10

Freshwater Marshes

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Wetland ecosystems dominate much of the Florida landscape, and marshes make up about one-third of those wetlands (Hefner, 1986). The largest of these marshlands, the Everglades, is a well-known symbol of natural Florida. Yet the history of Florida has been punctuated by campaigns to reclaim the wetlands; between the mid-1950s and mid-1970s alone, 24 percent of Florida's remaining marshes were drained (Hefner, 1986). Many more, including the Everglades, were severely altered by both drainage and unnatural flooding.

Marshes are wetlands dominated by herbaceous plants rooted in and generally emergent from shallow water that stands at or above the ground surface for much of the year. In general, less than one-third of the cover of a marsh consists of trees and shrubs. Marsh ecosystems include bogs, fens, mires, prairies, wet prairies, savannas, wet savannas, reed swamps, and swamps. The term *swamp*, however, is more appropriately restricted to forested or wooded wetlands. Marshes are classified as palustrine emergent wetlands by Cowardin et al. (1979). The Florida Natural Areas Inventory (1988) lists nine marsh types in Florida: basin marsh, bog, depression marsh, floodplain marsh, marl prairie, seepage slope, slough, swale, and wet prairie. In this chapter, marshes are classified either according to their general physiognomy, such as floodplain marsh, swale marsh, basin or depression marsh, and wet prairie, and by their characteristic plants, such as saw grass marsh and flag marsh.

Florida's marshes are characterized by their subtropical location, fluctuating water levels, recurring fires, and hard water. Owing to differences in climate and geology, the distribution and character of marshes vary across the state; yet notable similarities in appearance, constituent species, and controlling factors can be discerned among them.

Distribution

Marshes are not uniformly distributed throughout the state (fig. 10.1d). The greatest expanse is the Everglades of southern Florida (fig. 10.2). Several other relatively large marshes are associated with river floodplains, notably along the Kissimmee and St. Johns rivers. Smaller marshes are scattered throughout the peninsula, but the Panhandle has few marshes.

Topography is the principal factor controlling the distribution of marshes over the Florida peninsula (White, 1970) (fig. 10.1a). Land form and elevation affect marsh development primarily by determining the depth to the water table and the fate of runoff from local rainfall. Because the northern Panhandle and central core of the peninsula are elevated and well drained, they lack expanses of marshland. The remainder of the peninsula has a greater area of marshland because it is low, flat, and poorly drained. In southern Florida, water runs off slowly and is impounded by topographic rises and coastal ridges of limestone and sand. It is behind one of these coastal ridges that the enormous swale marsh of the Everglades is found. Elsewhere, marshes occur anywhere local topography and impermeable soils prevent rapid runoff or infiltration—either near rivers and lakes or in small basins and other depressions.

A relatively large surplus of annual rainfall over annual potential evaporation in Florida further contributes to the existence of marshland. This effect is particularly pronounced along Florida's southeast coast (figs. 10.1b, 10.1c), where it contributed to the development of the Everglades marshes, those in the vicinity of Lake Okeechobee, and those in the St. Johns River basin.

Thus the distribution of marshes in Florida (fig. 10.1d) may be explained through a combination of local and regional topography, rainfall, evaporation, and geology. Because these factors vary from one physiographic region to the next, it is possible to categorize the state's marshlands into five major groups. From higher to lower elevation, these are highland marshes, flatwoods marshes, the Kissimmee marsh complex, the St. Johns marshes, and the Everglades (fig. 10.2).

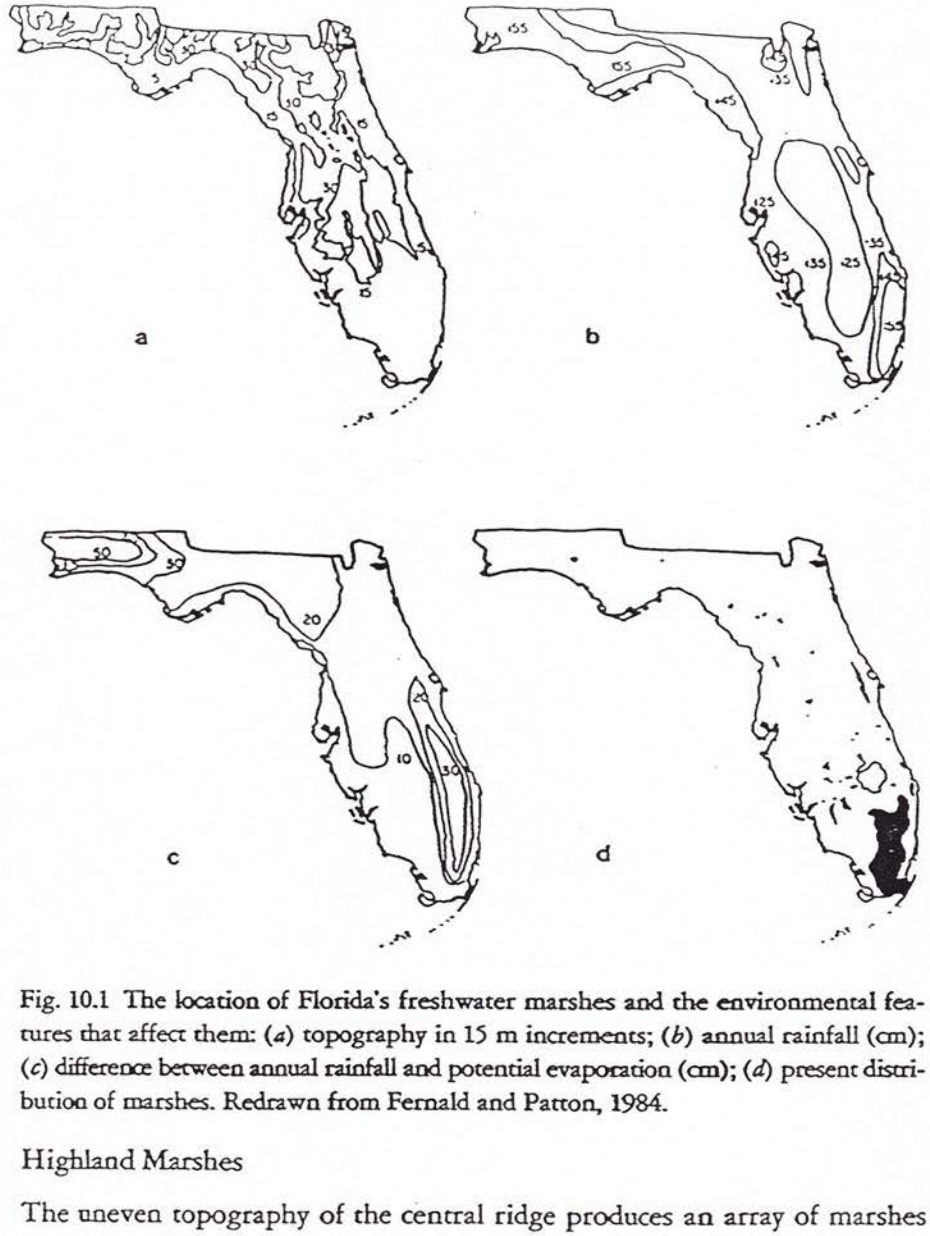

Fig. 10.1 The location of Florida's freshwater marshes and the environmental features that affect them: (*a*) topography in 15 m increments; (*b*) annual rainfall (cm); (*c*) difference between annual rainfall and potential evaporation (cm); (*d*) present distribution of marshes. Redrawn from Fernald and Patton, 1984.

Highland Marshes

The uneven topography of the central ridge produces an array of marshes occupying different types of depressions: former lake basins, shallow peat-filled valleys between existing lakes, and depressions landward of swamps that ring some lakes. Many of these marshes exist because of the shifting balance between two processes: the compaction of surficial sediments that retards loss of surface water and the periodic development of solution features that drain surface water into the aquifer (Pirkle, 1956; Pirkle and Brooks, 1959). Marshes and lakes in this region are unstable because subsurface drainage patterns change frequently as solution features appear or previous drainageways become plugged. A single site may alternately be lake, marsh, and dry land within a relatively short time span.

Fig. 10.2. Former distribution of major marshland areas in Florida and names of larger examples. Not shown are areas that include numerous small flatwoods marshes, wet savannas, and wet prairies scattered throughout much of the state.

Paynes Prairie, a large highland marsh located near Gainesville, is a famous example of this phenomenon (fig. 10.3). The character of Paynes Prairie has varied substantially during recorded history in response to changes in inflows, drainage, and fluctuations of the Floridan Aquifer. When William Bartram visited the area in 1774, the basin consisted of a dry grassland known as the Alachua Savannah (Bartram, 1791). In the early 1870s, Alachua Sink—the prairie's major drainageway—became plugged, and the basin became a lake deep enough for steamboat operations. The lake level began falling in 1891, and a marsh formed within two years.

Other large highland marshes are the Peace Creek marshes near Lake Wales; the Lake Apopka marsh near Zellwood; the Clermont marsh between Lake Minneola and Lake Minehaha; Emeralda and Fruitland Park marshes near Lake Griffin; Eustis Meadows near Eustis; Florahome, Fowler's, Hawthorne, and Levy's prairies in Putnam County; Jumper Creek marsh in Sumter County; Lake Panasoffkee marsh and Black Sink Prairie in Marion County; and the marshes of Orange Lake in Alachua County. Numerous small marshes dotted the Oklawaha River valley before it was impounded in the 1960s.

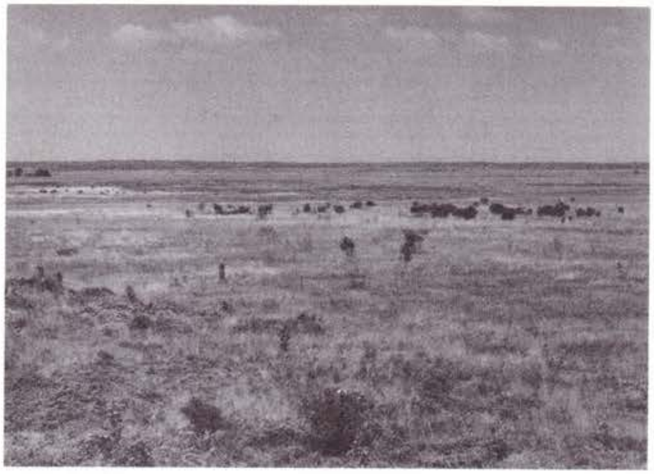

Fig. 10.3. The Alachua Savannah of William Bartram's day is now known as Paynes Prairie. It is an example of a large, highlands-type marsh created by the coalescence of solution holes. Photo by R. Myers.

Flatwoods Marshes

Flatwoods marshes, also known as flatwoods or seasonal ponds, occur throughout Florida's extensive pine flatwoods but are most common between the central highlands and the Atlantic and Gulf coasts (fig. 10.4). These marshes occur within slight depressions in an otherwise flat landscape. Although shallow (less than a meter deep) and small (usually only ten to a few hundred meters across), they reach a density of seventy per square kilometer in Sarasota County (Winchester et al., 1985). In places they make up a large portion of the area covered by flatwoods (Laessle, 1942; Abrahamson et al., 1984). The best-studied area where these marshes occur is the Ringling-MacArthur Reserve in Sarasota County (Winchester et al., 1985; Winchester, 1986). Preserved as a water recharge area, it encompasses 13,400 ha of flatwoods and associated flatwoods marsh habitat.

