3

Freshwater Wetlands

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INTRODUCTION

The purpose of this chapter is to introduce the major types of freshwater and inland wetlands with emphasis on their salient characteristics. As discussed more fully in Chapters 2 and 5, wetlands are ecosystems having shallow water standing above the soil surface or having a soil saturated with water for periods of time that are sufficient to produce characteristic soils or vegetation. Thus, freshwater wetlands are identified by specific water conditions including their shallowness, soils, and plants. Specifically, inland freshwater wetlands are those having consistently low concentrations of ocean-derived salt (less than about 0.5 parts per thousand) in the water and in the hydric soils, plants adapted to fresh water, and limited influence of diurnal tides. Estuarine and marine wetlands, which lack this suite of characteristics, are described in Chapter 4.

There are many types of freshwater wetlands. Approaches to describing, identifying, and delineating wetlands for legal purposes are discussed in Chapters 5 -7. As noted there, these can be controversial, reflecting both the high stakes in the outcome of classification and delineation exercises, and the inherent difficulty one has in achieving a universally acceptable nomenclature for any set of natural ecosystems that vary in a continuous rather than discrete manner. It is important to regulators to have a consistently applied way to delineate and name wetlands, so that they are able to distinguish wetlands and delineate their boundaries for permitting purposes. But such delineation is far less important to scientists, who are more interested in ecosystem function within a wetland than in drawing a boundary or insisting on a specific name. In the United States, the scheme of classification and nomenclature created by the U.S. Fish and Wildlife Service has been adopted and used with some success by some regulators (Cowardin et al., 1979). However, such universal classification schemes may or may not reflect vernacular names or reflect all the differences and similarities among wetlands that have ecological importance in a specific study.

Most wetlands are, in fact, readily identifiable, irrespective of the workings of universal classification schemes and controversial details of wetland delineation. For the purposes of this chapter, freshwater wetlands need only be categorized into vernacularly familiar types that are as easily recognizable by the nonscientist as the scientist. In this chapter several such readily identifiable types are reviewed that together encompass much of the diversity of freshwater wetland ecosystems in the United States. The divisions used here can be readily correlated with the more finely divided regulatory definitions of Cowardin et al. (1979).

Shallow freshwater ecosystems may be most conveniently divided into swamps, marshes, and bogs, as further described in Sections 3.1, 3.2, and 3.3, respectively. These may be subdivided in many ways, such as by dominant vegetation, geography, basin morphology, nutrient sources, or water supply. Recognition of a wetland by dominant plant type is one of the more common approaches to classification. By convention, "dominance" is the coverage of more than 30% of the surface area of a wetland by a plant type. Another important approach to classification is by basin morphology and water source. In this scheme, wetlands can be classified into palustrine wetlands or floodplain wetlands. Palustrine wetlands generally occupy basins. They are shallow with limited influence of flowing water and so often have an extensive cover of aquatic emergent or submersed vegetation. Such palustrine ecosystems are the ones most commonly thought of as wetlands by both scientists and the public. Floodplain wetlands are influenced by and associated with the flowing water of rivers and streams.

An important characteristic of wetlands is the shallowness of their water depths. However, freshwater wetlands and deep water habitats are not always ecologically separable. In many cases, emergent or submersed wetlands form a fringing habitat adjacent to deep water ecosystems, which are likely to have considerable interchange of water and materials. In general, wetlands are aquatic sites shallower than 2 m deep. Although somewhat arbitrary, an ecological basis for this demarcation that 2 m is about the depth to which erect, self-supporting aquatic plants could be expected to grow. Beyond the depth of rooted plants, the patterns and pathways of energy and nutrient flows differ from those in emergent wetlands. Of course, the 2 m limit is not always the case, because some shallower wetlands lack rooted plants and deep, clear aquatic systems support luxurious plant growth. Ponds may be wetlands in some classifications and not in others. They often are depressions within extensive emergent wetlands. For completeness and contrast, the major deep water aquatic systems, streams, and lakes, are briefly noted in Section 3.4.

3.1 SWAMPS

In different parts of the world, the term "swamp" has different meanings, an important point if one wishes to access the literature. In Europe, the term generally refers to herbaceous or forested wetlands with mineral-rich nonorganic soil. In other parts of the world, swamp refers to dense and extensive herbaceous wetlands, such as the reed swamps of Africa. In the North America, however, the term "swamp" typically means a wetland dominated by woody plants.

Swamps are of two types, swamp forests (or forested wetlands) and shrub swamps (or shrub wetlands). Swamp forests are wetlands dominated by trees, whereas shrub swamps are dominated by shorter woody plants. Since most swamps contain both tall and short woody plants, as well as herbaceous vegetation, a delimiting rule is useful. A forested wetland would be more than 30% covered by woody plants taller than 6 m; a shrub wetland would lack this dominance by tall trees and would be more than 30% covered by shorter woody plants (Cowardin et al., 1979).

Both swamp forests and scrub swamps may be dominated by broad-leaved trees or narrow-leaved trees, by deciduous trees or evergreen trees. Broad-leaved swamp trees include alder (*Alnus*), ash (*Fraxinus*), bay (*Persea*), or gum (*Nyssa*); narrow-leaved swamp trees include wetland conifers such as spruce (*Picea*), cedar (*Chamaecyparis*), cypress (*Taxodium*), or tamarack (*Larix*). Shrub wetlands may be dominated by broad-leaved plants, such as alder, ericaceous shrubs (*Vaccinium, Chamaedaphne, Andromeda, Ledum, Kalmia*), or birch (*Betula*), or by narrow-leaved plants such as dwarf cypress, spruce, or pine (*Pinus*). It is worth noting explicitly that in wetlands, narrow-leaved trees are not necessarily evergreen, nor broad-leaved plants deciduous. Two of the most important North American swamp trees, the cypress of the south and the tamarack of the north, are deciduous conifers.

These and other tree and shrub species can combine into a large variety of dominant plant communities, depending on how finely one wishes to subdivide vegetative descriptors. Some of the major and readily identifiable sorts of swamps in the United States include the cypress swamps of the southeastern United States, palustrine hardwood swamps found over much of the continent, shrub wetlands, and floodplain forests associated with river valleys. These categories, of course, overlap to a great extent.

3.1.1 Cypress Swamps

Cypress swamps are characterized by a peculiar, ancient conifer, the bald cypress (*Taxodium distichum*), which gets its common name from its deciduous habit. The best development of this swamp association occurs typically in relatively deep moving water of the humid southeastern USA (Figure 3.1; Plate IV-V) (Ewel and Odum, 1984). Those occurring in floodplains are a type of southern bottomland forest (divided in this chapter between cypress and hardwood forests). They are often associated with hardwoods and after disturbance may be succeeded by hardwood swamps. Cypress swamps also develop as stillwater, palustrine swamps, and as shrub swamps. They have many colloquial names, some of which have a high degree of technical specificity, such as domes, heads, strands, sloughs, scrub, and brakes.

Geophysical Characteristics. Cypress swamps occur in a wide variety of geomorphic situations ranging from broad, flat floodplains to isolated basins. These swamps are found throughout much of the lowlands of the southeastern and south-central United States. The most northern example of this type of swamp is in southern Illinois (Anderson and White, 1970). Several sorts of cypress swamps are easily recognizable.

Cypress domes are small, more or less circular swamps up to about 10 hectares, having taller trees in the center and smaller trees

Figure 3.1: Cypress swamp, showing cypress trees in the Okefenokee Swamp, Georgia. (J.A. Kushlan)

along the margin, giving the canopy a domed appearance. Also called cypress heads, they are stillwater, palustrine systems, occupying topographic depressions in clay or sandy soils, topped by a layer of peat in the center, and underlain by an impermeable clay or hardpan layer. Dwarf cypress covers much of southern Florida both east and west of the Everglades. Trees are generally of shrub stature and are locally called scrub cypress, with interspersed domes or strands of taller cypress trees. These swamps occur in sandy soils, sometimes thinly veneering, intermittently outcropping limestone bedrock. Although the surface water does flow, it does so slowly that these swamps are more like basin wetlands.

Cypress strands are similar to cypress domes but elongated in the direction of surface water flow. Also like domes, taller trees occur in the center of the strand with shorter trees toward the periphery. Cypress strands, often called sloughs, are riverine systems, essentially shallow, slow-moving, intermittent streams in a very gently sloping topography. Cypress riverine swamps are floodplain systems that occur in periodically to permanently flooded depressions within a river flood plain. Fringing cypress swamps occur along the sloping margins of lakes and ponds.

Wetland Criteria Characteristics. *Vegetation.* The cypress swamp takes its name from its dominant tree, the bald cypress, a deciduous conifer (Ewel and Odum, 1984). The wide distribution of these swamp types is due to the broad tolerances of the cypress with respect to water levels, anaerobic sediments, and nutrient conditions. Historically, two species have been recognized taxonomically, with the smaller pond cypress being distinguished by leaf morphology. Whether the pond cypress (called *Taxodium ascendens*) is taxonomically different from the bald cypress at the species, subspecies, or varietal level remains unresolved. Useful references on cypress swamp vegetation include Monk (1966), Musselman et al. (1977), Schlesinger (1978), Clark and Benforado (1981), Wharton et al. (1981, 1982), Conner and Day (1982, 1987), Schomer and Drew (1982), Drew and Schomer (1984), Dorge, et al. (1984), Duever et al. (1984), Conner et al. (1986), Tiner (1988), Hook and Lea (1989), Ewel (1990), Mitsch and Gosselink (1993), and Wilen and Tiner (1993).

Bald cypress can be very large trees, not atypically up to 40 m tall with a trunk diameter in excess of 1.5 m. Trunk diameters in excess of 5 m and heights in excess of 50 m have been reported. Many of the oldest and largest bald cypress trees were lumbered early in the present century, since their soft wood is rot resistant. It is likely that some of these lumbered trees were 400-600 years old. Trees over 200 years old remain in some swamps.

A characteristic adaptation of the tree is its growth of trunk buttresses and root protuberances called knees. Buttressing occurs especially in deeply flooded water, such as occur in fringing swamps and deep strands. The buttresses are reminiscent of those of tropical rain forest trees, which function in providing support for a shallow rooted large tree. It is almost certain that this is their function in bald cypress as well. The height of buttresses on old trees can be an indication of water levels prior to drainage. The knees also occur primarily under flooded conditions. They are elongated, tapered structures that emerge from the water to as much as 1 m or more above the soil. At present, the function of the knees is unclear, but they are similar to the pneumatophores of many swamp trees, and so most likely function in root respiration.

Despite the wide tolerances of adult trees, conditions for establishment of cypress seedlings are more restricted (Conner et al., 1986, Huenneke and Sharitz, 1986). An important requirement of cypress seeds is that they need nonflooded soil to germinate. As a result, seasonal or periodic drydowns may be required to establish a forest. Drying is seasonal in forests, such as dwarf cypress or domes, but is less frequent in fringing cypress swamps. After seed germination, shoot elongation is relatively rapid to keep pace with rising water levels. Since cypress can persist for decades or even centuries, germination events need not be frequent for a forest to maintain itself without logging or other human disturbance. Natural regeneration in existing cypress swamps appears to be low.

The stature of a cypress depends primarily on the quality of its growing conditions. The taller stature of trees in the center of a cypress dome or strand reflects deeper soils and longer hydroperiods. The trees become smaller towards the periphery where the organic soil is shallower and hydroperiods shorter. Dwarf "pond" cypress growth form occurs under even poorer growing conditions, particularly in shallow, nutrient poor, sandy soils. Dwarf cypress swamps also experience shallow water depths, shorter hydroperiods, limited surface water flow and, therefore, nutrients, and recurrent fires.

A co-dominant in deepwater cypress swamps is the water tupelo (*Nyssa aquatica*). The tupelo is sometimes found in pure stands within a cypress swamp, and dominance of this and other broad-leaved trees in cypress swamps appears to have increased as a result of logging that opened the canopy in previous decades. Other typical and co-dominant trees include the black gum (*Nyssa sylvatica* var. *biflora*), pumpkin ask (*Fraxinus profunda*), and slash pine (*Pinus elliottii*) in shallower sites.

