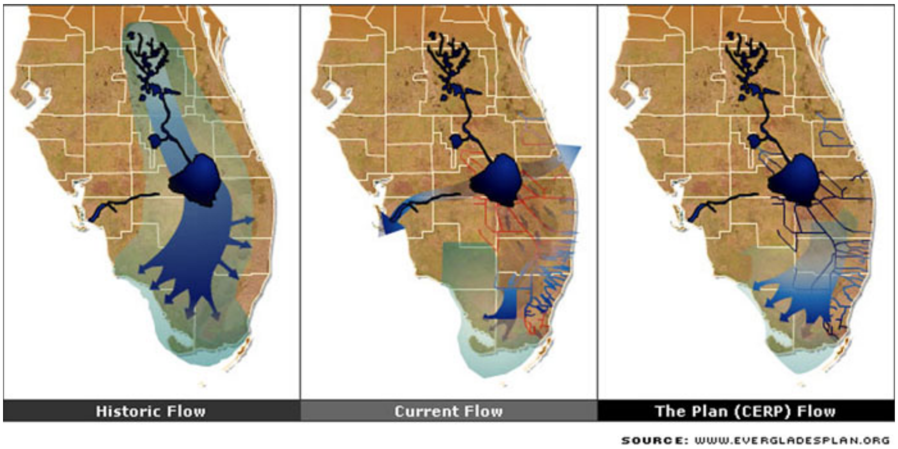


Fig. 11 Historic, current, and planned water flow conditions under CERP in the Everglades Watershed (Source: http://www.evergladesplan.org)

Everglades ecology. These areas would have to bear the increased flow and water depths, which in all likelihood would damage the tree island habitats (Hofmockel et al. 2008) and lead to a loss of key species. Leading the objections were the Miccosukee tribe, who have over 100,000 ha of holdings in the central Everglades and view the tree islands as key to their hunting and ceremonies. The Miccosukee also worried that the extra water would be laden with excess nutrients (Kloor 2000). A case in point is the EAA makeup water, which is currently too high in nutrients to meet the current standards (Richardson 2008).

Importantly, the original CERP plan (CERP 2005) is continually being altered following the concept of adaptive management, and in recent years more consideration is being given to studies on hydrologic flow conditions and its effects by Wu et al. (2006), Givnish et al. (2008), Wetzel et al. (2005), Harvey and McCormick (2009), and Harvey et al. (2009). However, the correct timing and volumes of future water delivery schedules are not the only aspects of water delivery that need to be restored to maintain the original Everglades fen peatland complex with it's linmogenous, soligenous, and ombrogenous water flow systems. Currently the Everglades is influenced by sulfur and nutrient laden EAA waters mixed with calcium-laden mineral groundwater from deep cut canals traversing the landscape and thus large portions would be classified as managenous or managed. The question is how much of the original peatland hydrodynamics and nutrient conditions can be restored in future water management plans. If they are not, the normal successional patterns and development of the Everglades mire will forever be altered. Unfortunately, in the future it appears that large portions of the Everglades will be maintained mostly as managed peatland systems, even with the planned removal of a number of dikes and canals. With only 50% of the original Everglades remaining and hundreds of control structures remaining in place to protect urban and agriculture areas some say this is the only choice available. Peatland ecologists would argue that we have the opportunity with adaptive management to test alternative peatland restoration techniques and restore key components of the former Everglades in spite of these constraints. For example, restoration experiments on tree island habitats (South Florida Water Management District 2006) are showing some success, but larger scale work is needed on alternate flow regimes and delivery system effects on the peatlands themselves. Harvey et al. (2009) suggest that water managers could, in addition to managing water depth, manipulate frequency and duration of input flows, which would better control flows velocities, water resident times, sediment settling and biogeochemical transformations. These approaches could provide the necessary information needed to restore and maintain the ridge and slough habitats. Hopefully, the ombrogenous interior portion of WCA-1 will be maintained by not allowing surface water flows into the region so that the normal succession stage of marsh-fen-bog development can continue. Another major continuing problem for water managers in the future will be trying to balance conditions to maintain soligenous peatlands conditions for the central Everglades habitats while being pressured continuously to alter hydrologic levels and flows for survival of endangered species at specific locations or for human water needs. Finally, it is essential that the variety and range of specific hydrologic, nutrient, and fire conditions that originally shaped the diversity of Everglades habitats be maintained. The future of the Everglades depends on it.

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