The St. Johns Marshes

The St. Johns marshes once encompassed the upper reaches of the St. Johns River floodplain (St. Johns River Water Management District, 1977). Before alteration by humans, all but the northernmost 100 km of the 480 km river basin was an extensive freshwater system of swamps, marshes, and lakes. The river originated in the 120,000-ha Blue Cypress Lake marsh, and other marshes occurred along the flat river floodplain, which falls less than 1.5 m over the entire upper St. Johns River basin (Lowe et al., 1984).

The Kissimmee Marsh Complex

The Kissimmee marsh complex includes the drainage basin of the Kissimmee River, Lake Istokpoga–Indian Prairie, and Fisheating Creek. The marshes along the Kissimmee River floodplain historically occupied 5000 km^2. Prior to its channelization in the 1960s, the river followed a 160-km

Fig. 10.4. Flatwoods marshes of the Ringling-MacArthur Reserve in eastern Sarasota County. Photo by Allan Horton.

meandering course from its headwaters at Orlando to its terminus in Lake Okeechobee. Undulating topography within the Kissimmee Valley created numerous isolated swale marshes, which blended into drier grasslands known as the Kissimmee Prairie.

One of the largest marshes in the Kissimmee complex was the 12,000 ha Istokpoga or Indian Prairie, which originated at Lake Istokpoga and then drained southward to Lake Okeechobee. It was once covered by shallow marsh, embedded with numerous deeper marshes. Similar marshes dot the swamp forests within the Fisheating Creek basin, located southwest of the Kissimmee River valley. The Ordway-Whittell Prairie Preserve and Avon Park Bombing Range also contain portions of the Kissimmee marsh complex (Tanner et al., 1982).

The Everglades

The Everglades marsh, the largest in Florida, originally encompassed over 10,000 km^2 in an elongated basin spanning 100 km and sloping a mere 3 cm/km (fig. 10.5). The basin, a bedrock depression known as the Everglades trough, is juxtaposed between the Atlantic coastal ridge, the Immokalee rise, and Big Cypress Swamp. Formerly, the marsh covered the entire central portion of southern Florida, from Lake Okeechobee southwestward to Florida Bay.

Some other marshes in southern Florida were hydrologically linked to

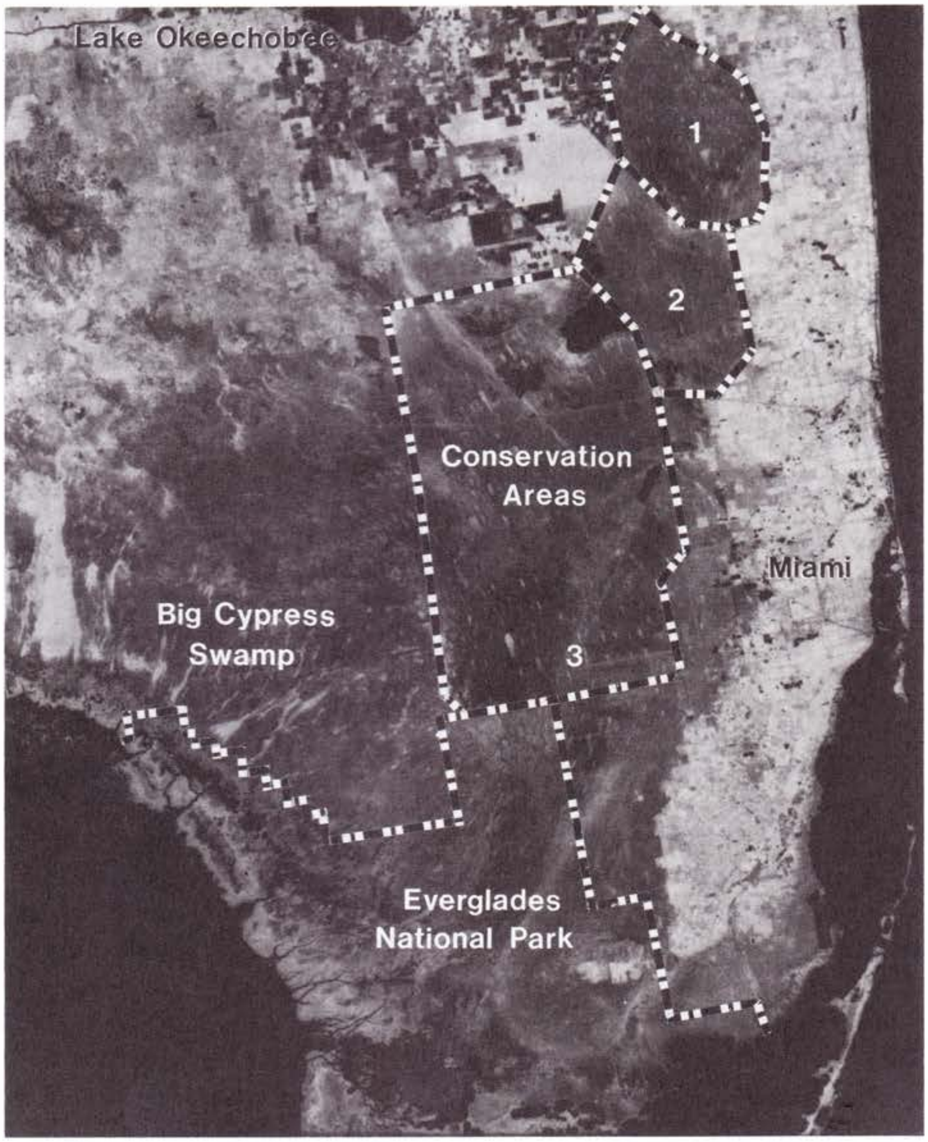

Fig. 10.5. Aerial image of southern Florida showing interior marshes of the Everglades as they exist today. Conservation Area 1 encompasses the Arthur R. Marshall Loxahatchee National Wildlife Refuge. The agricultural lands in the upper part of the Everglades basin are "muck farms," primarily sugarcane, commercial sod, and vegetable crops.

the Everglades or to Lake Okeechobee (Davis, 1943; Parker et al., 1955). For example, the Allapattah marsh, the Loxahatchee marsh and Hungryland Slough, and the Hillsborough Lakes marsh, together covering 81,000 ha, all drained into the northern Everglades. On the other hand, the southeast saline Everglades, or East Glades (Egler, 1952), and Taylor Slough drain south or southeast and are, for the most part, hydrologically independent of Everglades flow except during periods of high water. Big Cypress Swamp, situated topographically higher than the Everglades basin, contains a mosaic of various marshes and cypress swamps (Duever et al., 1986). Much of its waters historically flowed into the Everglades basin.

Physical Environment

Geology

Most of Florida is underlain by permeable sand or limestone; neither of which is particularly conducive to the formation of marshes. Where marshes do occur, one of three geological conditions is present: surficial deposits are impermeable, the water table emerges through the permeable substrate, or the marsh is hydrologically connected to a river.

Marshes perched above impermeable surficial deposits include many of the highlands and flatwoods marshes. Paynes Prairie, for example, is situated over a 2-m layer of sandy clay, which was deposited in the basin by ancient surface water flow. Many flatwoods marshes, particularly the deep, peat-filled ones, are underlain by an impermeable clay layer. Some low-lying flatwoods marshes, on the other hand, lack the clay deposit (Winchester, 1986), demonstrating the second condition: where water tables are high or overflow occurs, marshes do not require an impermeable basement deposit. The third condition holds in floodplain marshes, where the peat substrate clearly maintains both subsurface and surface connections with the river basin water table.

The southern Everglades fits into the second category: peat directly overlies permeable limestone, but the water table emerges through the limestone. In the northern Everglades, as in some other marshes, the determining factor has not been conclusively identified. A layer of marl underlies the peat, but it is uncertain whether it is responsible for the marsh's existence (Gleason et al., 1984).

Soils

The occurrence and character of the three principal soil materials of Florida marshes—peat, marl, and sand—are influenced by hydroperiod, height of flooding, and depth to the water table during the dry season.

Peat tends to accumulate in deep water marshes exhibiting long hydroperiods (over nine months in southern Florida; Duever et al., 1978) and limited recession of surface water during the dry season. The lengthy flooding maintains the anaerobic conditions conducive to peat formation and prevents oxidation because the peat typically remains somewhat damp throughout the year, even during seasonal dry periods. Completely dry peat, on the other hand, undergoes oxidation, consolidation, and compaction, which cause reduced porosity and irreversible loss of part of its water-holding capacity (Stephens and Johnson, 1951; Parker et al., 1955; Bay, 1966; Stephens, 1984).

The capacity of peat soils to retain water in the dry season is crucial to marsh development. Not only does peat hold water longer into the dry season than do other soils, but it also absorbs and retains scarce dry season rainfall (Parker et al., 1955). Such water retention maintains the high soil moisture necessary for the survival of marsh plants. Even in severe droughts, water typically is held within the root zone of the plants. Some marshes may lack surface water for many months during infrequent droughts, with no effect on soil or plant associations. However, deep, long-term drying of the soil causes changes in plant composition, productivity, and subsequent rates of peat accumulation.

Peat varies in color, structure, and acidity, depending on the source of plant material and the hydroperiod (Davis, 1946). It can range from red to brown to nearly black, from fibrous to spongy, and from neutral to acidic. Peats can be classified by their major plant components (Cohen and Spackman, 1984). For example, there are distinctive peats derived from saw grass and from water lilies.

Peat accumulation reached depths of 4 m at the south end of Lake Okeechobee. This mass of peat blocked water flow, thereby defining the lake. South of Lake Okeechobee, peat thickness ranges from 1.5 m in the upper reaches of the Everglades to 0.75 m in the lower end, and the peat layer smooths out the topographic irregularities of the basin.

In marshes with moderate hydroperiods and seasonal drying sufficient to oxidize organic matter, a marl substrate may develop. Most marl derives from precipitation of carbonates by the metabolic activities of encrusting algae, which form a "periphyton" mat on the surfaces of submerged sediments and plant stems. Occasionally, a substantial water level decline results in marl subsidence (Winchester, 1986).

A sand substrate is maintained on sites with short hydroperiods and extensive drying of the soil in the dry season. Frequent or extensive oxidation and fires preclude the accumulation of either peat or marl.