Many of the cypress swamps in southern Florida are undergoing invasion by a exotic swamp tree, the cajeput or paperbark (*Melaleuca quinquenervia*, see discussion in Section 2.2.2). In Australia this tree dominates swamps that are subject to wide extremes of flooding, drying, and fire. As a result it is highly predisposed for success in the less stringent cypress swamps of semitropical North America. Melaleuca strands and domes are replacing cypress strands and domes. Those swamps that have experienced invasions by melaleuca appear to have suffered reduced biodiversity among both understory plants and associated animals.

The understory of cypress swamps varies greatly, depending on such factors as geography, light penetration, history of logging, water depth, and availability of hummocks, knees, or fallen timber, where plants can gain a foothold. In domes and strands, in addition to the gums, and depending on location, the understory may include swamp bay (*Persea palustris*), sweet bay (*Magnolia virginiana*), holly (*Ilex cassine, Ilex glabra*), lyonia or fetterbush (*Lyonia lucida*) willow (*Salix caroliniana*), red maple (*Acer rubrum*), wax myrtle (*Myrica cerifera*), buttonbush (*Cephalanthus occidentalis*), and virginia willow (*Itea virginica*). In lake-edge swamps, tupelo, ash (*Fraxinus caroliniana*), and maple (*Acer* spp.) are associated with the cypress. In floodplain swamps the understory includes buttonbush, hackberry (*Celtis laevigata*), willow (*Salix nigra*), and swamp rose (*Rosa palustris*). In dwarf cypress, the understory is sparse but includes wax myrtle, holly, smaller cypress and pines.

The herbaceous layer includes aquatic species, although more terrestrial annuals occur during the dry season. The cypress dome herbaceous layer includes ferns (*Woodwardia virginica, Osmunda cinnamomea*), lizard tail (*Saururus cernuus*), red root (*Lachnanthes caroliniana*), pipewort (*Eriocaulon compressum*), various vines, and panic grasses (*Panicum* spp.). The cypress strand has the most diverse herbaceous layer, owing to the abundance of fallen logs and knees that provide a substrate for colonization. However, the density and coverage of herbaceous plants may be restricted where light penetration is low due to the dense canopy cover. The herbaceous layer in cypress strands includes ferns (*Blechnum serrulatum, Nephrolepsis exaltata, Thelypteris kunthii*), and grasses (*Andropogon* spp.). The deeper water pools are characterized by water fern (*Azolla* sp.), duckweed (*Spirodela polyrhiza*), and water lettuce (*Pistia*), and in recent years, water hyacinth (*Eichornia crassipes*). The dwarf cypress has a diverse understory of grasses and flowering herbs. Where light penetration is sufficient in cypress swamps, epiphytic algae can be important contributors to production (Atchue et al., 1983).

Cypress has rough bark, which along with the moderate climate in the closed canopy of a cypress forest makes the tree an excellent substrate for vines and epiphytic plants. These especially include ferns, such as resurrection fern (*Polypodium polypodies*), spanish moss (*Tillandsia usneoides*), and other bromeliads (*Tillandsia* spp.), and orchids in the extreme south.

Soils. The base substrate of cypress swamps may be sand, clay or organic. As a result, soil chemistry varies from acidic to neutral Ph, low to high ion exchange capacity, and low to high organic content. Peat deposition is characteristic of deeper water sites, such as the center of a cypress dome or strand. The thickness of the deposit decreases toward the edge. Strands tend to deposit peat in the deeper pools and adjacent to the central drainage way. Peat does not usually accumulate in shallow water, short hydroperiod sites, or particularly at sites subject to periodic burning.

Hydrology. Cypress swamps are wet for much of the year but most experience a seasonally fluctuating water regime. Because water conditions vary from year to year, intermittent droughts may last several months, during which the swamp can be without surface water. Higher productivity appears to occur in cypress swamps with greater water flow probably because flowing water aerates the soil and imports nutrients. Decomposition and solubilization products, such as tannin, may stain the water brown.

Water flow patterns vary among cypress swamps. Cypress domes are stillwater systems, flooded by rainfall and surface flow. Cypress strands occur in slowly flowing waters, following the downstream trend of the watercourse. Water flow in dwarf cypress is even slower. Fringing cypress swamps are connected hydrologically with their adjacent lake during high water seasons and subject to wind and density driven exchanges of water. Floodplain cypress swamps experience river flows during flood and are more isolated from the river during other parts of the year.

Hydroperiod also differs among swamps. Fringing and floodplain cypress swamps have the longest hydroperiod since both connect to the deeper water habitats in the wet season. They may not dry in some years. Domes and strands have the next longest hydroperiod, usually experiencing a seasonal dry period, although the deeper central ponds of the dome or strand may retain water through a normal dry season. Dwarf cypress swamps have the shortest hydroperiods and may be dry for several months per year.

Cypress swamps can be affected by environmental alterations. Drainage decreases the hydroperiod, whereas damming water courses increases the hydroperiod. The basic forest that developed in response to the naturally fluctuating hydrology may persist for some time under altered conditions, but recruitment patterns may be altered leading to succession to other forest or wetland types.

Because most cypress swamps are underlain by impermeable soil layers and the wetter swamps lay down a peat layer on top of the substrate, there is little vertical discharge or recharge. Ground water recharge does occur at times of high water along the edges of cypress domes and presumably in other cypress swamps that occupy distinct basins.

Relations between cypress and hydrology are reciprocal. The needle-leaved cypress has lower evapotranspiration than the nearby upland forest, and its deciduous habit further reduces evapotranspiration during the dry, winter season in Florida. Invasion of the evergreen malaleuca may increase annual water loss in these swamps.

Characteristic Fauna. The cypress swamp fauna is characteristic of southeastern swamps. The types of animals comprising the invertebrate community depend on water depth and duration of flooding, current, substrate, food availability, and oxygen levels (Sklar, 1985). Characteristic groups include oligochaetes, fly larvae, amphipods, isopods, crustaceans (especially crayfish), and mollusks. The large amount of detritus and deep water conditions in the deeper cypress swamps produce a substantial invertebrate community contrasted with those in shorter hydroperiod sites.

Fish communities respond to fluctuating water levels, with larger individuals being found in deeper ponds during the dry season (Kushlan, 1976). Species adapted to endure low oxygen levels have higher survival during dry periods (Kushlan, 1974a). These include fish that can breath atmospheric air, such as bowfin (*Amia calva*) and gar (*Lepisosteus* spp.), those that can endure low oxygen, such as bullheads (*Ictalurus* spp.), and those that can use the oxygenated surface layer, such as mosquitofish (*Gambusia affinis*). The larger species are, therefore, common in the deeper swamps and those with deeper ponds that serve as dry season refugia, whereas mosquitofish are common in shallow systems, such as dwarf cypress. Fringing and floodplain cypress swamps serve as spawning sites during flooding.

Various aquatic vertebrates of the southern United States are also found in cypress swamps. Water snakes (*Nerodea* spp.) and the cottonmouth (*Agkistrodon piscivorus*) can be exceptionally abundant, especially around ponds in the dry season. The American alligator (*Alligator mississippiensis*) is common throughout its range, and is often responsible for maintaining deep water ponds (Kushlan, 1974b).

Birds are abundant in cypress swamps, especially in winter. Among those frequently found there are the pileated woodpecker (*Dryocopus lineatus*), prothonotary warbler (*Protonotaria citrea*), and blue-gray gnat-catcher (*Polioptila caerulea*). Wood ducks (*Aix sponsa*) nest in tree cavities. Limpkins (*Aramus guarauna*), with their piercing call, are especially typical in Florida. Wading birds feed in shallow water, with green-backed herons (*Butorides virescens*) occurring throughout the swamps. Larger species of herons, ibises, and the wood stork (*Mycteria americana*) nest in colonies in cypress trees and feed in shallow water. Two extinct birds species were found in cypress swamps, the Carolina parakeet (*Conuropsis carolinensis*) and the ivory-billed woodpecker (*Campephilus principalis*).

Mammals are less abundant than in other nearby habitats. Those that are found typically include the white-tailed deer (*Odocoilus virginiana*), the black bear (*Ursus americanus*), panther (*Felis concolor*), fox squirrels (*Sciurus niger*), mink (*Mustella vison*), and raccoon (*Procyon lotor*). The introduced wild boar (*Sus scrofa*) occurs over much of the area.

Wetland Values. The hydrologic values associated with cypress swamps are many. Floodplain swamps serve to retard runoff during floods, decreasing the severity of downstream flooding. Cypress domes probably recharge ground water at their periphery. Because of their leaf morphology and deciduous habit, cypress trees transpire less water annually than an equivalent evergreen or broad leaved tree.

Cypress domes have been shown to be capable of serving as sinks for nutrients, and probably serve this function in some locations (Atchue et al., 1983; DuBusk and Reddy, 1987; Dierberg and Brezonik, 1983). Cypress swamps are highly productive in supporting wildlife, including hunted species, such as squirrels, deer, and hogs, and nongame wildlife. Some species, such as the limpkin, common in cypress swamps, have a limited distribution in the United States. The wood stork, which nests and feeds in cypress throughout its North American range, is an endangered species. Floodplain cypress swamps may be important as nursery grounds for game fish, but this is not well understood. Cypress has been harvested for many decades for its wood. Even today, lumbering of cypress knees and trees to make curiosities and of dwarf cypress for poles continues in some areas. Given the slow growth rates, sustainable harvest of timber may not be practical. Cypress swamps create some of the more spectacular landscapes in North America. They epitomize southern swamplands.

Unusual Characteristics. Cypress itself is an unusual species, with its knees, buttresses, deciduous habit and ancient lineage. Fire is an important element of cypress swamps. Short-hydroperiod dwarf cypress swamps burn relatively frequently, often with little harm to the tress as the fire moves quickly across the sparse herbaceous layer and does not ignite the mineral soil. Longer-hydroperiod swamps burn infrequently. A dry season fire in a cypress dome or slough can kill large trees by burning out their roots, toppling the trees, and burning the accumulated peat, in some cases resulting in the formation of deeper pools, which inhibits recolonization of the site by cypress.

3.1.2 Palustrine Hardwood Swamps

Palustrine hardwood swamps are stillwater wetlands that occupy basins (Figure 3.2; Plate I) (Monk, 1965, 1966; Wharton et al., 1982; Vince et al., 1989). Hardwood swamps are dominated by various species of broad-leaved hardwoods, which may be deciduous or evergreen. (In this context, hardwoods are distinguished from softwoods, such as cypress and pine.) These woody plants are of tree stature (6 m or greater), or would reach that stature given sufficient developmental time. These forests are often associated with cypress swamps. In some cases, they have developed in former cypress swamps following logging. Their rapid growth rates and the intolerance of cypress for shading probably account for the shift in dominance. Palustrine swamps are in some places called heads or hammocks. Some of North America's finest examples of wetlands fall in this category, including the Okefenokee Swamp and Great Dismal Swamp. Additional useful references on palustrine hardwood swamps are Dabel and Day (1977), McCormick and Somes (1982), Cohen et al. (1984), Tiner (1985a, 1985b, 1988, 1991c), Jahn and Anderson (1986), Erickson and Leslie (1988), Faber et al. (1989), Veneman and Tiner (1990), Metzler and Tiner (1992), and the references in Section 3.1.1.

Figure 3.2: Palustrine hardwood swamp in Virginia. (R.W. Tiner)

Geophysical Characteristics. Palustrine swamps develop in topographic depressions where interrupted drainage and sufficient rainfall or groundwater seepage flood the soil. They may occur in relatively isolated depressions surrounded by upland, in low spots along floodplains, or in various depressional landscapes. Suitable conditions are found broadly over the eastern, southern, and central states. Wet conditions may lead to the development of highly organic, enriched surface layers and organic deposition, which further enhances wetland development. Streams may enter or leave palustrine swamps, but their hydrology is not dominated by moving water.

Wetland Criteria Characteristics. *Vegetation.* The vegetative character of palustrine swamps depends on environmental factors, including rainfall, soil, drainage, drought, frost, fire and storms. The vegetation is more diverse in mild southern states than in the more climatically harsh north. Where water is relatively deep and hydroperiods relatively long, palustrine swamp forests are generally dominated by a few species. The diversity of plants tends to increase towards the edges of the swamp as hydroperiods and peat accumulation decrease.

Swamp black gum and red maple (*Acer rubrum*) are dominant trees of the flooded palustrine hardwood swamps in the southeast. The gum is flooding tolerant and develops adventitious pneumatophore roots when deeply flooded. Like cypress, with which it is often found, it requires dry conditions for seed germination. Loblolly pine (*Pinus taeda*) can co-dominate in many forested wetlands in the South. Along the Atlantic coast, white cedar (*Chamaecyparis thyoides*) dominates sites having shorter hydroperiods, forming evergreen cedar swamps. Other trees that may become prominent in places depending on hydroperiod include water tupelo, sweet gum (*Liquidambar styraciflua*), swamp bay (*Persea palustris*), ash (*Fraxinus caroliniana*), sweet bay, beech (*Fagus grandifolia*), laurel oak (*Quercus laurifolia*), swamp white oak (*Quercus bicolor*), overcup oak (*Quercus lyrata*), fetterbush (*Lyonia lucida*) and loblolly bay (*Gordonia lasianthus*), the latter being particularly invasive after disturbance. Willows (*Salix* spp.) are common either as trees or in the understory. Various hollies (*Ilex* spp.), arrowwood (*Viburnum dentatum*), and buttonbush are also common in the understory in the southeast.

A subtype of the southern palustrine swamp is the bay swamp. Also called bayheads, these found at the headwaters of streams and on peat filled basin. They are dominated by broadleaved, evergreen "bay" trees that make up the understory of other swamps. These include sweet bay, swamp bay, loblolly bay, and sometimes slash pine.

Further north and inland, northern conifers become more important components of palustrine swamps. These include tamarack (*Larix laricina*), fir (*Abies*), and northern white cedar (*Thuja occidentalis*). Hardwood trees include ash (*Fraxinus nigra*), red maple, poplar (*Populus balsamifera*), northern pin oak (*Quercus palustris*) and formerly, American elm (*Ulmus americana*). The understory is better developed further north, due to the sparser canopy. It includes many shrubs such as red-osier dogwood (*Cornus stolonifera*), speckled alder (*Alnus rugosa*), winterberry (*Ilex verticillata*), and spicebush (*Lindera benzoin*), as well as herbs and grasses. The understory is less developed in cedar shrub swamps.

These species combine into a number of recognizable swamp types. In the northern midwest, hardwood swamps are dominated by red maple, black ash, yellow birch, and formerly by American elm. Further north, tamarack is a pioneer tree, and its swamps occur on glacial outwash and in depressions. Northern white cedar swamps include tamarack, white spruce, balsam fir, and yellow birch. At each site, the diversity of plant species depends on hydrology and nutrients, with greater diversity in swamps having higher nutrients levels.

Fires can significantly impact the vegetation of these wetlands. Fires are more common in short hydroperiod wetlands, or in those having been drained, and can result in loss of organic soil. Pond pine (*Pinus serotina*), pitch pine (*Pinus rigida*), black titi (*Cliftonia monophylla*), and titi (*Cyrilla racemiflora*) require fire for regeneration.

Soils. The underlying base soil can be important in the colonization of certain plants into a wetland. Many cedar swamps, for example, occur on calcareous soils. Most basin swamps have mineral soils, since they occur in situations where relatively short hydroperiods lead to the oxidation of organic matter that might otherwise accumulate. Some tend to accumulate organic matter leading to the creation of an organic or peat soil. Greater organic matter accumulation occurs where decomposition rates are reduced due to prolonged flooding, acidic water and soil, low dissolved oxygen concentrations, and low nutrient content of leaves and stems.

Hydrology. The water source for hardwood swamps is primarily rainfall or ground water. Surface water flow is less important and, if present, is derived from a relatively small catchment basin and perhaps delivered via small streams. Any surface flow is therefore very sluggish, seasonal, and usually broadly spread over the landscape. This contrasts with the strong, directional, and more channelized flow affecting floodplain swamps or the water level influenced flow in fringing swamps. Surface flow ceases early in the dry season, and the hardwood swamps become isolated and the water stagnant.

The locally driven, dynamically restricted hydrology is a critical factor in determining the vegetation and soils of palustrine swamp forests. Water saturation of the soil creates longstanding anaerobic conditions, such that only a few tolerant tree species can survive where hydroperiods are long. Additionally, the surface water may be depleted of oxygen for extended periods of time, affecting plants, animal survival, and water and soil chemistry. The pattern of water level fluctuation, resulting in periodic dry seasons, affects seed germination and survival of plants permitting establishment of species requiring aerobic germination and requiring surviving plants to be capable of enduring both flooded and dry conditions.

The source of water to a palustrine swamp forest and its nutrient content are important determinants of water quality and productivity. Generally, low overland flow means that these wetlands are exposed to a limited nutrient regime, contrasted with wetlands having greater water flow. Export of nutrients and organic material is also low.

Characteristic Fauna. In the anaerobic sediment and, sometimes, waters of palustrine swamps, the benthic invertebrate fauna is dominated by groups well adapted to such conditions, especially midge larvae (chironomids). Crayfish (*Cambarus* spp., *Procambarus* spp.) are characteristic of this swamp.

The isolated location of many palustrine swamps combined with periodic dry downs and deoxygenation events means that fish populations are usually small unless the swamp periodically has surface water connections to other wetlands or to a river. In part because of low fish numbers, amphibians such as frogs and salamanders are common in these wetlands. Snakes and turtles may occur or not. Song birds nest and feed in the trees. Larger species include the barred owl (*Strix varia*) and pileated woodpecker. The presence of aquatic birds, such as herons, depends on food availability. Among mammals, deer, black bear, squirrels, raccoons, and beaver (*Castor canadensis*) are typical over much of North America, the latter creating conditions conducive for the development of still water swamps and marshes.

Wetland Values. Basin hardwood swamps serve as flood retention features in their relatively small catchments and may serve as recharge zones at their periphery. It is likely that the organic peat can serve as sinks for materials. Swamp trees have produced important forest products, especially high value hardwood lumber. They are productive for birds and mammals, including those traditionally hunted.

Unusual Characteristics. Because of their dependence on rainfall and localized water flows, palustrine swamp forests are susceptible to external forces, including human modification of their watershed. Drainage, diversion, impoundment, and extraction of water can all affect the sensitive annual pattern of water level fluctuation. Within the wetlands, forest product harvest and pollution load can substantially alter its character. Changes include reduced tree growth, shift in canopy dominance, loss of peat, and reductions in animal populations. The addition of nutrients can increase production and carbon accumulation, and also shift vegetation patterns.

Fire can be an important factor in the long-term development of these swamps. As palustrine swamps often occur under fluctuating water regimes and deposit organic soil, there will be times when the highly flammable peat will dry and be susceptible to fire. Such fires, if they burn deeply into the peat, can persist for weeks burning ever deeper and changing the hydrological character of the site. In this way fire also sets back any successional trajectory (see Section 2.2.3). In southeastern North America, periodic burning generally favors cypress over hardwoods.

3.1.3 Shrub Swamps

Shrub wetlands are separable from forested wetlands by the stature of their dominant plants (Figure 3.3) (Richardson, 1981; Lugo et al., 1989; Schalles and Shure, 1989). In many cases, the dominant plant species are among those also found in forested swamps. For the most part, their dwarf stature is due to stunting in response to edaphic conditions. These shrub swamps or shrub carrs are treated separately here to call attention to those naturally limiting conditions and to reinforce the understanding that shrub swamps are fully functioning natural wetlands. Evergreen shrub swamps of the southeast United States are called pocosins. In situations where the catchment basin is small and water is derived mostly from rainfall, pocosins may be considered to be southern shrub bogs.

Geophysical Characteristics. Shrub wetlands develop in similar situations as swamp forests, but usually under more nutrient limiting conditions, caused principally by limited surface water flow. Scrub swamps range from a few to thousands of hectares. Most form in

Figure 3.3: Willow shrub swamp in Maine. (R.W. Tiner)

depressions and at ground water seeps, such as spring heads. They also form between streams on the southeastern coastal plain of the U.S., with their base growing over time as peat accumulation overtops the surrounding land. Carolina bays are elliptical basins of uncertain origin that generally support shrub swamps. Shrub swamps are common in the upper midwest (Minnesota, Wisconsin, Michigan). These systems tend to be transitional from marsh to upland.

Wetland Criteria Characteristics. *Vegetation.* Shrub wetlands are characterized by their short stature, usually due to nutrient deficiencies and also, in some cases, recurring fires. As a result of the short stature and lack of shading by a tall canopy, these wetlands usually develop into impenetrable thickets of shrubs and vines. Shrub may be successional features, succeeding from marshes following a reduction in fire frequency.

Many shrub swamps in North America are characterized by buttonbush, alders, willows, and dogwoods (*Cornus* spp.). Tree saplings are also common, especially red maple and poplars. Useful references on shrub swamps are Moore and Bellamy (1974), Richardson (1981), Larsen (1982), Schomer and Drew (1982), Drew and Schomer (1984), Tiner (1985a, 1985b, 1988, 1991c, 1993c), Windell et al. (1986), and Crum (1988).

Pocosins are shrub swamps identifiable more from their setting and hydrological situation than by their vegetation, which they share with other wetlands (Figure 3.4). These may be shrub swamps or swamp forests, depending on the tree height, although shrub stature is more typical. The shrubs are evergreen, usually with scerophylous characteristics, although this is certainly not universal. Dominants include red maple, swamp cyrilla or titi (*Cyrilla racemiflora*), loblolly bay, lyonia or fetterbush (*Lyonia lucida*), sweet bay, and redbay (*Persea borbonia*), Atlantic white cedar, cypress, and pond pine, which forms the canopy of most forest pocosins. Other shrubs and vines include holly (*Ilex glabra, Ilex coriacea*), laurels, blueberries, huckleberries (*Gaylussacia* spp.), and greenbriar (*Smilax laurifolia*). Peat moss (*Sphagnum* spp.) occurs where the canopy is sufficiently broken to

Figure 3.4: Ocean Bay, a Carolina Bay pocosin in Francis Marion National Forest, Berkeley County, South Carolina. (R.W. Tiner)

allow sunlight penetration to the floor. Pocosins support several unique plants including white wicky (*Kalmia cuneata*), arrowleaf shieldwort (*Peltandra sagittaefolia*), spring flower goldenrod (*Solidago verna*), and rough-leaf loosestrife (*Lysimachia asperulaefolia*). Useful references on pocosins are Richardson (1981), and Sharitz and Gibbons (1982).

Also in the South are shrub swamps associated with standing or fluctuating surface water, which may or may not be peat depositing. The most widespread is the dwarf cypress swamp (see Section 3.1.1). Shrubby swamps are also dominated by swamp privet (*Forestiera acuminata*), elm, willow, alder, and birch. In the upper midwest, shrub swamps are dominated by willow, elder, red-osier dogwood, and buttonbush. Along the gravel flood plains of intermittent streams, shrub swamps are dominated by buttonbush and willow. In the north, shrub swamps are dominated by buttonbush, willows, alders, silky dogwood, or red-osier dogwood. In the northern peatlands, stunted trees and shrubs invade bogs, creating a shrub bog (see Section 3.3).

Soils. Soils differ ranging from mineral soils (sandy humus) to organic soils (muck, peat). Usually, due to limited outflow, they are more generally organic. Peats are most common in basins but are also laid down over alluvial clays in flood plains. In the East, shrub peatlands have expanded by paludification over thousands of years, much as have northern bogs. Peats deposited in basins, such as in Carolina bays of the southeast, may be over 4 m thick. Peat accumulation is inhibited by periodic fires. Highly organic soils are generally nutrient and cation deficient. This, combined with the limited surface and ground water inflow, accounts for the low nutrient conditions in most shrub wetlands.

Hydrology. Hydrologic conditions also differ among shrub wetlands, so generalizations are difficult. As peat accumulates, the substrate tends to hold water and sustain wetland conditions divorced from ground water, which may create a shrub wetland perched above the water table. These perched shrub wetlands discharge water to the adjacent lower landscape, especially in winter when the soil is saturated and evapotranspiration is low.

In most shrub wetlands, being nutrient limited, overland flow is limited and confined to that resulting from high rainfall events. Except for perched wetlands, surface drainage is usually minimal, and evapotranspiration may be the most important water output. Evapotransporation is seasonal and also dependent on characteristics of the plants. In pocosins many plants appear to be adapted to conserve water. Rainfall is generally seasonal, which leads to water depth fluctuations. Even in perched wetlands, ground water varies seasonally, decreasing during summer periods of high evapotranspiration.