Hydrology

The marked seasonality of Florida's rainfall and evaporation plays an important role in the functioning of marsh ecosystems by creating a seasonal fluctuation in surface water (fig. 10.6). This seasonal fluctuation is most

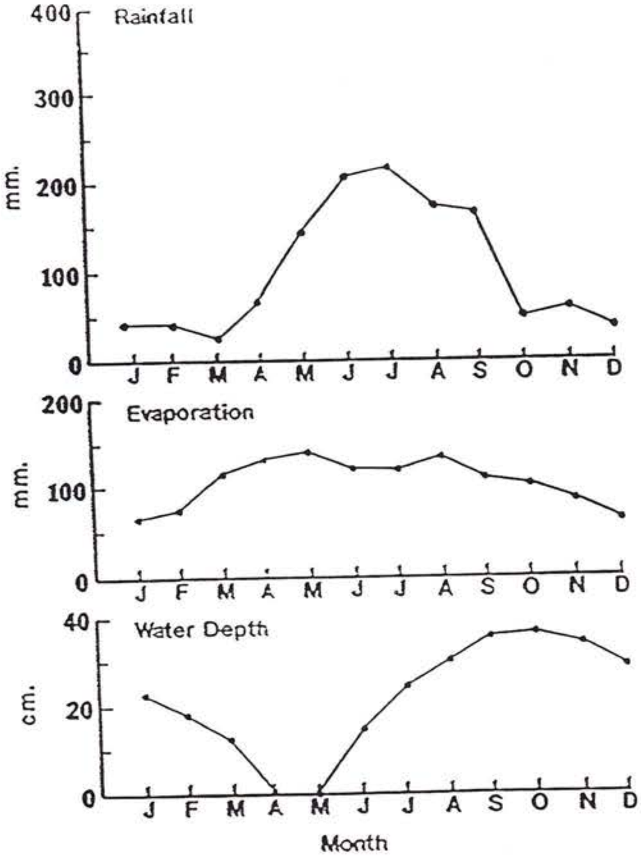

Fig. 10.6. Mean annual fluctuation of rainfall, evaporation, and water depth in the Everglades.

pronounced in southern Florida because it experiences less winter rainfall than occurs farther north. Water levels rise during the summer rainy season, gradually decline during the winter, and annually reach drought conditions as evapotranspiration increases in the spring. In most years, standing water is absent from southern Florida marshes at the height of the dry season, a condition that may last from a couple of weeks to several months. In northern Florida, water levels remain high through the winter and early spring because of higher winter rainfall.

Most marshes flood during each rainy season, but some may flood only in very wet years. Annual variation in rainfall may cause substantial differences in the depth and extent of flooding in various years at a single marsh site.

The timing and extent of water level fluctuations determine flooding depth, drying depth, drying rate, and hydroperiod (Duever et al., 1975; Pesnell and Brown, 1977). Various marsh plants, plant assemblages, and animals require specific ranges of these variables. In general, marshes in Florida have hydroperiods of seven to twelve months, water depths of less than 50 cm, and drying depths of less than 30 cm.

Those marshes of the highlands and flatwoods that are perched above the water table depend on local rainfall, sporadic surface runoff, and seepage from adjacent uplands for their water. In flatwoods marshes of the coastal lowlands, however, water source and water level fluctuation are linked to the water table (Winchester, 1986). These marshes tend to dry almost completely during periods of low rainfall, but the central peat zones usually retain water, and the marshes reflood rapidly as the water table rises during the wet season.

Some of the Kissimmee and St. Johns marshes are hydrologically connected to water flows in their river systems, whereas others are more isolated. Along the Kissimmee River, lower lying, river-edge marshes receive overflow water, but others are isolated in swales and obtain water from rainfall, localized runoff, and the seasonal rise in the water table. Historically, water level fluctuations averaged 1 m but may have been as great as 3.7 m during floods (Perrin et al., 1982). During the wet season the entire floodplain became inundated, while during the dry season only deeper sloughs, ponds, and the river channel retained surface water. Similar conditions prevailed in the St. Johns basin, where water accumulated in the marshes of the headwaters before flowing slowly over 20 km of marshland to Lake Helen Blazes, where the river channel itself begins.

Historically, the Everglades originated at Lake Okeechobee, which in turn received its inflow from the extensive catchment that included the entire Kissimmee basin. Outflow from the lake into the Everglades occurred intermittently in high water periods (Parker et al., 1955) but did not markedly affect the hydrology of the marsh farther south. Surface water conditions in the Everglades resulted primarily from *in situ* rainfall and extremely slow runoff from marshes immediately up-gradient (Leach et al., 1972).

Fire

Fire plays a crucial role in the ecology of Florida's marshes by limiting the invasion of woody vegetation, affecting the composition of the herbaceous community, and retarding, or occasionally reversing, peat accumulation (Alexander, 1971; Vogl, 1973a; Hofstetter, 1975; Van Arman and Goodrick, 1979; Wade et al., 1980). A sharp demarcation of plant associations in Florida marshes often indicates the boundary of a previous burn. Fires also burn dead but undecayed plant material, thereby releasing nutrients.

Fires have always been frequent occurrences in Florida's marshes. In the Everglades and elsewhere, charcoal embedded in the peat attests to a history of repeated fires (Parker, 1984). In fact, Everglades peat owes its black color to charcoal from ancient fires (Smith, 1968).

Summer, when lightning is most frequent, is the natural fire season. Thus, natural fires generally occur when soil moisture levels are high and plants are growing. Because organic soils fail to ignite when moisture content is above 65 percent (Wade et al., 1980), wet season fires are typically confined to the above-water vegetation and seldom consume the soil. All of Florida's marsh plant associations carry fire to varying degrees. In sparse stands, fire can be carried by the burning alga mat that forms on the top of the soil. Except during severe droughts, deeper water marshes serve as natural firebreaks.

Fire periodicity in most deep water marshes is about three to five years, whereas shallow water marshes burn on one- to three-year cycles, provided plant growth is sufficient to carry a fire (Wade et al., 1980).

Nutrients

The water in most Florida marshes is highly buffered because it is in contact with limestone, marl, or calcareous sand. In most cases, pH is circumneutral to slightly basic, but in some flatwoods ponds, where the groundwater is acidic, pH may be lower. Dissolved solids (especially carbonates and bicarbonates) and conductivity are generally high (Gonyea and Hunt, 1970; Flora and Rosendahl, 1982b). Oxygen concentrations are usually low (Kushlan, 1979c; Kushlan and Hunt, 1979; Perrin et al., 1982), yet decomposition can be rapid (Reeder and Davis, 1983).

Nutrients in flatwoods, highlands, and Everglades marshes are derived primarily from rainfall rather than from upland runoff or bedrock, so levels are typically low (Waller, 1975; Waller and Earle, 1975; Flora and Rosendahl, 1982a). Even given the influence of anthropogenic discharges, 78 percent of the nitrogen and 90 percent of the phosphorus entering the northern Everglades are from rainfall; 74 percent and 96 percent, respectively, of the incoming nitrogen and phosphorus are retained within the marsh (Waller, 1975). Inorganic nitrogen concentrations in Everglades waters are less than 0.1 mg/L. Phosphorus levels (Boyd and Hess, 1970) are especially low and limiting, being on the order of 0.003 to 0.005 mg/l in the water. Peat soils are typically deficient in minor elements (particularly copper, manganese, zinc, and boron), high in organic nitrogen, and low in phosphorus and potash (Forsee, 1940; Bryan, 1958). In contrast, floodplain marshes gain additional nutrients from river overflow.

Hurricanes

Hurricanes have little long-term influence on inland freshwater marshes in Florida (Craighead and Gilbert, 1962). Water depths may increase during storms, but basin overflow and runoff limit excessive levels. For example, hurricane-enhanced water levels in the Everglades in 1947, before the institution of control measures, did not exceed 0.3 m above normal high water. Freshwater marshes along the coast, on the other hand, can be adversely affected by the intrusion of saline water, especially in areas where runoff has been artificially blocked (Alexander, 1967a).

Marsh Plants

Flora

Although much of the flora of Florida is tropical (Long, 1974), many of the plants in Florida marshes (table 10.1) are from highly cosmopolitan taxa (Long and Lakela, 1971). The dominant marsh species are primarily temperate.

Although most Florida marshes are dominated by only a few species, the entire flora of a marsh may be large. For example, several Kissimmee marshes contained more than 100 species of forbs, grasses, and sedges (Tanner et al., 1982). Deep water marshes in southern Florida have more than 110 species (Long, 1984). In shallower wet-prairie sites, the species number increases to about 175 (Long, 1984). In the Paynes Prairie complex, 326 species of herbaceous and woody hydrophytes were found in a mosaic of deep water marshes, shallow wet prairies, and pasture (Easterday, 1982; Patton and Judd, 1986).

Table 10.1. Dominant plant species in marsh associations of Florida

	Marsh association[a]					
Species	WL	SB	CT	FL	SG	WP
Nymphaea odorata (white water lily)	x					
Orontium aquaticum (neverwet)	x					
Nelumbo lutea (yellow lotus)	x					
Najas guadalupensis (naiad)	x	x				
Utricularia spp. (bladderwort)	x	x		x		
Potamogeton spp. (pondweed)		x				
Typha spp. (cattail)			x			
Pontederia lanceolata (pickerelweed)				x		
Sagittaria latifolia (arrowhead)				x		
Eleocharis spp. (spikerush)				x		
Panicum hemitomon (maidencane)				x		x
Thalia geniculata (fire flag)				x		
Scirpus spp. (bulrush)			x			
Rynchospora tracyi (Tracy's beakrush)				x		x
Cladium jamaicensis (saw grass)					x	x
Muhlenbergia fillipes (muhly)						x
Spartina bakeri (cordgrass)						x
Dichromena colorata (white-topped sedge)						x
Hypericum fasciculatum (St. John's-wort)						x

a. WL = water lily marsh; SB = submersed marsh; CT = cattail marsh; FL = flag marsh; SG = saw grass marsh; WP = wet prairie.

Major Associations

Throughout Florida, freshwater marshes support a similar set of plant associations (table 10.1). Each association occurs under a particular range of environmental conditions defined by the hydrologic regime, fire frequency, and soils (table 10.2). Of these factors, hydroperiod (the percentage of time a marsh is flooded) and timing of drying are the most important.

The abilities of various species to become established and persist under specific environmental conditions determine the composition of the plant community at a specific site. The establishment phase is critical, as most species cannot germinate under water. Thus, the timing and length of the dry season relative to the types of seeds available in the substrate determine which species gain a foothold. Once established, individuals may persist under conditions that might otherwise be unsuitable for germination. Their subsequent spread is primarily vegetative.

Plant associations vary markedly along hydrological gradients, but species tolerances to inundation overlap broadly. For example, in the marshes of the upper St. Johns River, both maidencane and saw grass grow where the hydroperiod exceeds 290 days (Lowe, 1983). Other flood tolerances include white water lily, 90–100 percent inundation; naiad, 95–100 percent; arrowhead, 85–95 percent; pickerelweed, 70–95 percent; spikerush, 70–90 percent; and white-topped sedge, 10–65 percent. The importance of water level fluctuation and hydroperiod are apparent from the changes in plant distribution that have been brought about by water level stabilization (Ager and Kerce, 1970, 1974; McPherson, 1973b; Goodrick and Milleson, 1974).