Characteristic Fauna. The fauna of shrub wetlands is little studied. The fish fauna depends on the shrub wetlands' connections to more permanent water bodies. Seasonal drying inhibits the persistence of many fish species. Shrub wetlands are important to amphibians, including the endangered pine barrens tree frog (*Hyla andersoni*). They appear to be less important for reptiles because of their seasonality, although rattlesnakes (*Crotalus adamanteus*) and alligators occur in the South. Mammals and birds characteristic of nearby uplands frequent shrub wetlands during low water conditions. These include bear, deer, bobcat (*Lynx rufus*), gray squirrel (*Sciurus carolinensis*), and marsh rabbit (*Sylvilagus floridanus*).

Wetland Values. The peat development of peat-forming shrub swamps controls aspects of local hydrology by maintaining higher soil water levels than would otherwise be the case. Shrub wetlands also affect runoff and transpiration.

Although of small stature, some plants such as cedars have forestry importance. Shrub wetlands also are important wildlife habitat, especially as refuges for upland game species during the dry seasons.

Unusual Characteristics. Shrub wetlands are typically maintained in this form primarily by low nutrients. It is important to note that these are fully functioning wetlands and are not necessarily less valuable because of the small stature of their trees. Many shrub swamps have been logged, especially for their cedar and cypress. Others have been drained for farming or mined for peat, thereby altering their wetland character.

Recurring fire has been an important factor in the development of pocosins, as evidenced by the root sprouting capabilities of pocosin plants and the serotinous cones of the pond pine. All of the typical pocosin plants recover quickly after a fire and may rapidly become dominant. Some herbs and grasses sprout only after fire passage.

Pocosins are considered fire subclimax associations.

3.1.4 Floodplain Forests

Wetland forests occurring in floodplains take their character from the influence of the nearby river, which controls ground water levels and the surface water flow regime, and therefore material transport. Floodplain wetlands are dynamic, productive, and intimately constrained by the hydrology of the river valley and its watershed (Figure 3.5) (Clark and Benforado, 1981; Wharton et al., 1982; Conner and Day, 1982; Lugo et al., 1989; Ewel, 1990). In the humid southeast, they are in some places known as bottomland hardwood swamps, bottoms, or backswamps.

Geophysical Characteristics. These forests occur within a river floodplain, delimited at one margin by a natural levee created by coarse sediment deposition at the river's edge and at its other margin by terrestrial conditions toward higher elevations. Between these borders, poorly drained soil and a high water table controlled by the river

Figure 3.5: Floodplain forest swamp, showing the swamp adjacent to the Myakka River, Florida. (J.A. Kushlan)

elevation often result in wetland conditions. The topography may be one of gradually rising land surface or a more complex arrangement of alternating highs and lows.

The river valley is a dynamic landscape. The river channel changes as it downcuts or as it meanders across a steady state floodplain, altering the location of wetlands, including forests. Often topography can be complex, with ridges representing old depositional events, swales representing old erosional and flow features, and oxbows representing former river channels. When surface flows are high during exceptional flood events, the waters can uproot, smother or damage standing trees, deposit materials from the river, and alter basin topography itself. In northern climates, ice floes similarly can destroy trees and alter the topography.

Wetland Criteria Characteristics. *Vegetation.* Well developed floodplain forests, especially in warm, humid climates, generally are dominated by densely spaced plants of tree stature. Their diversity and structure are less well developed in drier and in cooler climates. In most cases, the floodplain forest is more diverse and better developed than forests of the adjacent upland. In the best developed systems, the understory is reduced due to limited light penetration combined with the effects of flooding depth and frequency.

Forest development and the wetland character of the vegetation depend on the ground water, flooding regime, and ice conditions. In most cases, riverine control of the water table leads to saturated soil conditions. Where a hydraulic gradient exists, the various forest communities (following the individual adaptations of the constituent plants) may follow the gradient from hydric to mesic forests, or they may respond to the more complex pattern of topographic highs and lows with wetlands occupying the low sites (Larson et al., 1981). In some cases, a river edge forest may seldom flood and be fully terrestrial. In the moist floodplain, nutrients and water are highly available, but adaptation to periodic soil anaerobiosis is required of plants. Wetland adaptations required depend on the timing, duration, and depth of flooding. Where hydroperiods are long, trees may give way to herbaceous marsh. Ice floes may limit vegetation development by periodic scouring. Useful references on floodplain forests are Brinson et al. (1981), Clark and Benforado (1981), Larsen et al. (1981), Wharton et al. (1981, 1982), Ewel (1990), Faber et al. (1989), Hook and Lea

(1989), Minshall et al. (1989), Gosselink et al. (1990), and Sharitz and Mitsch (1993).

Floodplain forests occur under a wide variety of conditions throughout the U.S. from the broad floodplains of the lower Mississippi to the narrow riparian fringes of the arid southwest. As would be expected, they show substantial differences in their vegetation.

The river floodplains of southern North America are often dominated by cypress swamps, as described in Section 3.1.1. In the south, non-cypress floodplain forests tend to occur in drier and less deeply flooded sites than the cypress. The vegetation of these bottomland hardwood swamps is variable, depending especially on hydroperiod. In deeper sites, along with cypress, water tupelo occurs with planertree (*Planera aquatica*), and Carolina ash (*Fraxinus caroliniana*), with a sparse understory including buttonbush. Slightly higher sites support overcup oak (*Quercus lyrata*) and water hickory (*Carya aquatica*). On shallower sites, a more complex forest develops of red maple, green ash (*Fraxinus pennsylvanica*), American elm (which has been eliminated by disease over much of its range), and laurel oak (*Quercus laurifolia*). Shorter hydroperiod conditions, such as on ridges, support sweetgum, and black gum.

In the floodplains of the eastern and midwestern states, silver maple (*Acer saccharinum*) is often dominant, with red maple, elm, eastern cottonwood (*Populus deltoides*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). The understory includes American hornbeam (*Carpinus caroliniana*), hackberries (*Celtis* spp.), and willows.

To the north on mineral soil in floodplains, the swamps are dominated by conifers, especially northern white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), and white spruce (*Picea glauca*), along with the broad leaved black ash (*Fraxinus nigra*) with speckled alder (*Alnus rugosa*) in the understory. Even further north in Canada and Alaska, floodplains are dominated by willows and alders and at higher elevations by balsam poplar (*Populus balsamifera*).

In drier climates, development of the floodplain forest depends on rainfall. In the eastern grasslands, the fringing forest is composed of river birch (*Betula nigra*), sweetgum, black gum, American sycamore (*Platanus occidentalis*), and cypress. In relatively dry areas, willow and cottonwood dominate the river edge forest, occurring in an open canopy with boxelder (*Acer negundo*) and bur oak (*Quercus* *macrocarpa*). In the deserts, floodplain vegetation is naturally dominated by screwbean mesquite (*Prosopis pubescens*), cottonwood (*Populus fremontii*), and willows. Tamarisk (*Tamarix pentandra*), introduced within this century, has invaded many riparian wetlands and become dominant in places.

Soils. The base soil of the floodplain develops from the mineral rich alluvium transported by the river. In some locations, colluvium from the adjacent upland forms or contributes to the soil base. These soils are high in nutrients, although nutrient availability is affected by soil moisture in that anaerobic conditions usually persist for much of the year. Under the influence of riverine conditions, organic matter tends not to accumulate as it is oxidized by overflow water or by air during the dry season, or is physically removed by surface water flow. Fires, also not uncommon, also remove organic accumulation. Thus, these swamps tend not to deposit peat except in topographic depressions having a long hydroperiod, usually associated with an elevated water table. Such situations become basin wetlands.

Hydrology. Floodplain forests are characterized by the influence of the flowing water of the river itself. Groundwater levels in the floodplain are often controlled by river elevation. Relatively flat floodplains have a high water table and waterlogged soils. Periodic surface flooding leads to rapid and sometimes prolonged periods of inundation, often seasonal. In the South, periodicity of flow depends primarily on seasonal variation in rainfall, whereas in the midwest and northern areas, flow seasonality tends to depend on the timing, duration, and amount of the spring thaw.

The surface hydrology may therefore fluctuate seasonally from deep water during flooding to a lack of surface water at other times. In addition to rain and snowfall, the topography and slope of the valley and the river, distance from the river channel, frequency of flooding, icefloes, soil characteristics, and bedrock conditions all affect the hydrology of the floodplain. The hydrologic gradient from the river, in turn, determines vegetation development.

With fluctuating water levels and hydroperiods shorter than in basin wetlands, floodplain swamps are dynamic. They have relatively high dissolved oxygen concentrations during flow conditions and a nutrient store replenished by river water materials. With both groundwater and surface water inputs, floodplain forests have access to a substantial nutrient pool, resulting in high productivity.

Characteristic Fauna. Floodplain forests are among the most productive wildlife habitats (Wharton et al., 1981). Fish populations are high seasonally, as they enter the floodplain during high water and retreat to the river when water levels fall (Guillory, 1979; Finger and Stewart, 1987). In the wetland, they can access this high productivity. It is likely that floodplain forests of the United States provide important nursery grounds for stream fishes, as has been so well demonstrated in tropical floodplain forests (Goulding, 1980).

Beavers are characteristic of this environment and have the ability to change floodplain forests to palustrine forests or marshes by impounding water. Otter, swamp rabbits, and raccoon are other typical aquatic mammals. Upland game animals enter the forest during low water conditions. Populations densities may be highest at the swamp-upland ecotone.

Birds are locally quite abundant. The floodplain forests of the lower Mississippi provide a primary wintering habitat for waterfowl from the central North American flyway. They also serve as nesting and feeding areas for wood duck, ibises, wild turkey (*Meleagris gallopavo*), barred owl (*Strix varia*), downy woodpecker (*Picoides pubescens*), red-bellied woodpecker (*Melanerpes carolinus*), pine warbler (*Dendroica pinus*), common yellowthroat (*Geothlypis trichas*), Canada warbler (*Wilsonia canadensis*), ovenbird (*Seiurus aurocapillus*), northern waterthrush (*Seiurusnoveboracensis*), wood peewees (*Contopus virens*), veery (*Catharus fuscens*), wood thrushes (*Hylocichla mustelina*), and grey catbird (*Dumetella carolinensis*).

Floodplain forests are particularly important in the arid West where they serve as nesting habitat for many birds, including mourning dove, verdin (*Auriparus flaviceps*), and orioles (*Icterus galbula*) (Wauer, 1977). They also are important habitat for migratory birds.

Wetland Values. Floodplain wetlands have proven to be crucial flood retention features of the landscape. As a river floods its valley, the downstream movement of water is slowed. Although the total amount of discharge is the same per event, its release is delayed, decreasing flood stages downstream over what would have occurred without the floodplain forests. Floodplain forests are intimately tied to the ground water table, and serve as water sources to the river during lowering water conditions. These forests have superior value as wildlife habitat, both for hunting and for nonhunted wildlife. In the south, these forests serve as a primary wintering area for migratory waterfowl. Deer are characteristic and heavily hunted in most areas. It is likely that these forests have important fishery values, as nursery areas for river sport and food fishes. Forest products are an important value of these wetlands. They also have important aesthetic values in the floodplain.

Unusual Characteristics. Not only are floodplain forests determined by hydrological conditions, they significantly influence the overall water regime of the river. Floodplain forests have been recognized as important flood control features. Floodplain forests are highly productive, owing to the capture of nutrients and materials from the river. This productivity is translated into forest products and both hunting and fishing. Floodplain forests also provide corridors for the dispersal of plants and animals between remnant patches of upland habitat, a function that may become increasingly important as forested habitats are altered.

3.2 MARSHES

Marshes are wetlands dominated by herbaceous, usually emergent, plants (Good et al., 1978; Weller, 1981; Gore, 1983; Kushlan, 1990). Various marshes are similar in structure, and presumably function, although the species of dominant plants differ from one site to the next. Freshwater marshes are found in many situations, including those in palustrine and floodplain environments, discussed in Sections 3.2.1 and 3.2.2. The largest contiguous marsh systems in North America are the Everglades and the prairie potholes, which for this reason are treated separately in Sections 3.2.3 and 3.2.4, respectively.