Six major categories of freshwater marsh are recognized in Florida:

Table 10.2. Important environmental characteristics of marsh associations in Florida

Marsh association	Hydroperiod[a]	Fire frequency[b]	Organic matter accumulation[c]
Water lily	Long	Low	High
Submersed	Long	Low	High
Cattail	Moderate	Moderate	High
Flag	Moderate	Moderate	Moderate to high
Saw grass	Moderate	Moderate	Moderate to high
Wet prairie	Short	High	Low

a. Short = < 6 months flooding; moderate = 6 to 9 months; long = > 9 months.

b. Low = < once per decade; moderate = about once per decade; high = > once per decade.

c. Low = a few centimeters to nonexistent; moderate = usually < 1 meter deep; high = usually > 1 meter deep.

water lily marsh, submersed marsh, cattail marsh, flag marsh, saw grass marsh, and wet prairie. Each is characterized by a distinct assemblage of dominant plant species (table 10.1).

Water Lily Marsh

Water lily marsh is dominated by floating-leaf plants including white water lily, neverwet, and yellow lotus (fig. 10.7). These marshes generally occur in the deepest water, where emergent plants cannot thrive. They are usually rooted in poorly decomposed plant material, which seldom dries out completely.

Submersed Marsh

Submersed marsh occurs in deep water where emergent plants are thinly distributed. The more important species are naiad, pondweed, and bladderwort. In the Everglades, water hyssop (*Bacopa caroliniana* and *B. monnieri*), primrose willow (*Ludwigia repens*), spikerush (*Eleocharis elongata*), *Chara*, and string lily (*Crinum americanum*) are also characteristic.

Cattail Marsh

Cattail marsh is found in relatively deep, nutrient-rich water, usually on deep soils (fig. 10.8). It is not generally dominant over large areas but forms

Fig. 10.7. Water lily marsh along the shore of Lake Jackson, Leon County. Dominants are water lotus, white water lily, and maidencane. Photo by R. Myers.

Fig. 10.8. Cattail marsh at the transition between freshwater saw grass marsh and salt marsh, Collier County. The abundance of cattail may be the result of freshwater damming by U.S. 41 (Tamiami Trail). Photo by R. Myers.

nearly monospecific stands in some places, particularly those that are disturbed.

Flag Marsh

Flag marshes are named after pickerelweed, fire flag, arrowhead, and other species with flag-like leaves. These are diverse associations and may be dominated not only by flag species but also by maidencane, spikerush, beak-rush, or bulrush. Flag marshes occur where the wet season water depth is between 0.3 and 1 m and the hydroperiod extends more than 200 days per year. They require seasonal drying; under prolonged inundation plants up-root and die.

Pickerelweed- and maidencane-dominated marshes are the most wide-spread types of flag marsh (fig. 10.9). Of these two, pickerelweed is more dependent on continually wet conditions. Beakrush and maidencane, at the other extreme, cannot tolerate long-term flooding. Both types disappear from marshes in which the seasonal drawdown has been eliminated, as occurred in parts of the northern Everglades in the 1970s. Spikerush can tolerate both flooding and drying, and thus is less affected by changes in hy-drological conditions.

Fig. 10.9. Maidencane marsh flanking Myakka River in Myakka River State Park, Sarasota County. Photo by Allan Horton.

Saw Grass Marsh

Saw grass marsh is widespread in Florida and is the predominant association in the Everglades, where it once covered over 800,000 ha; it still accounts for 70 percent of the remaining Everglades landscape (Loveless, 1959a; Stephens, 1984) (fig. 10.10). The nearly total dominance of this species over such a large area is one of the distinguishing features of the Everglades.

Saw grass marsh is impressive. The plants may exceed 3 m in height and form an impenetrable mass. Two categories of saw grass marsh are recognizable: dense and sparse. The dense type occurs on higher ground and is underlain by deep organic soils. Although it appears monospecific, dense saw grass marsh includes other tall emergents such as cattail, ferns, and small shrubs. The transition between dense saw grass and adjacent marsh communities is often sharply defined, probably owing to fire effects. Where flooding conditions increase, flag marsh or water lily marsh replaces saw grass marsh. Under prolonged dry conditions, woody vegetation becomes more prevalent. Where nutrients are elevated, cattail tends to invade and may eventually displace saw grass.

Sparse saw grass, which usually occurs at lower elevations than the dense saw grass, occupies similar sites to those of flag marsh and thus may include spikerush, arrowhead, and maidencane. The substrate under sparse saw grass marsh is shallow peat or marl.

Periphyton is a typical component of these sparse stands of saw grass and of similar marshland environments with alkaline water (fig. 10.11). It consists of an algal mat composed mostly of filamentous blue-green algae (Swift, 1981), but its composition varies with ionic and nutrient concentrations and with hydroperiod (Van Meter-Kasanof, 1973; Swift, 1981).

Periphyton becomes attached to submerged surfaces, such as sediment and plant stems, and its development is enhanced in sparse communities because light penetrates into the water. In deeper-water marshes, it often

Fig. 10.10. Saw grass marsh with elongated tree islands that lie parallel to the direction of water flow, Shark Valley, Everglades National Park. Photo by J. Snyder.

Fig. 10.11. Sparse saw grass marsh with periphyton, Shark Valley, Everglades National Park. Photo by R. Myers.

attaches to the floating purple bladderwort (*Utricularia purpurea*) and thereby covers much of the water surface.

Wet Prairie

Wet prairies are the least frequently flooded of any Florida marsh type. Their short hydroperiods (50–150 days per year) preclude peat development. In southern Florida, the substrate is a periphyton-derived marl, but the acid substrates of shallow flatwoods marshes and wet savannas of the Florida Panhandle also support wet prairie vegetation. Species composition varies greatly depending on hydroperiod, soils, and site history. Because of their short hydroperiods, wet prairies are the most species-rich of Florida's marshes and include a variety of grasses, sedges, and flowering forbs (fig. 10.12). Dominants include maidencane, cordgrass, beakrush, or muhly. Saw grass may be present, but it is sparsely distributed and of shorter stature than in saw grass–dominated marshes.

Wet prairie species have considerable tolerance to both flooding and drying. Many shallowly rooted species typical of the wet prairies associated with coastal flatwoods (like St. John's-wort) are killed by drying but reseed readily. As a result, their zone of dominance migrates up- and downslope in response to changing water conditions (B. H. Winchester, personal communication). Higher wet prairies may, under some conditions, be invaded by saw palmetto (*Serenoa repens*).

Geographic Differences among Plant Associations

Although the six major marsh plant associations occur throughout the state, their extent differs within and among Florida's major marsh systems (table 10.3).

Large highland marshes, such as Paynes Prairie, typically include a mosaic of saw grass marshes; water lily marshes; and arrowhead, beakrush, and maidencane flag marshes (White, 1975; Easterday, 1982; Patton and Judd, 1986). Water lily marshes of Paynes Prairie are dominated by white water lily, banana water lily (*Nymphaea mexicana*), fanwort (*Cabomba caroliniana*), bladderwort (*Utricularia foliosa*), naiad, and water pennywort (*Hydrocotyle ranunculoides*). Floating mats of water hyacinth (*Eichhornia crassipes*), pickerelweed, and pennywort also develop in stabilized deep water, particularly in the canals, but also in waters having high nutrient content (Morris, 1974) (fig. 10.13). Saw grass and pickerelweed marshes occupy the middle ground, while maidencane marshes, intermixed with southern cut-

Fig. 10.12. Shallow flatwoods marsh supporting wet prairie vegetation, Lake Kissimmee State Park, Polk County. Photo by R. Myers.

grass (*Leersia hexandra*) and rush (*Juncus acuminatus*, *J. effusus*), dominate higher ground.

Flatwoods marshes typically consist of concentric rings of marsh associations defined by hydroperiod and water depth. Maximum depth usually occurs in the center; thus water lily marshes or flag marshes occupy this zone. Arrowhead flag marshes are most common, but in some cases the central zone is open water, creating what is known as a flatwoods pond. In a number of places, pickerelweed, maidencane, redroot (*Lachnanthes caroliniana*), cordgrass, or saw grass predominates. The abundance of pickerelweed relative to arrowhead frequently depends on the severity of the drought period. Arrowhead, because of its greater drought tolerance, is the usual dominant. Over time, peat accumulation may elevate the central portion of the marsh above peripheral plant zones.

The intermediate zones of flatwoods marshes are generally dominated by Tracy's beakrush or maidencane marsh. Maidencane marshes on sandy substrates typically have a *Sphagnum* moss mat. In many of the coastal flatwoods, however, there is a dense mat of periphyton (B. H. Winchester, personal communication).

The upper zone, which completely dries out each year, supports wet prairie associations. Species composition is particularly variable from one place to the next. It may be dominated by St. Johns wort, blue maidencane

Table 10.3. Predominant plant associations in the marsh systems of Florida

Marsh	Predominant marsh association
Highlands marshes	Water lily marsh
	Arrowhead flag marsh
	Beakrush flag marsh
	Maidencane flag marsh
	Dense saw grass marsh
Flatwoods marshes	Beakrush marsh
	Maidencane marsh
	Wet prairie
The St. Johns marshes	Dense saw grass marsh
	Maidencane flag marsh
	Pickerelweed flag marsh
The Kissimmee marshes	Pickerelweed flag marsh
	Maidencane flag marsh
	Beakrush marsh
The Everglades	Dense saw grass marsh
	Sparse saw grass marsh
	Spikerush flag marsh
	Beakrush flag marsh
	White water lily marsh
	Wet prairie

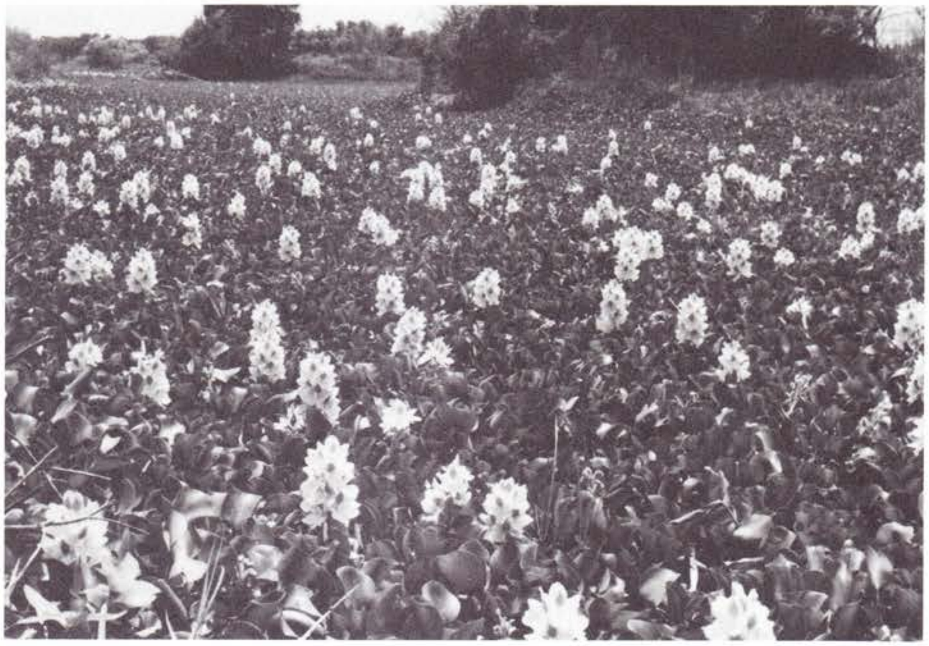

Fig. 10.13. Water hyacinth, a troublesome exotic, clogs drainageway of Rainey Slough, Glades County. Photo by M. McMillian.

(*Amphicarpum muhlenbergianum*), cutthroat grass (*Panicum abscissum*), or yellow-eyed grass (*Xyris* spp.). The St. John's-wort marsh is particularly characteristic of southeast peninsular flatwoods in Sarasota County (Winchester et al., 1985).

Flatwoods marshes often abruptly terminate in a border of saw palmetto, buttonbush (*Cephalanthus occidentalis*), willow (*Salix caroliniana*), pop ash (*Fraxinus caroliniana*), gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*), slash pine (*Pinus elliottii*), or dry prairie.

At one time the marshes of the upper St. Johns basin were similar to the Everglades (Sincock, 1959; Lowe, 1983, 1986). White water lily marsh predominated in deeper areas, but saw grass marshes covered extensive areas. Maidencane marshes have expanded at the expense of saw grass marshes following deep-burning fires. They now cover 37 percent of the headwater wetlands (Lowe, 1983). Pickerelweed flag marshes are common in places, while flag marshes of water hemp (*Amaranthus australis*), moonflower (*Ipomoea alba*), dog fennel (*Eupatorium capillifolium*), arrow arum (*Peltandra virginica*), string lily, and redroot also occur.

The marsh associations of the Kissimmee basin are particularly complex (Goodrick and Milleson, 1974; Milleson et al., 1980; Perrin et al., 1982; Pierce et al., 1982). The most widespread are pickerelweed flag marshes (Tanner et al., 1982). Associated species include arrowhead, maidencane, torpedo grass (*Panicum repens*), smartweed (*Polygonum* spp.), primrose, pennywort, horsehair sedge (*Eleocharis equisetoides*), Tracy's beakrush, southern cutgrass, and several woody plants, such as swamp hibiscus (*Hibiscus grandiflorus*) and buttonbush.

Maidencane flag marshes dominate large areas where sandy substrates occur. Maidencane makes up 50 percent to 60 percent of the biomass in some of these marshes (Van Arman and Goodrick, 1979). Associated with it are pickerelweed, arrowhead, pennywort, beakrush (*Rhynchospora inundata*), and smartweed. Beakrush flag marshes replace maidencane marshes as higher ground is approached. Both associations contain much the same complement of species, differing only in their relative abundances.

Saw grass marshes occur in a few locations in the Kissimmee basin, primarily as patches within maidencane and beakrush marshes. Maidenhair sedge (*Eleocharis vivipara*), blue maidencane, and shrubs such as buttonbush and hibiscus are associates.

Some sites support marsh associations not distinguished by any consistent dominants but rather by a mixture of torpedo grass, maidencane, broomsedges (*Andropogon* spp.), water grass (*Hydrochloa caroliniensis*), southern cutgrass, and false maidencane (*Sacciolepis striata*).

The Everglades are predominantly saw grass and flag marshes. As elsewhere, inundation patterns determine species distribution. Deeply flooded areas support water lily marshes, whereas in slightly shallower zones, beakrush marsh and spikerush marsh predominate (Loveless, 1959b; Goodrick, 1984). Redroot and yellow-eyed grasses are common in the Loxahatchee Wildlife Refuge but are rarely found farther south. Flag marshes often support periphyton mats that cover floating bladderwort. Saw grass marshes, of course, are the characteristic association of the Everglades. Sparse saw grass occurs throughout the southern part, especially along the periphery, while dense saw grass covers much of the core. In some places, standing stocks exceed 28,000 kg/ha (Hofstetter, 1976). A common pattern in the Everglades is strand and slough physiography—saw grass marshes alternating with flag or water lily marshes (fig. 10.10).

In the Everglades, wet prairies are primarily oriented laterally to the main drainage (Gleason and Spackman, 1974). Interspersed among vast expanses of these wet prairies are deeper-water marshes and unflooded rises. The most prominent species in Everglades wet prairies are muhly, foxtail grass (*Setaria corrugata*), black rush (*Schoenus nigricans*), plume grass (*Erianthus giganteus*), love grass (*Eragrostis* spp.), and white-topped sedge.

Adaptations of Marsh Plants

As mentioned, marshes are characterized by three key environmental factors: rainfall, evaporation, and water level. The timing and extent of water level fluctuations influence the colonization and survival of marsh plants by creating extremes either of submergence and waterlogged substrates or of drought conditions conducive to fire. Additional adaptive challenges are presented by such factors as periodic freezes and water chemistry.

Flooding

Living in a flooded environment requires special adaptations. Inundation results in saturated substrates and, if prolonged, an anaerobic environment. To counteract anaerobiosis and the attendant presence of toxic chemicals, some marsh plants possess internal air channels that facilitate oxygenation of their roots. Oxygen leaks from these channels, forming an aerobic microlayer around the roots.

Most marsh plants can neither germinate nor survive as seedlings under water (Teskey and Hinckley, 1977; Pesnell and Brown, 1977; van der Valk, 1981); thus, most propagate vegetatively. Even dominants such as saw grass seldom sprout from seed (Alexander, 1971). Germination and establishment are rare events, and many marsh species rely on seed stored in persistent seed banks in the marsh substrate. The seeds germinate when the marsh is dry. Interestingly, few of the long-lived dominants in marshes form large, persistent seed banks.

Besides being the period for germination, the dry season serves to release the bulk of nutrients tied up in the vegetation and detritus. As water levels recede, leaves and stems fall over, die, and decay. The nutrient release, coupled with aerobic soil conditions, initiates a burst of aerial vegetative growth. Upon reflooding, decaying plant material becomes available to the marsh food chains. Thus seasonal drying is essential to maintaining energy and nutrient flows.

Excessive drying of the marsh substrate during drought also limits plant growth. Root systems of most marsh plants are shallow, mostly within the upper 15 cm of soil, and few roots extend below 50 cm (Duever et al., 1986).

Because of their relatively short hydroperiods, flatwoods marshes experience marked seasonal variation. One outcome is seasonal dominance by different species. For example, in maidencane flag marshes, maidencane and floating heart (*Nymphoides aquatica*) are dominant in spring, but beakrush and bald rush (*Psilocarya nitens*) become more apparent as the dry season progresses (Winchester et al., 1985). Similarly, flowering phenology is related to seasonal hydrology (Abrahamson et al., 1984). The species of shorter stature bloom in early spring before water levels rise, whereas the taller emergent species flower in summer and fall.

Fire

Plants in Florida marshes are also adapted to recurring fires. Most marsh plants—including long hydroperiod species, such as saw grass, pickerelweed, arrowhead, and maindencane—regrow quickly following fire, their growth enhanced by the release of bound-up nutrients and reduced competition for space (Loveless, 1959b; Forthman, 1973; Goodrick and Milleson, 1974; Wade et al., 1980). Fire is at least partly responsible for the mosaic of marsh associations and for the sharp demarcations between them (Craighead, 1971; Lowe, 1986). Fire's impact depends on how fast and how deeply the organic soil burns and how slowly the water rises after the fire.

Saw grass is particularly suited for surviving fire (Wade et al., 1980). Its growing bud is buried in the soil and surrounded by overlapping leaves that insulate it from fire. Saw grass leaves are highly flammable and can support fire even when standing water is present. Saw grass responds quickly after a fire, reaching a height of as much as 20 to 40 cm in two weeks (Forthman, 1973). The rapid regrowth permits saw grass to outpace rising water levels. If complete submergence occurs, however, the resprouting stem is killed. If large areas are affected in this way, saw grass may be eliminated from the site. Saw grass declines when there is extended flooding coupled with a lack of fire; this decline is reversed by drying and burning.

Flag marsh species also respond rapidly after fire. Significant regrowth of maidencane occurs within one month after fire (Loveless, 1959b; Vogl, 1973a), and within six months little evidence of fire remains (Van Arman and Goodrick, 1979). Fire influences the competitive relationship between saw grass and maidencane; the latter frequently invades marshes after fires severe enough to kill saw grass. Saw grass, however, eventually reinvades (Lowe, 1983, 1986).

Fires limit peat build-up and prevent invasion of trees and shrubs into marshes (Craighead, 1971). In the absence of fire, invasion by wax myrtle (*Myrica cerifera*), willow, buttonbush, and nonnative woody species such as Brazilian pepper (*Schinus terebinthifolius*), Australian pine (*Casuarina* spp.), and melaleuca (*Melaleuca quinquenervia*) occurs rapidly if seed sources are nearby and water levels are conducive to establishment (fig. 10.14). The spread of melaleuca, an Australian native, is also enhanced by fires, which open serotinous seed capsules (see Myers, 1983, 1984, and Ewel, 1986, for assessments of melaleuca's invasibility in south Florida marshes).

Nutrients

Most plant species in Florida marshes have low nutrient requirements and tend to accumulate available nutrients (Steward and Ornes, 1975). The ability of saw grass to sequester nutrients beyond its immediate needs may account for its competitive advantage over other species in nutrient-poor Florida marshes. Although marsh systems have considerable assimilative capability (Sloey et al., 1978), this capacity may not be unlimited. Increased nutrient loading in streams entering many marshes may have affected species composition. For example, high nutrient loads have been responsible for an increase in cattail along canals and perhaps elsewhere.

Fig. 10.14. Melaleuca, an aggressive exotic pest plant from Australia, scattered in a wet prairie/dwarf cypress landscape, Big Cypress National Preserve. Melaleuca is a serious threat to the marshes and wet prairies of southern Florida. Frost limits its northerly advance. Photo by R. Myers.

Periphyton growth is limited by low nutrient concentrations in the marsh and altered by changing nutrient loads. Periphytic blue-green algae can fix nitrogen and may be important sources of this nutrient in Florida marshes.

Temperature

Seasonal variation in temperature has important effects on Florida marshes, though the presence of surface water during the coldest months of the year tends to offset the effect of drastic temperature changes to some extent. Frost, however, determines the northward spread of tropical species. A notable example is pond apple (*Annona glabra*), which finds its northern limit on the marshy fringes of islands in Lake Istokpoga.

Above-ground stems of water lilies, maidencane, pickerelweed, and other more northerly ranging species die back in winter and resprout from roots or tubers in spring (Milleson, 1976). Saw grass, on the other hand, is one of the most cold-tolerant of Florida's marsh species (Steward, 1974). Cold-death of leaves is limited, and above-ground biomass shows no seasonality.

Plant growth in Florida's more northerly marshes, such as Paynes Prairie, varies markedly with season (White, 1975). Standing crop is greatest in July and August. In late fall and winter, above-ground portions of many plants (including pickerelweed, arrowhead, cattail, water lily, spadderdock, and maidencane) die, creating great rafts of recumbent leaves in late winter.