3.2.1 Palustrine Marshes

Palustrine marshes are emergent herbaceous wetlands that form in basins (Figure 3.6; Plate I-II). These may be tiny and isolated or may cover thousands of square kilometers. The largest single marsh in the U.S. is the Everglades, and the largest marsh complex is the prairie pothole region. Other marshes include those along the Gulf and

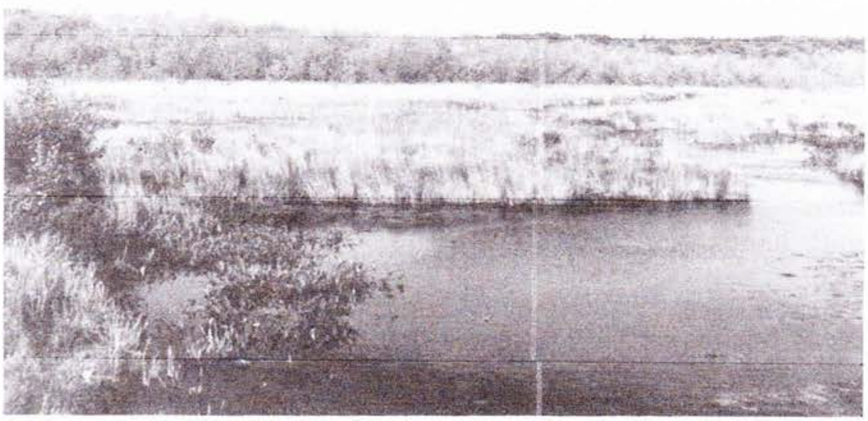

Figure 3.6: Palustrine marsh in central Maryland, with red maple swamp in the background. (R.W. Tiner)

Atlantic coast, marshes inland of the tidal freshwater marshes, the playas of the high plains of Texas and New Mexico, northern fens, the tule marshes of the west, and the many small to large marshes found elsewhere where water pools at the soil's surface. Useful references on palustrine marshes are Weller (1981), Schomer and Drew (1982), Nelson et al. (1983), Simpson et al. (1983), Drew and Schomer (1984), Odum et al. (1984), Tiner (1985a, 1985b, 1988, 1991c, 1993c), Herdendorf et al. (1986), Windell et al. (1986), Herdendorf (1987), Conner and Day (1987), Nachlinger (1988), Kushlan (1990), and Mitsch and Gosselink (1993).

The water sources of basin marshes may be rainfall, surface water, and groundwater in any combination, with the latter two dominating overall. Outflow typically is restricted. As a result of minerals and nutrients transported into the wetland by these water sources, palustrine wetlands can be very productive and can accumulate peat.

Geophysical Characteristics. Palustrine marshes typically develop in topographic depressions. They also develop on flatter ground where drainage is sufficiently retarded and in river valleys (see Section 3.2.2) behind drainage restrictions. They may occur on any soil, even over highly permeable karst topography when rainfall is high and drainage restricted by peat deposition. In some cases, marshes represent a fire subclimax, with periodic burning inhibiting shrub invasion. Appropriate marsh-forming conditions occur over most of the non-arid United States, resulting in the wide distribution of these wetlands.

Other marshes develop on floating mats suspended above the basin bottom. Freshwater floating marshes are particularly common in coastal areas, such as in Louisiana, and along the margins of deeper water habitats.

Wetland Criteria Characteristics. *Vegetation.* Marsh vegetation is rather uniform in its overall aspect, consisting of emergent and submersed plants growing in shallow water to damp soil and submersed or floating leaved plants in deeper areas. Many of the same plants are found throughout North America, although in differing relative abundance and stature in different regions and sites. Herbaceous wetland plants are adapted to flooded conditions in several ways. Annuals sprout during periodic dry periods, to be succeeded by emerging perennials over the following wet periods. Some species have long-lived seeds that can spend many years in the soil, which becomes a seed bank, before sprouting when conditions turn appropriate. Perennials may allocate a substantial proportion of their energy to root production, especially storage structures, which are used for overwintering or dry season survival. After establishment, vegetative spreading is a typical way for marsh plants to reproduce and dominate a site. Often, the history of colonization determines which plants become dominant. Because of seasonal drying, fires can be recurring. Wetland plants, both annuals and perennials, resprout soon after a light, fast burn. In Winter, above soil portions of the plants die back.

The sedges, grasses, and other herbaceous plants that can dominate a marsh site are relatively few, although many more species are found peripherally. Typical marsh species include common reed (*Phragmites australis*), wild rice (*Zizania aquatica*), cattail (*Typha* *latifolia, Typha angustifolia*), maidencane (*Panicum hemitomon*), cutgrass (*Leersia oryzoides*), reed canary grass (*Phalaris arundinacea*), bluejoint (*Calamagrostis canadensis*), sawgrass (*Cladium jamaicense*), bulrush (*Scirpus* spp.), spikerush (*Eleocharis* spp.), arrowhead (*Sagittaria* spp.), pickerelweed (*Pontedaria cordata*), smartweeds (*Polygonium* spp.) arrow arum (*Peltandra virginicum*), sedges (*Carex* spp.), rush (*Juncus* spp.), and marsh fern (*Thelypteris palustris*). These species can form a variety of recognizable marsh types, depending on their relative abundance and cover.

Common reed is a predominant marsh plant at many sites, especially in disturbed areas. Cattail marsh occurs similarly, with best development under conditions of high nutrient loading and deep sediments. Reed and cattail dominate a large proportion of small North American basin marshes. Both of these species have superior production efficiencies.

Floating marshes often have maidencane, arrowhead and various vines and herbs growing on a floating mat of roots, tubers, and detritus. In more hydrologically complex marshes, rooted plants sort themselves out by water depth and hydroperiod. At the higher margins of a wetland, various grasses and sedges predominate. Toward deeper water, tall, herbaceous emergents occur. Floating leaved and submersed plants occur next, adjacent to open water if present. To what extent this zonation recapitulates successional patterns differs among situations.

Palustrine marshes occur in the far north, especially where permafrost underlies the tundra. These marshes are dominated by a few species such as bulrush (*Scirpus cespitosus*), cottongrasses (*Eriophorum angustifolium, Eriophorum spissum*), beakrush (*Rhynchospora alba*), sedges (*Carex* spp.), and pendant grass (*Arctophila fulva*). These northern marshes contain mosses, such as sphagnum, but it does not dominate the water quality of the site as it does in true bogs (see Section 3.3). Northern marshes that deposit peat can develop into sphagnum bogs under appropriate conditions.

In temperate latitudes, a myriad of identifiable marshes occur. Among the more notable are tule marshes, beaver dams, and savannahs. The tule marshes of the western U.S. occur (or occurred) along the lower reaches of rivers. These are dominated by *Scirpus* of several species, along with cattail, common reed, and sedges. In the lower prairies of North America, there are many marshes, dominated by cattail, bulrush, and sedges (*Carex* spp.). Also present are common reed, cutgrass, arrowhead, spikerush, and burreed (*Sparganium* spp.). These marshes undergo a multiyear cycling, based on hydrological conditions (Weller, 1981). During periods of high water level, emergent plants (cattail, bulrush, arrowhead) flourish, covering much of the open area of the marsh. As wet conditions continue, the emergents begin to die, especially due to muskrat cutting of the emergent stems, opening up the marsh. During droughts, the emergent plants reestablish themselves, beginning with annuals such as *Bidens* spp. and *Rumex* spp. and the "marsh cycle" begins again.

In arid regions, palustrine marshes can be quite saline (Chapman, 1974). Vegetation includes saltworts (*Salicornia* spp.), sea blites (*Suaeda* spp.), iodine bush (*Allenrolfea occidentalis*), sacaton (*Sporobolus airoides*), and grasses (*Distichlis spicata*).

Beaver ponds are common throughout most of North America. Beavers, in damming drainage features and cutting down trees, create a palustrine environment that supports herbaceous vegetation (Figure 3.7). Along the southeast coast, marshes called savannahs occur under short hydroperiod conditions. These frequently burning marshes are dominated by grasses (*Andropogon virginicus, Ctenium aromaticum, Aristida stricta*).

Marshes known as "fens" occur in the north (Figure 3.8). These are peat accumulating wetlands that receive drainage from surrounding mineral soils, such that water and wetland soils are rich in minerals. Fens generally support marsh vegetation such as reeds, sedges, and grasses (see Glaser, 1983, 1987), and are occasionally considered to be transitional stages in the development of a bog (Mitsch and Gosselink, 1993).

Further south, on the southeast coastal plain and in Florida, marsh vegetation becomes more complex, and species change dominance over surprisingly small increments of elevation and hydroperiod (Kushlan, 1990). In short hydroperiod marshes, beakrush, maidencane, redroot (*Lachnanthes caroliniana*), or sawgrass may predominate in a sparse stand. In slightly deeper water sawgrass, pickerelweed, arrowhead, fire flag (*Thalia genticulata*), maidencane, bulrush, or spikerush predominate, alone or together. In locations of high nutrient or deep soil conditions, cattail often flourishes. Submersed and floating leaved plants may occur in even deeper water. These include bladderwort (*Utricularia* spp.), water lily (*Nymphaea* spp.), fanwort (*Cabomba caroliniana*), water hyssop (*Bacopa* spp.), primrose

Figure 3.7: A beaver pond in Minnesota. (R.W. Tiner)

willow (*Ludwigia repens*), and chara (*Chara* spp.).

Soils. The base substrate of a marsh may be varied, including sand, clay, organic soil, or even bedrock. The important circumstance is that a combination of substrate permeability and water supply are together sufficient to initiate marsh development. Retarded drainage may be due to the impervious character of the soil, the existence of a hard pan, decreased percolation in organic soil, or a high water table even in a substrate having high porosity.

Organic content of the soil is usually relatively high in palustrine marshes. In many, perhaps most, palustrine marshes peat deposition occurs, even in warm, circumneutral waters. Under such conditions, accumulation is the result of high production despite relatively high decomposition rates. Deposition increases in deep, deoxygenated water, under permanently flooded conditions, and in cool climates. Oxidation of the soil is higher in shallow, oxygenated water and during dry periods. Deep reaching fires can burn out peat deposits, lowering soil elevation, and changing the water regime at a site.

Figure 3.8: A fen in Minnesota. (R.W. Tiner)

Hydrology. Water in inland, freshwater marshes comes from three sources: rainfall, groundwater and surface water. Marshes in well watered areas gain most of their water supplies from overland and ground water flow. Marshes in arid areas depend more on periodic rainfall and short-term runoff for their water supply. The western playas occupy small basins with a relatively restricted watershed and are dry for considerable periods (Barclay and White, 1981).

In freshwater marshes situated on the coastal plain (inland of tidal freshwater marshes), water levels are controlled by sea level elevation. However, in most inland marshes, water levels fluctuate with variations in rainfall and runoff. Palustrine marshes may lack standing surface water seasonally or infrequently in dry years. This characteristic of inland marshes is important relative to wetland delineation, in that surface water might not be present in a marsh at all times.

The importance of fluctuating water levels in most palustrine marshes cannot be overstated. Much of the plant and animal life found in these systems either depend on or can acclimate to appropriately fluctuating water depths (Kushlan, 1989a). The permanence of flooding, hydroperiod, and hydropattern decisively affects the character of the palustrine marsh ecosystem.

Some marshes discharge to ground water, particularly at their margins, and by surface flow when the marsh edge is overtopped. However, most basin marshes have limited surface outflow.

Palustrine marshes tend to develop where surface and ground water effects predominate. Because these inputs carry loads of dissolved and suspended materials, marshes can have high levels of nutrients and minerals, including carbonates. As a result, marsh waters are well buffered, generally circumneutral, and have high specific conductivity.

Characteristic Fauna. Among invertebrates, flies are the most uniformly present group in palustrine marshes. These include such characteristic groups as midges, blackflies, and mosquitoes. Macroinvertebrates such as prawns, crayfish, and snails are often common. Fish are abundant where drydowns are not severe or if recruitment sources are available during higher water periods. Those that are most abundant are often small stature species better adapted for survival during the low oxygenation conditions of the dry period. Aquatic snakes, turtles, and the alligator may be typical, depending on location. Marshes are highly productive for aquatic mammals and birds. Muskrat (*Ondotra*), raccoon, otter, and rice rats (*Oryzmyzes*) are typical mammals. Beavers create and sustain many palustrine, herbaceous wetlands. By their dam building activities, they turn bottom land, especially swamp forests, into herbaceous marshes.