Succession

The extant wetland communities in Florida have existed in their present form for only a few thousand years (Long, 1984), and there is clear evidence for large-scale primary succession within this period. Some highland marshes represent late successional stages in the filling of solution basins by endogenous peat and allochthonous sediment. Marl and older peats underlying surficial peat layers indicate that Lake Okeechobee and the Everglades basin have filled by successional processes. In some cases, shallow marshes can be completely replaced by woody thickets within five to ten years. In the Everglades, peat derived from tree islands overlies peat derived from marsh vegetation, demonstrating that tree islands have developed on former deep-water marsh sites (Stone, 1978). In many places, it is clear that present-day emergent marshes have succeeded from deeper water associations.

Relatively frequent fires coupled with fluctuating water levels maintain the integrity of Florida marshes. For example, Winchester (1986) found no major change in the zonal configurations of flatwoods marshes over forty years. The importance of fire frequency and water level in arresting succession is demonstrated by the rapid change that occurs when these factors are altered. Succession occurs quickly when water levels are raised or stabilized or when lowered (McPherson, 1973b; Alexander and Crook, 1984; Pierce et al., 1982; Lowe, 1983; Lowe et al., 1984). The vegetation history of Paynes Prairie demonstrates that successional processes are reversible, given changes in the hydrology and fire regime.

Marsh Animals

Fauna

Aquatic animal populations are among the great glories of Florida's marshes and are in fact the stated reason Congress established Everglades National Park. Although abundant, this animal life, with the exception of birds, is not diverse. The aquatic invertebrates, fishes, reptiles, amphibians, and mammals are derived from temperate North America, and their diversity decreases southward down the peninsula. In contrast, the bird fauna is enhanced by species derived from both North America and tropical sources, especially waterbirds (Robertson and Kushlan, 1984).

Invertebrates

Small invertebrates serve as important components of marsh food chains. Amphipods are extremely abundant where they are secure from predation, especially within periphyton, naiad, bladderwort, or water grass. Dragonflies and mayflies are diverse and abundant in marshes throughout Florida. Fly larvae are also common and locally abundant. These include the infamous mosquitoes and gnats as well as the larger deerflies and horseflies. Many species of water bugs and water beetles are widely distributed. When fish numbers decrease after dry periods, ostracods may become abundant. Leeches are not common in Florida marshes but do occur locally, especially on turtles and alligators.

Macroinvertebrates figure importantly in food chains. Among the most conspicuous in many marshes are prawns, crayfish (*Procambarus alleni* in the south and *P. fallax* in the north), and snails such as the apple snail (*Pomacea paludosus*) (Kushlan, 1975; Kushlan and Kushlan, 1979). Prawns abound in submersed marshes where they are sheltered by aquatic plants such as naiad and water grass (Kushlan and Kushlan, 1980b).

Fishes

The fish fauna of Florida marshes is depauperate, especially toward the southern end of the peninsula. Nearly all fish species are derived from temperate North America, with the exception of a few species in the Everglades (e.g., *Rivulus* spp.) that have affinities with the West Indies (Loftus and Kushlan, 1987). In some places, particularly the lower Everglades, the fish fauna is augmented by marine and estuarine species that are able to penetrate inland because of the chemically hard water (Odum, 1953).

Most of the fish found in Florida marshes are small, minnow-sized species, typically the livebearing mosquitofish (*Gambusia affinis*) and least killifish (*Heterandria formosa*), along with the cyprinodonts: flagfish (*Jordanella floridae*), golden topminnow (*Fundulus chrysotus*), seminole killifish (*F. seminolis*), and bluefin killifish (*Lucania goodei*). Also abundant are small sunfishes, such as pygmy sunfish (*Elassoma spp.*), bluespotted sunfish (*Enneacanthus gloriosus*), and dollar sunfish (*Lepomis marginatus*). Smaller individuals of larger species, such as warmouth (*L. gulosus*) and redear sunfish (*L. microlophus*), may be found in fluctuating marshes.

Dominance of small fishes arises from differential mortality during drying periods, when the smaller species are at an advantage (Kushlan, 1974a). Thus the size and relative abundances of species vary seasonally. One study found that small fishes—especially mosquitofish and least killifish—as well as prawns and crayfish, increased rapidly during the first six months following reflooding of a previously drained marsh (Milleson, 1976). In floodplain marshes, alternating water levels produce an explosive expansion of fish production as water levels rise (Perrin et al., 1982).

If water levels become stabilized, larger fish survive and assume dominance (Kushlan, 1980). These larger species, such as Florida gar (*Lepisosteus platyrhincus*), bullhead catfish (*Ictalurus natalis* and *I. nebulosus*), bowfin (*Amia calva*) and pirate perch (*Aphredoderus sayanus*), occur in deep marshes, ponds, and rivers and lakes adjacent to marshes. At one time, the St. Johns River supported a large freshwater fishery that was probably based on marsh productivity (Cox et al., 1976). Decreases in river fish populations followed by decline of the fisheries occurred in both the St. Johns and Kissimmee rivers after they were channelized (Perrin et al., 1982).

The fishes of the Everglades are the most studied in Florida (Kushlan and Lodge, 1974; Dineen, 1984; Kushlan, 1976a, 1980; Loftus and Kushlan, 1987). The fish community is dominated by mosquitofish, which can compose 60 percent of a sample, followed by other livebearers and killifishes, such as golden topminnow, bluefin killifish, and seminole killifish. Under typical fluctuating conditions, sunfishes are rare and small, except near canals and ponds.

Fishes of the Kissimmee marshes are also numerically dominated by mosquitofish, but Florida gar accounts for the greatest biomass (Perrin et al., 1982). Other common components are the least killifish, bluefin killifish, sailfin molly (*Poecilia latipinna*), bluegill (*Lepomis macrochirus*), flagfish, and redear sunfish. Game species, including crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*), and channel catfish (*Ictalurus punctatus*), are common in the river but not in the marsh.

Nonnative fish species have spread via canals throughout the state (Courtenay and Robins, 1973). By the mid-1970s the exotic walking catfish (*Clarias batrachus*) was present throughout the southern Florida canal system and had invaded the Kissimmee marshes (Courtenay, 1978; Perrin et al., 1982). As of the mid-1980s, nonnative species had not become a problem in the fish communities of undisturbed parts of the Everglades, though a substantial threat exists, especially from the blue tilapia (*Tilapia niloticus*) (Kushlan, 1986b).

Amphibians and Reptiles

Amphibians characteristic of deeper Florida marshes include the leopard frog (*Rana sphenocephala*), pig frog (*Rana grylio*), bullfrog (*Rana catesbeiana*), green tree frog (*Hyla cinerea*), fire-bellied newt (*Notophthalamus viridescens*), and dwarf newt (*Pseudobranchus striatus*). Water snakes, abundant in some Florida marshes, include the green water snake (*Nerodia cyclopion*), swamp snake (*Seminatrix pygaea*), cottonmouth (*Agkistrodon piscivorus*), and mud snake (*Farancia abacura*). Turtles of the deeper marshes include the mud turtle (*Kinosternon bauri* and *K. subrubrum*), musk turtle (*Sternotherus odoratus*), Florida cooter (*Chrysemys floridana*) in the north, and the red-bellied turtle (*C. nelsoni*) in the south.

Shallower marshes and wet prairies support more species of amphibians and reptiles. These include the little grass frog (*Limnaoedus ocularis*), narrow-mouthed toad (*Gastrophryne carolinensis*), leopard frog, pygmy rattlesnake (*Sistrurus miliarius*), and chicken turtle (*Deirochelys reticularia*).

The American alligator (*Alligator mississippiensis*) (fig. 10.15) assumes a dominant ecological position in many of Florida's marshes because of the "gator holes" it creates and maintains. These ponds supply dry season habitat for other aquatic organisms (Kushlan, 1974b) and serve as staging areas for recolonization of the marshlands when floodwaters return. Alligator populations throughout the state were depressed by hunting, and for a period during the 1960s the species was threatened with extinction. With protection, populations have rebounded to the point where, in some places, alligators are becoming a nuisance. Management of these large reptiles, including the reinstitution of hunting, is a matter of concern in wildlife conservation (Hines and Woodward, 1980; Jacobsen and Kushlan, 1986).

Mammals

Mammals are not as abundant in Florida marshes as they are elsewhere in North America. The Florida water rat (*Neofiber alleni*) is found throughout the state, replacing the larger muskrat (*Ondatra zibethica*), which is a dominant influence in many North American marshes. The white-tailed deer (*Odocoileus virginianus*) inhabits shallow marshes throughout Florida and is surprisingly well adapted to wetland conditions. Deer in the Everglades are distinguished from populations elsewhere by their small size and aquatic habits (Loveless, 1959a). It has recently been found that the endangered

Fig. 10.15. Alligator in an artificial "gator hole" at the mouth of a culvert, Shark Valley Loop Road, Everglades National Park. Photo by R. Myers.

Florida panther (*Felis concolor coryi*) uses marshland extensively (C. Belden, personal communication).

Birds

Waterbirds that are particularly dependent on freshwater marsh habitat include the least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), green-backed heron (*Butorides striatus*), white ibis (*Eudocimus albus*), glossy ibis (*Plegadis falcinellus*), limpkin (*Aramus guarauna*), rails (such as the king rail, *Rallus elegans*), marsh wren (*Cistothorus palustris*), common yellowthroat (*Geothlypis trichas*), red-winged blackbird (*Agelaius phoeniceus*), and boat-tailed grackle (*Quiscalus major*). A few species characteristic of Florida marshes are now considered to be rare or endangered. The original distribution of the snail kite (*Rostrahamus sociabilis*) was coincident with that of Florida's marshes (fig. 10.16; cf. fig. 10.1d) (Sykes, 1979, 1983a,b, 1984; Kushlan and Bass, 1983b). Its historic habitat included the Everglades, the marshes surrounding Lake Okeechobee and Lake Istokpoga, those along the Kissimmee and St. Johns rivers, and numerous smaller marshes. At present, the kite population is in most years limited to stabilized, deeply flooded marshes of the Everglades Conservation Areas (fig. 10.5). The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) occurs in muhly-dominated wet prairies bordering the southern Everglades (Kushlan and Bass, 1983a). Resident and wintering sandhill cranes (*Grus canadensis*) (fig. 10.17) are found primarily in the marshes of north and central Florida but range into the southern marshes in limited numbers (Williams and Phillips, 1972; Walkinshaw, 1976; Kushlan, 1982).

Wading birds, including the endangered wood stork (*Mycteria americana*) and a variety of herons, egrets, and ibis, depend on freshwater marshes, particularly those of southern Florida (Kushlan, 1973, 1976b, 1978; Kushlan and White, 1977). Resident species often nest in swamp forest vegetation and forage in nearby marshes. Mixed species colonies, usually dominated by white ibis, have exceeded 35,000 birds. Other birds that nest over much of the eastern United States use Florida's freshwater marshes in winter, when they number in the tens of thousands. For example, more than 14,000 birds were counted in the eastern Everglades each year during the mid-1970s.