Birds sort themselves according to vegetative habitat, and populations of marsh birds change as the emergent vegetation goes through multiyear cycles. Characteristic are: redwinged blackbird (*Agelaius phoeniceus*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), long-billed marsh wren (*Telmatodytes palustris*), swamp sparrow (*Melospiza georgiana*), sang sparrow (*Melospiza melodia*), black tern (*Chlidonius niger*), spotted sandpiper (*Actitis macularia*), killdeer (*Charadrius vociferus*), mallard (*Anas platyrhynchos*), pintail (*Anas acuta*), blue-winged teal (*Anas discors*), ring-necked duck (*Aythya collaris*), ruddy duck (*Oxyura jamaicenis*), least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), Virginia rail (*Rallus limicola*), sora (*Porzana carolina*), sandhill cranes (*Grus canadensis*), whooping cranes (*Grus americana*), American coot (*Fulica americana*), common gallinule (*Gallinula chloropus*), and pied-billed grebe (*Podilymbus podiceps*).

Some marshes are particularly important for animal life. Fifteen species of waterfowl bred on marshes in the upper midwest (Smith et al., 1964). Morning doves (*Zenaida macroura*) nest in the playa marshes of Texas (Gutherie, 1981). The marshes of the southeastern and southern United States support many thousands of colonial waterbirds (herons, ibese, storks). The tundra marshes of the Arctic are the primary nesting areas for shorebirds, geese (*Branta canadensis, Anser albifrons*), and certain ducks, such as the pintail (*Anas acuta*).

Wetland Values. Freshwater marshes have important hydrological functions. They absorb floods and runoff, delaying its down gradient movement, thereby reducing flooding conditions elsewhere. They often serve as groundwater recharge sites, especially in porous soil and along their margins. It is now well established that these marshes can serve as a sink for contaminants and fertilizers. These materials are sequestered in the sediments, taken up by plants, or transformed by microorganisms. Of the various wetlands, it appears that marshes dominated by herbaceous plants appear to have the greatest ability to sequester and transform environmental contaminants. Marshes support both wildlife and fishes, particularly waterfowl. Rare and endangered species of birds and amphibians depend on palustrine marshes.

Unusual Characteristics. Palustrine herbaceous wetlands are widespread and, as such, may be the most important wetlands in many areas. Water recharge, discharge, nutrient sinks, wildlife habitat, and fish production are some of the important functions of these marshes. The fluctuating water conditions means that these sites are not always flooded, yet fulfill important wetland functions.

3.2.2 Floodplain Marshes

Floodplain marshes occur in river valleys. Although similar to palustrine marshes, they are influenced by river flows and are exposed to periodic flooding by river water, with attendant stresses and nutrient pulses (Figure 3.9). These may occur in basins in floodplains where

Figure 3.9: Floodplain marsh along the Rio Verde in Arizona. (R.W. Tiner)

periodic flow conditions are conducive to herbaceous growth. They often occur interspersed with floodplain swamps and shrub swamps (see Sections 3.1.2 and 3.1.3). They also occur in situations where water flows over the floodplain for long periods during the year.

Geophysical Characteristics. These marshes occur in many kinds of situations within the floodplain. The most common site is in basins, which may be oxbows or shallow drainageways (sometimes called sloughs). They also occur along the river edge in situations where trees cannot survive, such as where flooding is great or icefloes occur. These are particularly extensive within the floodplain forests along the large rivers of North America, such as the Mississippi and the lesser rivers along the Gulf and Atlantic coastal plain. They also occupy large areas of floodplain where slightly sloping topography and seasonal rainfall lead to extensive flooding over many months of the year. This is the case in Florida along the St. Johns and Kissimmee Rivers. The largest of the flood plain marshes is the Everglades, which is distinguished by lacking a core river, except as it approaches the coast (see Section 3.4)

Wetland Criteria Characteristics. *Vegetation.* The vegetation of floodplain marshes is similar to palustrine marshes, consisting of the same suite of species. Most are the same as was described for palustrine marshes (Section 3.2.1). Some floodplain marshes remain deeply flooded and support dense stands of emergents. Others flood less frequently or for shorter duration and support a sparser vegetation that includes annuals and upland species.

In the south, shallowly sloping floodplains of coastal plain rivers support extensive marshes (called prairies or wet prairies). These are dominated by water lily, pickerelweed, sawgrass, maidencane, torpedo grass (*Panicum repens*), or smartweed, depending on the hydroperiod. More terrestrial species are added toward the gently sloping margins of more upland sites.

Soils. Floodplain soils are either mineral or organic depending on the intensity of the scouring action of the flow. However, most have an organic soil. In basins and other sites protected from erosive water flows, peat can accumulate. The type and degree of accumulation depends on elevation, which determines the length of the dry period.

Hydrology. These marshes differ from palustrine marshes by their hydraulic connection to riverine conditions. High water tables are maintained by the head of the river. Periodic flooding events carry nutrients and materials into the marsh. Depending on the region, seasonal flooding is related to a wet-dry rainfall cycle, or to the Spring snow melt. In northern regions, the scraping and gauging of icefloes can benefit floodplain marshes over woody swamps. Some floodplain marshes are flowthrough systems where water moves across the surface in a sheet flow for many months of the year. Hydroperiod and flood frequency, of course, depend on elevation relative to the river.

The combination of herbaceous growth, flowing water sources, and warm climate leads to high productivity in these wetlands.

Characteristic Fauna. These marshes contain all the characteristic species of palustrine marshes, but in addition support more mobile species seasonally. During the high water period, fishes can move from the river into the floodplain marsh and may spawn there. They retreat back to the river as the marshes dry. Similarly, migratory and regionally mobile birds use the marsh, determined by the water depths. Snakes and turtles are similarly common. In the south the American Alligator may be abundant in this habitat. Wading birds (herons, ibis) feed on fish being concentrated by decreasing water level in the dry season. Water fowl use flooded areas in the winter. Sandhill cranes (*Grus canadensis*) often feed and nest when the marshes are flooded. These are highly productive habitats for fish and game.

Wetland Values. Like floodplain forests, floodplain marshes serve to retard flooding. They also recharge ground water, and can discharge to the river under low water conditions. Like palustrine marshes they can serve as sinks and transformers of materials. They are important wildlife habitat, especially for waterfowl. Also like palustrine forests and in conjunction with connecting riparian habitats, these marshes serve as wildlife corridors.

Unusual Characteristics. Floodplain marshes vary from small potholes to large expanses covering most of a shallow river valley. They are deeper and more permanent near the river than on the higher land farther from the river. They usually occur where fires are rather frequent, and most plants are well adapted to rapid burning.

3.2.3 The Everglades

The Everglades is the largest continuous freshwater marsh in the U.S. (Gleason, 1974; Kushlan, 1989b, 1991). Located in southern Florida, it is a flowthrough, floodplain wetland 100 km long by as much as 65 km wide. The Everglades is dominated by herbaceous, emergent vegetation but also contains extensive stands of submersed marsh and shrub swamp (Figure 3.10).

Geophysical Characteristics. The Everglades overlies a trough in the limestone bedrock of southern Florida (Hoffmeister, 1974). The trough has filled with peat over the Everglades' 10,000 year history. The result of this depositing is that the Everglades occupies a relatively uniform, shallow basin, deeper along the center of its basically north-south axis, shallower to both sides rising to slightly higher ridges.

Along this north-south axis, a ridge and swale topography is elongated in the direction of water flow, with higher ridges showing hydrodynamic sculpting. Deeper pools occur, as do patches of higher

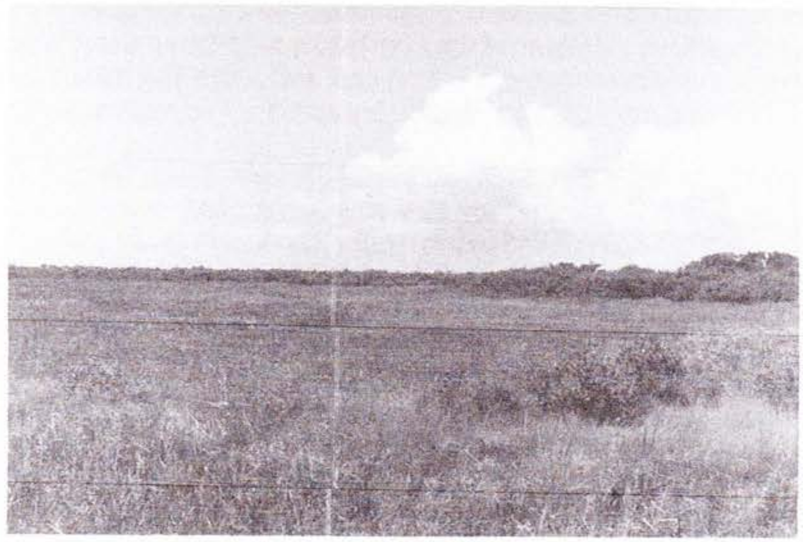

Figure 3.10: The Everglades, showing a ground view of a sawgrass dominated marsh. (J.A. Kushlan)

ground, on peat mounds or limestone highs. Because of the extensiveness of the wet landscape, these high ground patches are called islands. The limestone and sand deposits underlying the Everglades are highly permeable.

Wetland Criteria Characteristics. *Vegetation.* The vegetation of the Everglades is dominated by herbaceous emergents, especially sawgrass, with more complex communities occurring on progressively higher ground. The presence of a particular dominant plant species depends on water depth and duration of surface flooding, nutrients, fire, and recruitment history.

The deepest sites are open water ponds that support submersed (*Najas* spp.) and floating vegetation, such as water lily and spatterdock (*Nuphar luteum*), or submersed plants especially bladderwort

(*Utricularia*). Bladderwort, as characteristic of the southern Everglades as sawgrass, supports a thickly growing community of epiphytic algae. These deepest marshes are elongated in the direction of the surface current and serve as the primary flow ways.

On slightly higher ground and slightly shorter hydroperiods, emergent plants take over. Depending on the water depth and hydroperiod, these may be dominated by spikerush, cattail, maidencane, pickerelweed, arrowleaf, or sawgrass, which is the most widespread plant cover of the Everglades. On higher sites, shrubs such as willow (*Salix caroliniana*), holly, and buttonbush may form shrub swamps on the ridges and on islands. At the periphery of the Everglades, the shallow, short hydroperiod marsh supports foxtail (*Erianthus giganteus*), black rush (*Schoenus nigricans*, and muhly (*Muhlenbergia fillipes*). Ground that is emerged for most of the year supports a more complex forest of tropical hardwoods.

Soils. The soil of the core of the Everglades is an endogenous peaty muck, unconsolidated at the surface and compacted below. The deepest deposits, near Lake Okeechobee, were historically up to 6 m deep. This thins to less than a few cm in the southern portion of the marsh. Along the periphery, and mixed with the organic soil in the interior, are marl substrates. These have formed in situ from calcium carbonate precipitation by epibiotic algae that cover the plants and bottom. The peat is deficient in trace nutrients but is highly organic. Dry season fires can burn the peat and the organic marl, either superficially or deeply depending on water conditions.

Hydrology. The water source of the Everglades is rainfall and overland flow. Rainfall is seasonal with 85% of the 130 cm of annual rain falling in six months. Water moves from topographic highs near Lake Okeechobee toward the coast over a gradient of about 0.3%. Because of the slowness of the flow, the Everglades has characteristics of both palustrine and floodplain marshes. The flow is sufficient to create the ridge and swale lineations that further direct the flow patterns.

In the dry season, flow decreases and finally stops, and water levels drop. The marsh surface becomes exposed first along the higher periphery, moving inland with the drying season toward the central trough of the marsh. In some years, all but the deepest sloughs and ponds will be without surface water. The rainy season begins in late May, on average, and the Everglades fills up rather quickly.

There appears to be no definitive aquiclude between the groundwater moving through the porous limestone and the surface water. However, the peat and marl deposits no doubt inhibit rapid movement of water between the two. Recharge probably occurs along the periphery and through canals that have been cut through the peat into the limestone baserock.