The number and variety of nesting waterfowl are limited in Florida marshes. Wintering waterfowl are also not abundant (relative to sites farther north), as most of them frequent estuarine areas (Chamberlain, 1960; Goodwin, 1979; Kushlan et al., 1982; Perrin et al., 1982; Johnson and Montalbano, 1984). Mottled ducks (*Anas fulvigula*) are among the most common, and fulvous whistling duck (*Dendrocygna bicolor*) populations are increasing in the state's interior marshes. Canvasback ducks (*Aythya valsineria*) were once common winter residents of the marshes that existed

Fig. 10.16. Historic (*left*) and present (*right*) ranges of the snail kite in Florida. After Sykes, 1984.

Fig. 10.17. Nesting sandhill crane. Photo by J. N. Layne.

along the Kissimmee River, and the river floodplain was historically a major waterfowl corridor (Belrose, 1976). The most common duck overwintering in freshwater marsh habitats is the ring-necked (*Aythya collaris*). It is found throughout the state, especially in the peripheral marshes of Lake Okeechobee, along the St. Johns River, and in the deep water areas of the Everglades. Coots (*Fulica americana*) still winter in large numbers throughout Florida's fresh waters.

The diversity of other bird groups is limited by seasonal high waters.

Nesting species in the Everglades include the red-winged blackbird, common yellowthroat, boat-tailed grackle, cardinal (*Cardinalis cardinalis*), Carolina wren, king rail, purple gallinule, and red-shouldered hawk (*Buteo lineatus*); their density averages about 96 birds per km² (Kushlan and Kushlan, 1978). In winter, bird density increases to about 380 individuals per km² and includes such migrants as the eastern phoebe (*Sayornis phoebe*), belted kingfisher (*Ceryle alcyon*), palm warbler (*Dendroica palmarum*), yellow-rumped warbler (*Dendroica coronata*), and marsh wren (Kushlan and Kushlan, 1977).

Adaptations of Marsh Animals

Like the plants, animals living in marshes possess specific adaptations for surviving periodic fires and seasonal fluctuations in water levels, dissolved oxygen, and temperature (Kushlan, 1990a). An example of a bird adapted to Florida's fluctuating marshes is the snail kite (Sykes, 1983b; Kushlan, 1975; Kushlan and Bass, 1983b; Beissinger and Takekawa, 1983). These birds are nomadic, concentrating in marshes where water levels have been relatively high because their primary food, the apple snail (*Pomacea paludosus*), requires prolonged flooding. In drought, the birds are forced to use the small, widely scattered patches of marsh that remain. Historically the kites roamed throughout the state to find such patches of suitable marshes. As the density and abundance of these patches have declined through drainage, so have the kite populations.

The Cape Sable seaside sparrow requires not only specific water levels but also a predictable fire regime (Werner and Woolfenden, 1983). Marshes that burn on a five- to seven-year cycle provide optimum habitat; sparrow populations decline rapidly with longer fire-free periods.

Alligators are closely attuned to hydrological fluctuations and position their nest sites relative to water depths (Kushlan and Jacobsen, 1990).

Mammals also have specific adaptations to fluctuating water levels. Water rats move between higher and lower marshes as water levels fluctuate, and they burrow when water levels fall below the ground (Tilmant, 1975). To forage, deer wade or even swim through water that can be shoulder-deep.

The accommodations that marsh-dwelling animals make in response to hydrological fluctuations in southern Florida (Kahl, 1964; Kolipinski and Higer, 1969; Kushlan, 1974a,b, 1975, 1976a, 1977, 1979b, 1986d, 1990b; Kushlan et al., 1975; Kushlan and Kushlan, 1979, 1980b) appear to be generally applicable throughout the state (Collopy and Jelks, 1986; Perrin et al., 1982). The basic pattern consists of the annual cycle of water level fluctuation, which Dineen et al. (1974) called the "rejuvenation process." The pattern can best be illustrated by considering the annual cycle faced by marsh fishes and their major predators, the wading birds. During high water in the summer and fall, fish populations increase in number and in total biomass. When water levels recede in the late winter, standing surface water becomes shallow, higher elevations dry out, and fishes and other mobile aquatic organisms become increasingly concentrated in depressions. Densities in these pools can exceed hundreds of individuals per square meter of water surface. Alligator ponds provide one of the principal sources of dry-season pools. Another set of refugia is supplied by crayfish burrows.

A consequence of falling water levels is a decrease in dissolved oxygen. Aquatic organisms can survive in pools as long as densities are low enough that total community metabolism does not exhaust available oxygen. Predation by birds on fishes has the beneficial effect of increasing the probability that the remaining fish will survive through the dry season.

Dry-season refugia are also crucial to the survival of wading birds (Kahl, 1964; Kushlan, 1976c, 1977, 1979b, 1986d; Kushlan et al., 1975). Both wintering and nesting birds use the concentrated food resource, and continued low water level determines the nesting success of some species. The white ibis, for example, chooses its nesting colony sites near marsh areas where drying conditions are appropriate. Wood storks depend on specific falling water conditions over a prolonged four-month nesting season; the faster the marsh dries, the earlier they nest. If water levels rise, nesting success declines. This pattern is consistent in several herons (Frohring and Kushlan, unpubl.).

As the wet season commences, water levels rise. Invertebrates, which spend the dry season as eggs or cysts, hatch soon after reflooding. Mobile aquatic organisms recolonize the marsh, either from refugial ponds or from rivers. In flatwoods and highland marshes, recolonization depends on the degree of isolation. Fishes appear to be more abundant in flatwoods marshes that have a wet-season connection to deep-water habitats than in hydrologically isolated marshes (B. H. Winchester, personal communication).

Ecosystem Function

Standing crop of the vegetation in Florida marshes is quite variable. Saw grass can achieve 2800 g/m^2, while flag marshes may reach 688 g/m^2 (Hofstetter, 1976; Bayley et al., 1985). Periphyton standing crop can achieve 350 g/m^2 (Brock, 1970).

The productivity of Florida's marshes has not been thoroughly studied, but data suggest that natural rates of accumulation are relatively low. Net production is on the order of 320 g m^2 yr for a flag marsh and 150 g m^2 yr in a wet prairie (Duever et al., 1986). These values compare poorly with productivity of 700 to 2800 g m^2 yr in a marsh in the northern prairies (de la Cruz, 1978).

The relatively low productivity may be a function of the low nutrient levels of most Florida marshes. However, the primary factor influencing the productivity of Florida's marshes is the seasonal fluctuation of water level. Bayley et al. (1985) found that nutrient enrichment of a flag marsh did not increase production over that achieved by the drying and flooding cycle alone. The loss of biomass through dry-season death and decay stimulates production during the following wet period. Periodic drying and reflooding also mobilize nutrients bound in plant material and in the soil.

Human Influences and Management

Highland Marshes

Most small highland marshes have been drained for farming or used in conjunction with adjacent dry prairies for cattle grazing (Camp, 1932). Some, such as Florahome and Black Sink prairies, have been mined for peat (Davis, 1946).

Among the larger remaining highland marshes, few are afforded any permanent protection. At Paynes Prairie, which is a Florida State Preserve, the principal management goal is "to restore, as nearly as possible, the conditions that existed on and around the basin during Bartram's visit" (i.e., 1774) (Florida Department of Natural Resources, 1981). Management involves imitating natural processes with manipulations, including regulating water inflow and outflow, conducting controlled burns, controlling exotic plants, and grazing.

Because water depth and its fluctuations have determined the character of Paynes Prairie throughout its history, water entering and draining from the prairie is regulated by structural means to simulate water cycles that would have occurred naturally. Control of incoming nutrients is a problem that needs attention (Dugger, 1976). Managing as a historic landscape does ignore the fact that marsh systems such as Paynes Prairie are highly dynamic. An alternate management strategy has been proposed to manipulate water levels to reset successional patterns every thirty to fifty years (White, 1975). The objective of such a plan would be to perpetuate a natural successional cycle rather than to mimic perpetually the conditions that prevailed at a particular time in the past.

Flatwoods Marshes

Many flatwoods marshes have been drained, either by general lowering of the groundwater or by ditching. Most are used for cattle grazing, and the composition of plant associations is often the result of the grazing and burning (Laessle, 1942). St. John's-wort and maidencane become scarce in areas of heavy cattle use and may be replaced by smartweed and prairie grasses.

Rooting by hogs also adversely affects these marshes (Winchester et al., 1985). The recognition that complexes of flatwoods marshes serve as groundwater recharge areas has led to their use as well fields, but wells can draw down water levels, with attendant changes in plant associations (Rochow, 1985).

Management of flatwoods marshes involves protection from development followed by active management to counteract the effects of groundwater lowering. Additionally, these marshes require prescribed fire. It is likely that with proper management flatwoods marshes can be used judiciously as groundwater recharge areas and well fields while being maintained in a relatively natural state (Winchester, 1986).

The St. Johns Marshes

Alteration of the St. Johns floodplain began with the construction of a road and levee between 1910 and 1914, which cut off Blue Cypress Lake and the St. Johns River from their headwater marshes. Reclamation for agriculture and channelization of the river followed (Goolsby and McPherson, 1978). More than 70 percent of the basin is now used for cattle production, and the marshes and swamps feeding the river have been reduced by 65 percent (Lowe, 1983).

The results of these changes have been segmentation of the continuous floodplain, isolation of remnant marsh patches, loss of floodplain water storage capacity, rapid movement of water between previously unconnected basins, decrease in water storage, increase in flood stages in the river, and reduced dry-season river flow (Tai and Rao, 1982; Lowe, 1983). The remaining marsh is confined to a few reservoirs and lake edges.

These changes—particularly those that affect the frequency of inundation—caused the replacement of saw grass marshes by cordgrass and woody species, which increased in coverage by 89 percent between 1943 and 1980–81 (Cox et al., 1976; Lowe et al., 1984). Waterfowl and wading bird populations have decreased markedly in recent decades (Sincock, 1959; Florida Game and Fresh Water Fish Commission, 1981; Lowe et al., 1984). From 1948–58 to 1972–80, wintering waterfowl decreased 75 percent. Numbers of wading birds, which nested in nine colony sites in the late 1970s, are similarly much reduced. In 1930, for example, 15,000 white ibis were reported to have nested in the marshes of Lake Washington, but nowhere near that number of birds nests there today. Likewise, snail kites bred in considerable numbers in the early part of the century (Howell, 1932), but today they are rare.

After several decades of planning and implementing ill-advised flood control projects, the management plan of the St. Johns River basin now emphasizes the preservation and restoration of plant and animal resources and takes into account the importance of the hydrologic gradient and associated fire regimes. Primary management emphasis is placed on the river and its lakes because of their roles in water supply and flood control. However, the historic importance of the surrounding marshes in maintaining the quality of the deeper water habitats is now recognized (Brooks and Lowe, 1984). Plans call for a semistructural approach to flood control and water management to be implemented through purchase and restoration of the marshes and the development of water conservation areas (St. Johns River Water Management District, 1977, 1979; Brooks and Lowe, 1984).

A semistructural approach, which involves small structural modifications, may be the best management strategy for nearly all Florida marshes. This approach allows natural hydrologic regimes to be reestablished, corrects reversible changes, and maintains the managers' ability to manipulate the system if required.

Several other aspects of this plan merit special notice by the managers of Florida's marshes. One is its acknowledgement that acquisition of additional marshland is necessary. Another is the recognition that changes in the floodplain are mostly irreversible (Brooks and Lowe, 1984). Computer simulations indicate that drained marshes can never be restored to their primitive condition because elevations have been lowered by soil subsidence and oxidation. A third aspect is the realization that existing wetlands must be actively managed by structural means. Restoration of marsh function will require manipulation of the fluctuations and depths required by the plant communities and other aquatic organisms (Lowe, 1983; Brooks and Lowe, 1984).

The Kissimmee Marshes

Like the St. Johns basin, the Kissimmee floodplain has been drastically altered by drainage and flood control projects (Dineen et al., 1984). A plan to manage the river was authorized by Congress in 1948. It involved using lakes as reservoirs, connecting them by canals, and channelizing the river to carry floodwaters south into Lake Okeechobee. The resulting channel, which is half the length of the original river, is flanked by discontinuous spoil piles. Flow is regulated by six control structures that drop water in 2 m decrements. Water levels behind these structures were stabilized; the downstream portion of each pool is constantly inundated by up to a meter of water while the upstream portion remains relatively dewatered.

Hydrologic modifications and dewatering in the Kissimmee basin have resulted in the overall loss of marshes and alteration of those that remain (Goodrick and Milleson, 1974; Haeney and Huber, 1975; Pruitt and Gatewood, 1976). Grazing also has had an impact; improved pasture covers more than 30 percent of the original floodplain (Frederico et al., 1978). Milleson et al. (1980) found that more than 42 percent of the land in one area had been developed and that only 24 percent remained as marsh vegetation. The complexity of the present plant associations—such as floating tussocks, mixed grass marshes, and nearly floating pickerelweed marsh—is the result of stabilized high water levels (Milleson et al., 1980). Hydrologic modifications have also increased the rate of eutrophication of Lake Okeechobee and caused reductions in waterfowl populations (U.S. Fish and Wildlife Service, 1958; Perrin et al., 1982). Animals using the Kissimmee marshes and other parts of the basin have been greatly affected by the changes (Perrin et al., 1982). Fish populations in both the marsh and the river have been reduced by hydrologic stabilization. Waterfowl food, and therefore waterfowl populations, have also been reduced.

For decades, the appropriate management of the Kissimmee basin has been a matter of intense debate. It has centered on the recognized need to abate the environmentally adverse effects of channelizing the Kissimmee River (Marshall et al., 1972; Dineen et al., 1974). The largest remaining marshes are near the lake and in the southern flooded portions of each impoundment. As in the case of the St. Johns River, marsh acquisition is an important first step, and several sites in the Kissimmee basin have been proposed for preservation.

Management of the remnant marshes of the Kissimmee basin requires restoration of a fluctuating water regime. It is clear from the studies of Perrin et al. (1982) that restoration would enhance fish and wildlife habitat, improve water quality, increase water storage capacity, and restore aspects of the riverine-wetland ecosystem. It is generally believed that backfilling the canal is an important overall first step. The efficacy of the second step—semistructural management of isolated marshes—has been shown by Perrin et al. (1982), and the possibility of dechannelization is being studied in a demonstration project (Palmer, 1986). Other aspects of the state's management strategy are to purchase additional floodplain, expand management to abate nonpoint pollution, and develop a model of dechannelization effects.

It is clear, however, that complete restoration of the Kissimmee Marsh is not possible, given existing flood control requirements. As in the St. Johns marshes, the best alternative is to reestablish as much marsh and river flow as possible and otherwise impede the downgradient flow of water by structural controls. Restoration of functioning marshes both adjacent to and isolated from the river would require additional structural control.

The Everglades

The Everglades have been much altered by flood control and water management (Blake, 1980; Kushlan, 1986a,c, 1990b). Despite early attempts at drainage, the vastness of the Everglades prevented the near total loss of marsh habitat experienced in the St. Johns and Kissimmee valleys. Nevertheless, cross-Everglades canals were operable by 1921, and a levee around

Lake Okeechobee was completed in 1924. Drainage was most effective along the periphery, particularly along the east coast.

Most of the loss of marshland in the Everglades resulted from drainage for farming, the largest loss occurring immediately south of Lake Okeechobee (Jones, 1948). Additional land was "reclaimed" east of the Everglades, a loss consisting primarily of wet prairie and sparse saw grass marshes (Birnhak and Crowder, 1974; Hull and Meyer, 1973). Drainage of the Loxahatchee Slough began in 1913 and led to the near total reclamation of that marsh. Overall, 65 percent of the original Everglades has been irretrievably drained; in completely drained places, dewatered peat has subsided at a rate of about 3 cm per year (Stephens, 1984; Stephens and Johnson, 1951).

The central core of the Everglades proved exceptionally difficult to drain and was unsuited for agricultural development. The lack of control of seasonal and catastrophic high water, however, led to the establishment of a flood control district in 1949; this in turn led to the enclosure of the remaining Everglades and its isolation from reclaimed lands to the north and east.

Superimposed on the dramatic loss of peripheral marsh habitat were the effects of water impoundment within the leveed core of the Everglades for flood control and water storage. These impoundments are known as "conservation areas." The former Hillsborough Lakes marsh is enclosed in Conservation Area 1, the Loxahatchee National Wildlife Refuge (see fig. 10.5). South of the conservation areas lies Everglades National Park and the undeveloped wet prairie to its east, known as the East Everglades. The compartmentalization of the Everglades system preserved the marsh character of the landscape, but it also markedly altered water flow and flood cycles.

Flood control and water regulation have had profound effects on the marsh plant communities (McPherson, 1973b; Alexander and Crook, 1984). From 1940 to 1970, swamp trees and shrubs nearly disappeared from the flooded southern end of Conservation Area 3, and saw grass marsh was displaced by water lily marsh. Conversely, marsh associations have been replaced by drier communities in the dewatered northern end. In Conservation Area 2, prolonged flooding caused loss of swamp islands and flag marsh and changed the depositional characteristics of the peat (Worth, 1983).

Bird populations responded dramatically to the changes. The wood stork and other species of wading birds have decreased in numbers as a direct result of hydrologic alterations (Kushlan et al., 1975; Kushlan and Frohring, 1986; Kushlan, 1990b). These same alterations have had a beneficial effect on the snail kite (Sykes, 1983a, 1984). In addition, excessive water discharges from the conservation areas into the national park have increased the flooding of alligator nests (Kushlan and Jacobsen, 1990).

Water management practices have also changed the chemistry of Everglades water. In Conservation Area 2, for example, 57 percent of the surface water in the interior marsh is derived from canal inflows that have been mineralized by contact with the limestone bedrock (Millar, 1981). The ionic composition of water flowing into the southern Everglades has been similarly affected by canal deliveries. Chloride concentration has increased from 10 to 70 mg/L since 1959 (Klein et al., 1975; Flora and Rosendahl, 1982b).

Management of the Everglades, like the management of the Kissimmee marshes, has been the source of considerable debate. As in the Kissimmee marshes, appropriate management of the Everglades must take into account the irreversible loss of marsh habitat, the requirements of individual species, and the valid needs of the many human users of Everglades resources (Kushlan, 1979a, 1983, 1986a,c, 1990b). It must involve restoration of meteorologically based patterns of water level fluctuations in the natural-area zone, most notably Everglades National Park. However, flood control and human water supply needs must continue to be met by retaining water in the conservation areas, conserving water in the dry season, and releasing excess in the wet season. Thus, ironically, restoration may require additional structural and semistructural controls of water movement and active management of all component areas just as in the St. Johns and Kissimmee.

Conclusion

Given their distinctive plant and animal populations, Florida's marshes are clearly worth conserving for their own sake and for their scientific value. In addition, they maintain the overall quality of human life in the state. Environmental services performed by marshes include recreation, flood control, water storage and supply, production of fish and wildlife, provision of habitat for nonharvestable species including endangered and rare animals, some agriculture, water quality maintenance, and wastewater renovation. Concerning the last, state legislation—the Warren S. Henderson Wetland Protection Act of 1984 (FS 403.918)—mandates permit issuance, consideration of cumulative impacts, and establishment of regulatory criteria for using wetlands for wastewater disposal.

The principal cause of ecological degradation of Florida's marshes has been dewatering, a dominant force in the political and social history of the state. Loss of marsh has continued in recent decades, mostly due to agricultural conversion (Hefner, 1986). The initial objective of marshland conservation in the state is the purchase and reflooding of drained marshes. Considerable progress has been made in reclaiming Florida wetlands, especially after phosphate mining (Clewell, 1981; Shuey and Swanson, 1979; Erwin and Best, 1985).

Although the loss of marsh area is the most obvious component of the degradation of Florida wetlands, a second factor is more subtle but no less important: the loss of wetland function in those marshes that remain

(Kushlan, 1990b). Given the dependence of plants and animals on specific inundations, it should be clear that modifications of the hydrologic cycle alter the distribution and abundance of various species and, therefore, the character of the wetland ecosystem. Such changes have been repeatedly documented in Florida marshes. The natural history and population status of the snail kite and the wood stork in Florida reflect the history of drainage and functional alterations of the state's marshes.

The similarities in the ecology of Florida marshes and the demonstrated effects of changes in the plant and animal populations dependent on them hold promise for their effective management. Several generalizations emerge from a consideration of the history and character of Florida marshes.

1. Most of the loss of Florida marshes was due to drainage, and only a small but important part of this loss is reversible.

2. Loss of the natural fluctuation of water levels in the remaining marshes has caused drastic changes in the functioning of these ecosystems.

3. Marshes are useful for flood control and water supply management, and these services can be supplied conveniently to nearby developed areas.

4. Storage of water in wetlands has led to their alteration because the area available for storage now is so much less than when the entire natural marsh area was intact. There is more water to be stored on less land; thus water levels may be higher and dry seasons shorter. As a result, remnant marshes can have higher than natural water levels in the dry season.

5. Because of the above factors, structural control and continued managed manipulation of water levels is not only inevitable but desirable. Semistructural solutions emphasizing natural fluctuations, restoration of sheet flow, and reduction of canal flow except when absolutely required for health and safety would yield substantial returns.

6. The diverse demands placed on marshes, ranging from flood control to wildlife conservation, can be coordinated through management techniques that simulate the natural fluctuation of water levels but are constrained by criteria based on biological and hydrologic goals.

7. To the extent that these needs cannot be coordinated, management goals must be chosen for a particular patch of marsh; different patches may be zoned for different purposes. It may be that only in a large natural zone would the appropriate management goal be to restore a naturally functioning marsh ecosystem.

8. Because of history, conflicting demands, and management limitations, some of the natural functioning of Florida's marshes can never be recovered.

9. Only active management will assure the future of the remnants of Florida's once great marshlands.