Characteristic Fauna. The Everglades is well known for its wildlife (Kushlan, 1976, 1989b; Sykes, 1983; Frohring et al., 1988; Kushlan and Jacobsen, 1990). The small fish community is dominated in numbers by mosquitofish (*Gambusia affinis*), but includes a number of minnows (Cyprinids) and sunfish (*Lepomis* spp.), which survive the dry season in alligator ponds and deeper marshes and have fast population growth rates, allowing them to reinvade the marsh soon after rising water levels. Small invertebrate larvae are an important link in the food chain. These include dragonflies, mayflies, mosquitos, gnats, and deer flies. Macro-invertebrates include prawns (*Palaemonetes* spp.), crayfish (*Procambarus alleni*), and apple snails (*Pomacea paludosa*).

Amphibians and reptiles are common, including water snakes (*Nerodea* spp., *Agkistrodon piscivorus*), and turtles (*Pseudemys* spp.) as well as the American alligator. Mammals include the white-tail deer, Florida panther, roundtail muskrat (*Neofiber alleni*), and mink (*Mustella vison*).

At one time populations of wading birds nested in large numbers in this system. Prominent species include wood storks, white ibis (*Eudocimus albus*), great blue herons (*Ardea herodias*), great egrets (*Egretta alba*), tricolored herons (*Egretta tricolor*), snowy egrets (*Egretta thula*), and little blue herons (*Egretta caerulea*). Populations of these species have declined significantly in the past several decades due to hydrological changes that have taken place in the Everglades. Other characteristic birds include the snail kite (*Rostrhamus sociabilis*), which specializes on catching apple snails. Mottled ducks (*Anas fulvigula*) are found year round, with a few other species wintering in the marsh.

Wetland Values. The Everglades is the primary means of flood control and the primary water supply for the large human population in southern Florida. It has tremendous value for recreation, including hunting, fishing, and nature study. Everglades National Park attracts hundreds of thousands of visitors each year. The Everglades is a nutrient-poor system which can absorb nutrients only with changes in vegetation community. This system is recognized by all major international programs as a wetland of worldwide importance.

Unusual Characteristics. The Everglades is the largest expanse of wetlands in the United States and the only basically tropical wetland system located there. Its historical importance as a wildlife habitat led to the creation of national parks and wildlife refuges to preserve a portion of its landscape. Unfortunately its hydrology has been altered and degradation has occurred despite this concern (Blake, 1980; Kushlan, 1987). Considerable effort is being made to understand the system and reverse its degradation.

3.2.4 Prairie Potholes

Prairie potholes are small, palustrine marshes scattered over the northern prairies from South Dakota and Minnesota through Manitoba, Saskatchewan and Alberta (Figure 3.11) (Stewart and

Figure 3.11: Prairie pothole marsh in North Dakota. (R.W. Tiner)

Kantrud, 1972; van der Valk and Davis (1978); Leitch et al., 1979; Weller, 1981; van der Valk, 1985, 1989; Hubbard et al., 1988; Kantrud et al., 1989). The complex of marshes and prairie covers 780,000 square kilometers.

Geophysical Characteristics. The pothole marshes occur in basins formed by moraine and meltwater landforms left by retreating glaciers. The basins occupy depressions in till deposits formed by scouring, iceblocks, drainage dams, and riverine deposits. The accumulation of glacial silt sealed the basins. The irregularities of the landscape provided a variety of situations where marshes were able to develop within the prairie. Most marshes are less than 0.4 hectares (Cowardin et al., 1981).

Wetland Criteria Characteristics. *Vegetation.* The prairie pothole marshes are characterized by emergent plants interspersed with open water. The dominant plants include cattail (both species), bulrush (*Scirpus validus, Scirpus fluviatilis, Scirpus acutus*), burreed (*Sparganium eurycarpum*), sedges (*Carex* spp.), and arrowhead. Floating leaf and submersed plants include lilies (*Nymphaea* spp.), pondweed, stonewort, and bladderwort (van der Valk, 1985, 1989; Hubbard et al., 1988; Kantrud et al., 1989).

The vegetation follows a zonation based on water depth. Lilies, pondweed, and bladderwort occur in the deeper, more open areas. Bulrush occurs next to open areas, followed by cattail, then sedges and arrowheads, and finally the terrestrial prairie grasses.

Prairie potholes undergo a 5-20 year marsh cycle alternating periods of drying, regenerating marsh, and degrading marsh (Weller, 1981). The marsh cycle begins during drought with plants sprouting from the seed bed of the marsh. These include both annuals and the dominant perennials. After flooding, the annuals die out leaving the emergent perennials. Submersed and floating leaf plants next appear. These reach their maximum stands and then decline.

Soils. The base soil of prairie potholes is glacial till with a high percentage of clay and silt with low permeability. Higher percentages of sand and gravel occur on outwash areas. Soils underlying the marshes have a well developed soil profile.

Hydrology. The hydrology is driven by rainfall, snowfall, runoff, and ground water. Ground and surface water hydrology is further constrained by glacial topography and soil permeability. Annual precipitation is moderate (30 -60 cm) and evapotranspiration is seasonally rather high. In fact, evapotranspiration generally exceeds rainfall, so runoff and snowmelt are essential to maintain water in these marshes. Because of variation in watershed contribution and groundwater relationships among marsh basins, they differ in their water depths and permanence. Some prairie pothole marshes are only temporarily flooded, some are flooded seasonally, some semi-permanently, and some permanently.

Water level in the marshes tends to reflect the ground water, especially at high water stages. At lower stages, some marshes discharge to the ground water at their edges contributing importantly to the aquifer. Other marshes receive discharge from ground water and can be interconnected by subsurface water flow. Semipermanent marshes tend to be flowthrough systems, receiving ground water and discharging to groundwater.

Rainfall varies among years and this variation can substantially alter the hydrological situation on a marsh. A cycle of plant growth is initiated by periodic drying during low water conditions.

Water chemistry varies as these marshes have a wide range of salinity, due to variation in materials carried from the glacial materials.

Many of the potholes have been drained for farming. Others are plowed to the edge, disrupting the quantity and quality of their water source.

Characteristic Fauna. Fish are few to nonexistent since prairie potholes dry periodically and are not confluent with refugia that might allow fish to survive droughts. As a result of the limited ichthyofauna, the food chain of prairie potholes is based on the invertebrates found there. These include isopods, chironomids, amphipods, snails, cladocerans, and copepods. Populations of these groups vary seasonally and according to the marsh cycle. Isopods are most abundant early in the cycle, snails and amphipods in midcycle, and cladocerans and copepods of open water systems characterize late stages.

Fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*) are among the few native fish that can survive the difficult environment of the potholes, mostly in marshes with connections to deepwater refugia. A number of reptiles and amphibians use prairie potholes. Notable are the tiger salamander (*Ambystoma tigrinum*), the chorus frog (*Pseudacris woodhousei*), and the leopard frog (*Rana pipiens*).

The importance of these wetlands lies in the fauna they support (van der Valk, 1989). It is estimated that as much as 75% of the waterfowl produced in North America come from this region. The amount of recruitment is correlated with the number of potholes with water in them during the beginning of the breeding season. The most important species is the mallard (*Anas platyrhynchos*). Others include pintail (*A. acuta*), blue-winged teal (*A. discors*), gadwall (*A. strepera*), green-winged teal (*A. crecca*), canvasback (*Aythya valisineria*), redhead (*A. americana*), ring-necked duck (*A. collaris*), lesser scaup (*A. affinis*), hooded merganser (*Lopodytes cucullatus*), ruddy duck (*Oxyura jamaicenis*), wood duck, and Canada goose (*Branta canadensis*). Various species use marshes with specific hydrological conditions. Temporary marshes are used only by dabbling ducks (*Anas* spp.). Seasonal marshes and semipermanent are also used by diving (*Aythya* spp.) and the ruddy duck. Waterfowl appear to make best use of the potholes when the emergent vegetation and open water areas are interspersed, leaving both shelter and open feeding areas.

Many other birds use these marshes including, grebes, rails, coot, American bittern, killdeer, willet (*Cataptrophorus semipalmatus*), marbled godwit (*Limosa fedoa*), Wilson's phalarope (*Phalaropus tricolor*), black tern (*Chilonius niger*), marsh wren, yellow-headed blackbird, red-winged blackbird, and savannah sparrow. These species use specific vegetation stands, which change with the marsh cycle.

Mammals are exceptionally important in the ecology of prairie potholes. During the regeneration stage of wetland development, muskrat (*Ondatra zibethicus*) populations increase, and their activities are thought to hasten the decline of the marsh and its succession from emergent marsh to open aquatic habitat. Other aquatic mammals include beaver and mink. Shrews, mice, hares, weasels, fox, coyote, and deer use the marsh periodically.

Wetland Values. The prairie potholes serve a number of important functions, the most critical being flood retention and ground water recharge. They also function to maintain water quality, which is of importance given the heavy agricultural use surrounding them. The most important international value, of course, is the production of a significant portion of the continent's migratory waterfowl.

Unusual Characteristics. The importance of the prairie pothole ecosystem is the combination of intensive agriculture and waterfowl production. The combination makes this one of the most valuable systems in the world. With much of the marsh system having been drained, the future depends on an optimization of the several important values they serve.

3.3 BOGS

Bogs are wetland communities typified by the dense surface cover of aquatic moss, *Sphagnum* spp., which creates a highly acid water chemistry. These wetlands are found across the north temperate zone of North America and Eurasia and are similar in appearance and functioning (Figure 3.12, and Plate III) (Heinselman, 1970; Moore and Bellamy, 1974; Larsen, 1982; Gore, 1983; Larsen, 1982; Johnson, 1985;

Figure 3.12: A bog in New York. (R.W. Tiner)

Tiner, 1985a, 1985b, 1988; Damman and French, 1987; Glaser, 1987; Crum, 1988; Mitsch and Gosselink, 1993).

Bogs characteristically derive their nutrients primarily from rainfall. The low nutrient availability and high acidity results in peat deposition, which in turn influences the development of plant and animal communities. These nutrient poor peatlands may be herbaceous bogs or shrub bogs, with a successional relationship often existing between the two. Bogs are called muskegs in Canada and moors in Europe. They also are a type of mire, in European terminology.

Geophysical Characteristics. Bogs have been well studied and are known to occur in several situations. Basin bogs are those that occupy depressions including former lakes, which become filled with peat after which the bog begins to emerge above the landscape. As a result basin bogs are called raised bogs. Bogs also cover flat landscapes, often extensively. These blanket bogs have generally grown out from a foci such as a depression. Another type of bog occurs on slopes, where an undulating topography develops a series of peat bog ridges tending across slope separated by intervening pools. These are called string bogs. In all these bogs, the peat deposition process itself creates the final land form.

Peat grows not only up but out. As peat accumulates, new growth can also move sideways encroaching upon and overtopping the soil and plants adjacent to its margins. It is in this way that blanket bogs spread from basin loci through woodlands. Along the edges of lakes and pools, peat can grow out over the water, forming a floating shelf. These wetland situations are called quaking bogs.

Wetland Criteria Characteristics. *Vegetation.* Bogs are characteristically dominated by a few species of peat moss, a bryophyte. These included *Sphagnum cuspidatum, S. major, S. papillosum, S. magellanicum*, and *S. capillifilium.* Sphagnum is well adapted to survive and prosper under conditions of low nutrients and acid water. Acid water is not required for its survival, but it is competitive over other plants under such conditions. *Sphagnum* grows in densely packed mats. It has a high concentration of air in its cells, which keeps it floating toward the surface. Because decomposition is slowed by cool temperatures, acid water, deoxygenated conditions, and low nutrient concentrations, the peat located below the actively growing moss accumulates, creating the bog conditions.

Bogs have a low plant diversity relative to other wetlands because of the lack of mineral soil, lack of nutrient availability, and acidity. However, some are capable of invading acidic peat substrate. Cotton grass (*Eriophorum vaginatum, Eriophorum angustifolium*) is a common associate. It is a deciduous perennial, which conserves nutrients by translocation prior to leaf death. Sedges also are common associates. These include *Carex oligosperma, C. limosa, C. pauciflora,* and *Rhynchospora alba.* Other herbaceous plants include liverwort (*Cladopodiella fruitans*), the moss *Drepanocladus*, and orchids (*Calopogon tuberosus, Habenaria clavellata, Habenaria blephariglottis, Pogonia ophioglossides*, and *Arethusa bulbosa*). Carnivorous plants are also typical. These include the bladderwort (*Utricularia cornuta*), *Sarracenia purpurea, Drosera intermedia*, and *Drosera rotundifolia.*

Woody plants can also invade, although their growth is slow and stature usually slight; species that are trees elsewhere may only achieve shrub stature in bogs. Shrubs include cranberry and blueberry, heather (*Calluna vulgaris*), crowberry (*Empetrum* spp.), black spruce (*Picea mariana*), scotch pine (*Pinus sylvestris*), leatherleaf (*Chamaedaphne calyculata*), laurel (*Kalmia politifolia*), heaths (*Ledum groenlandicum*), Labrador tea (*Ledum palustre*), willow, bog birch (*Betula pumila*) and tamarack. Trees, such as black spruce, can occur on higher islands in the bog.

Most of these species are not restricted to acid conditions, but are competitive there. Among the adaptations for survival are: reduced oxygen consumption, aerenchyma and lacunae, root aeration, low nutrient requirements, sequestering of nutrients during the Winter, deep penetration of roots, symbiotic nitrogen fixation and carnivory, adventitious roots and shoot elongation to ovoid overgrowth by the moss (Crum, 1988).

As succession occurs, typical plants change. Bogs typically develop from mineral, groundwater marshes. First, sphagnum invades and eventually alters the water and soil chemistry. Then a mixed bog develops as other herbaceous plants and small woody plants invade. Finally a shrub bog develops.

Soils. The functional substrate of bogs is the sphagnum peat itself, which is waterlogged, acidic, and anaerobic at depth. Sphagnum also dominates water chemistry, particularly through its control of pH and the ability of living sphagnum to take up dilute nutrients.

Bogs deposit peat. Conditions leading to peat deposition and bog formation include cool climate, ample precipitation, high humidity, poor drainage and waterlogged conditions, low oxygen levels, and usually low pH.

Bog peat is deposited over various soil and geologic bases but is soon divorced from the influence of the underlying mineral soil. Bogs are generally successional ecosystems, having developed over mineral soils through the autogenic activities of the bog plants. In succession, the transition from soil dominated processes (owing to mineral soil or mineralized peat) to sphagnum dominated processes occurs rather sharply.

Hydrology. Bog vegetation occurs typically where ground and surface water inflow is minimal, thus the wetland depends primarily on rainfall. Ground and surface water may influence bogs more in the early stages of bog formation. Bogs develop along the edges of lakes that have a flow through hydrology. However, as bog development occurs, the bog is increasingly isolated from other water sources.

The water holding capacity of peat is many times its own weight, and as a result, affects such characteristics as effective water table, temperature, nutrients, and gases. Water is contained not only among the peat particles but also in water holding cells in the sphagnum. As the accumulating peat raises the bog, it carries with it its water table. The bog water supply may then become perched above the ground water and higher than flows of surface water, which bypass it. The bog may become a water source.

The limited inflow of surface and ground water results in the bog's low fertility and therefore explains many of its characteristics. The water is highly acidic with low concentrations of minerals and high cation exchange capacity in the peat. The acidity comes from the oxidation of organic compounds, especially those containing sulfur, by the sphagnum's extraction of cations from the water and exchange with hydrogen ions, the production of galacturonic acid at the growing tips of sphagnum, and the leaking of humic acid from decomposing peat (Clymo, 1964).

Characteristic Fauna. Animals are generally scarce in bogs, owing to the low production, low nutrient concentrations, acidity, and an inability to access and consume the dominant biomass - sphagnum. Insects are the dominant consumers, especially flies (psyllids, tipulids). Snails are nonexistent.

Among vertebrates, those that are mobile among habitats are the most common. Herbivores and carnivores enter the bog from the surrounding habitats or higher areas of the peat lands. Mammals include hares, lemming, and weasels. Large mammals, such as moose, occur along the margins. Birds include sora, sandhill crane, great gray owl (*Strix nebulosa*), short eared owl (*Asio flammeus*), palm warbler (*Dendroica palmarum*), northern waterthrush (*Seiurus noveboracensis*), and swamp sparrow (*Melospiza georgiana*).

Wetland Values. Bogs determine and create the water table of their basin. Since prehistoric times, bogs have been mined for their peat, which is used for fuel, and more recently for horticulture. Bogs cover much of the Northern Hemisphere and are part of the traditional live of that huge region. Berries are farmed in bogs and harvested commercially. It is likely that bogs influence atmospheric gasses, considering their wide distribution.

Unusual Characteristics. Peat creates its own wetland. Peat bogs have played an important role in human history for centuries. For example, they provide fuel. As a result, peat has been mined as a source of fuel in situations where fuel is limited. This practice continues in many parts of the world.

3.4 DEEP WATER AND OTHER INLAND AQUATIC ECOSYSTEMS

Wetlands are often found in association with deep water habitats, especially rivers and lakes. The environmental conditions in these ecosystems differ in important aspects from those in wetlands. Nonetheless they interact as water and organisms move between them.

3.4.1 Rivers and Streams

A river or stream is composed of water and its load that moves along a defined and repeated track, following or cutting a channel. The predominating physical and biological feature is the role of moving water in structuring this ecosystem.

Geophysical Characteristics. The stream channel is cut through the substrate, soil, sediment, or rock by the erosive force of water moving down gradient. The velocity and volume of water moving down the stream depend on the catchment area, the width, depth, and gradient of the stream bed, and the amount of rainfall, snowmelt, and upstream discharge. Typically, streams originate in upland areas, such a mountains or hills. There they are relatively swift, shallow, and narrow. Velocity decreases as the stream falls in elevation. The size of the stream increases with distance from its source, joining other streams and becoming wider, deeper and carrying a great load of sediment and other materials. When it reaches flatter land, such as in the coastal plain, it becomes more sluggish and meanders as it cuts along out along the outer bends and deposits materials along the inner bend. As meanders come closer together, the stream can break through the neck of land separating the channels, taking a more direct course and isolating oxbows from the main channel. Flow varies seasonally and from year to year, from no flow in intermittent streams to flood stage. Repeated flood stages, annually or less frequently, cut a valley larger than the stream itself. During floods, materials are both transported to and removed from the flood plain.

Ecological Characteristics. *Vegetation.* Vegetation in the channel itself it usually limited by the flowing water and lack of substrate in upper reaches, and by high flows and lack of light in lower reaches. Where the water is clear, algae grows on rocks. In slower streams, or in protected sites, submersed plants can form plant beds. Typical plants include *Potomogeton, Myriophyllum, Wolffia, Spirodela*, and *Chara.* In larger muddy streams, other submersed and floating leaf aquatic plants, such as water lilies, can grow in protected sites such as backwaters and coves.

Many streams are intermittent. Depending on the season and duration of no flow periods, the stream bed may be colonized by herbaceous annuals, especially grasses (*Panicum*). Streamside vegetation reflects the situation through which the stream flows and is often a zone of wetland type plants. Streamside plants may range from herbaceous, particularly in upper reaches, to an extensive floodplain swamp in the lower reaches. In arid areas, tamarisk is common.

Soils. Stream substrates depend on the bedrock and the materials that are being carried and deposited in the floodplain. The streambed reflects the parent material through which the stream flows and the material being transported to that point, either on a daily or intermittent basis. As the flow slows and volume of materials being transported increases from erosion, unconsolidated sediments are deposited in the channel and along the banks.

Typically, higher streams have a rocky substrate because of the rapid flow and relatively small volumes. The bottom of smaller streams may be bedrock, rubble, gravel, sand, or mud. Larger streams and those flowing through arid environments generally have a mud bottom. Along the coast, streams cut through organic substrate.

Hydrology. The water of streams originates from rainfall, ground water seepage, springs, surface runoff, or wetland surface flow. Variation in stream flow depends on rainfall, soil conditions, slope of the landscape, vegetation in the catchment basin, temperature, humidity and evaporation.

Characteristic Fauna. Given the limited primary production within a stream, a characteristic of this ecosystem is that the food chain is based on materials being carried into and along the stream. Additionally, organisms are adapted to life in flowing waters.

The invertebrates present depend on the substrate and the type of food source. On bedrock and rubble, animals are generally adapted to attach firmly to the substrate. These include snails (*Physa*), clams (*Pisidium*), worms (*Limnodrilus*), caddisflies, and mayflies (*Ephemerella, Caenis*). On cobble, there are more interstices for hiding, and additionally this bottom can support midges (*Chironomus*), mosquitos (*Anopheles*), mussels (*Mytilus, Modiolus*), flatworms, leeches, and crustaceans. In sand, crustaceans increase. In mud, burrowing and mud specialists can occur, including the horse and deer flies (*Tabanus*), crayfish, snails (*Lymnaea*), and clams (*Sphaerium*).

Fishes in the upper reaches are the swift flow specialists, especially the salmonids (trout) and bottom dwelling fish (*Percina, Ammocrypta, Etheostoma*). In the lower reaches, additional species occur.

3.5 PONDS AND LAKES

Lakes and ponds are open, deep water systems occupying basins. There is no substantive difference between a pond and lake, except that lakes are larger, but even that relation differs among areas. Ponds are still waters, generally with submersed vegetation covering significant portions seasonally. Ponds and lakes may be formed artificially by damming rivers and flooding their valley. These reservoirs bear many similarities to natural lakes and ponds.

Geophysical Characteristics. Basins may develop in many ways, ranging from a meteor impact crater to an alligator den. Some of the largest and most interesting lakes in North America have diverse origins, such as glacial scouring (Great Lakes), remnants of a former sea floor depressions (Lake Okeechobee), volcanic action (Crater Lake), solution of limestone, and earthquakes (Reelfoot Lake). Salt lakes occupy fossil basins of former large lakes (Great Salt Lake). Smaller ponds and lakes result from glaciers, such as kettle lakes that formed in the depression left by melting blocks of glacial ice; oxbow lakes that form in the former channels of rivers; beaver lakes form when beavers dam streams; and the many depressions in various habitats that are deep enough to have open water.

Ecological Characteristics. *Vegetation.* Lakes and ponds generally have a zonation of vegetation following water depth gradients. Along the edges in shallow water if wind and wave exposure is limited, typical marsh or swamp vegetation usually develops. Submersed and floating leaf vegetation cover slightly deeper areas, and can seasonally cover an entire pond or small lake. In deeper basins, primary production depends on phytoplankton. The nutrient and energy relationships between the open water system and the fringing wetland vegetation are just now becoming better understood.

Soils. Substrates of lakes are variable, depending on the parent substrate and on the materials carried into the lake by streams or runoff. Substrates may be sand, clay, or organic sediment. In deep lakes, an anoxic organic, sediment forms. Often in the herbaceous zones of lakes and ponds, peat is deposited if erosional processes are not excessive.

Hydrology. The water supplies of lakes and ponds may come from rainfall, ground water, surface runoff, stream flow, or wetland surface flow. Most lakes have both input and output streams; many ponds lack surface outflow, although they may recharge groundwater. Reservoirs have outflow tightly controlled for flood control and water management. Outflow in these situations is often from depth rather than at the surface, which can effect downstream rivers and wetlands. Changes in the timing of flows from the reservoir can also substantially change the flooding regime of the floodplain and its wetlands.

Direct water input into a lake, such as by stream flow, can create density gradients within the lake. Density gradients are also maintained by temperature stratification, which effectively isolates aerobic layers from cool anaerobic bottom layers. Temperate lakes can overturn seasonally when water temperature equilibrates to depth. This turnover is a characteristic of the water quality of deep, temperate lakes. The water supply of ponds may be more local, and its water chemistry is very dependent on local conditions.

Characteristic Fauna. The fauna of lakes and ponds differs from that of wetlands because of its open water component. Phytoplankton and zooplankton (cladocerans, ostracods, copepods) generally form the basis of the food chain. Sediments are anaerobic and are suitable for only specialized animals such as oligochaetes (*Tubifex* spp.). Fish occupy most lakes and ponds. Since lakes are more stable than wetlands, fish can grow to larger size. Gizzard shad (*Dorosoma cepedianum*), bass (*Micropterus*), sunfish (*Lepomis* spp.), walleye (*Stizostedion lucioperca*) are some important lake fish in the U.S. Many lakes and reservoirs are stocked with native or non-native fish to enhance the recreational fishery.