ONE

Ecology of Freshwater and Estuarine Wetlands: An Introduction

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What Is a Wetland?

The study of wetland ecology can entail an issue that rarely needs consideration by terrestrial or aquatic ecologists: the need to define the habitat. What exactly constitutes a wetland may not always be clear. Thus, it seems appropriate to begin by defining the word *wetland*. *The Oxford English Dictionary* says, "Wetland (F. wet *a*. + land *sb*.)—an area of land that is usually saturated with water, often a marsh or swamp." While covering the basic pairing of the words *we*t and *land*, this definition is rather ambiguous. Does "usually saturated" mean at least half of the time? That would omit many seasonally flooded habitats that most ecologists would consider wetlands. Under this definition, it also seems that lakes or rivers could be considered wetlands. A more refined definition is clearly needed for wetland science or policy.

Because defining *wetland* is especially important in terms of policy, it is not surprising that governmental agencies began to develop the first comprehensive definitions (see Chapter 8). One influential definition was derived for the U.S. Fish and Wildlife Service (USFWS) (Cowardin et al. 1979):

> Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. Wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominately hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year.

This USFWS definition emphasizes the importance of hydrology, soils, and vegetation, which you will see is a recurring theme in wetland definitions. The U.S. Army Corps of Engineers (USACE), the primary permitting agency for wetlands of the United States, adopted a slightly different wording (Environmental Laboratory 1987):

> The term "wetlands" means those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions.

> Wetlands generally include swamps, marshes, bogs, and similar areas.

This definition also incorporates hydrology, soils, and vegetation, but it is more restrictive than the USFWS definition. The USACE definition requires all three features to be present, while the USFWS Cowardin definition indicates that only one of the three conditions needs to occur. Despite its exclusive nature, the USACE definition has been adopted as the authority to define legal (or jurisdictional) wetlands of the United States.

In Canada, a very similar definition for *wetland* is used by the National Wetlands Working Group (NWWG). This definition also focuses on hydrology, soils, and vegetation, but is more expansive, acknowledging that aquatic processes and biologic factors other than just soils and plants may also be useful for classification (NWWG 1988):

> Wetland is defined as "land that has the water table at, near, or above the land surface or which is saturated for a long enough period to promote wetland or aquatic processes as indicted by hydric soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to the wet environment."

The NWWG definition is not an official legal standard in Canada but is widely used or adapted by various governmental agencies for setting policy about wetlands (personal communication, Barry Warner, University of Waterloo, Ontario, Canada).

An international definition for *wetland* was developed for the Ramsar Convention, an intergovernmental treaty regarding wetland conservation initiated in 1971 (which met in Ramsar, Iran). The most recent information (see www.ramsar.org) provides this definition:

> Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres.

The emphasis on soils and plant adaptations found in other definitions is absent from this one, possibly because it targets non-scientists who may not be familiar with what constitutes wetland conditions. However, hydrology remains a focal tenet. This definition is currently being applied to identify wetlands in countries in Asia (e.g., Gong et al. 2010).

As ecologists, we must realize that political definitions may not cover all habitats that function ecologically as wetlands. For example, mud flats devoid of vegetation, floodplains that primarily flood in winter outside the "growing season," and flooded areas of floodplains where anoxic soil conditions do not develop are all probably *ecological* wetlands but may not fit some legal definitions. In Georgia, for example, we have seen floodplains repeatedly covered by as much as 1 meter of water (Fig. 1.1), yet competent delineators following USACE criteria determined that the majority of the floodplain area did not meet the legal US definition of a wetland (hydric soil was not present). However, the determination that these floodplains were not jurisdictional wetlands did not affect the responses of soil-dwelling arthropods and herbaceous plants that were covered by the water or the functioning of waterfowl or fish that were swimming and feeding in those habitats. Although definitions do serve a purpose, especially for regulation (see Chapter 8), ecologists should not be constrained by them when studying wetlands.

Nonetheless, for ecologists seeking a biologically useful definition for wetlands, we recommend the simple, straightforward, yet inclusive, definition put forward by Paul Keddy (2000):

> A wetland is an ecosystem that arises when inundation by water produces soils dominated by anaerobic processes and forces the biota, particularly rooted plants, to exhibit adaptations to tolerate flooding.

Why Are Wetlands Important?

Wetlands comprise only about 6% of the earth's land surface, but ecologically they are disproportionately important. For example, 25% of the plant species in Malaysia occur in only one wetland type, peat swamps (Anderson 1983). Almost 10% of the world's fish fauna occurs in the Amazon basin (Groombridge and Jenkins 1998). The vast majority of amphibians are linked to wetlands, even if only for reproduction. Wetlands are particularly important habitats for birds, with many species occurring only in association with wetlands. Bird watching and waterfowl hunting are major human activities related to wetlands. Because wetlands support both terrestrial and aquatic biota, they are unusually diverse (Gopal et al. 2000). Those taxa unique to wetlands will contribute significantly to the overall diversity of regions containing numerous wetlands.

Besides supporting the plethora of plants and animals of interest to ecologists and nature enthusiasts, wetlands provide an assortment of ecosystem services of considerable value to all people. Costanza et al. (1997) estimated the economic values of services provided by the world's ecosystems and found that, on a per-hectare basis, estuaries and freshwater floodplains/swamps were the world's two most valuable ecosystem types (Table 1.1). The value of these wetlands to people stem primarily from their roles in nutrient cycling, water supplies, disturbance (flood) regulation, and wastewater treatment. However, recreation, food production, and cultural (aesthetic, artistic, educational, spiritual, or scientific) values are also important (Costanza et al. 1997). Many of these services are accomplished by wetland biota (microbes, plants, and animals). In Canada, an assessment of the economic values of the country's wetlands (see NWWG 1988, Table 10-15) came up with an esti-

FIGURE 1.1. Flooded riparian wetland of the North Oconee River, Georgia. Although the site floods almost yearly, it does so in winter, out of the growing season. Additionally, hydric soils are not extensive. As such, using current criteria for delineating wetlands in the United States, most of the floodplain is not considered a jurisdictional wetland.

TABLE 1.1.
Estimated Relative Economic Values per Hectare of Services Provided by the World's Ecosystems

Ecosystem Type	1997 US$ $ha^{-1}yr^{-1}$
Estuaries	22,832
Swamps/floodplains	19,580
Coastal sea grass/algae beds	19,004
Tidal marsh/mangrove	9,990
Lakes/rivers	8,498
Coral reefs	6,075
Tropical forests	2,007
Coastal continental shelf	1,610
Temperate/boreal forests	302
Open oceans	252

SOURCE: From Costanza et al. (1997).

mate of almost $10,000,000,000 (1985 Canadian dollars), of which almost half was attributed to recreational values (nature appreciation activities, fishing, and hunting). However, despite the considerable economic value of wetlands, there is a long history of humans destroying or degrading the world's wetland resources.

Characteristics of Selected Wetlands

Throughout the world, the types of plant and animal communities that occur in wetlands are a result of climate, geomorphology and landscape position, soils, water source and chemistry, and numerous environmental factors including disturbance. Wetlands are found on every continent except Antarctica and extend from the tropics to the tundra. Estimates of the extent of the world's wetlands vary, but generally range from around 7 to 10 million square kilometers (Mitsch and Gosselink 2007). Approximately 30% occur in tropical and 24% in subtropical regions, 12% in temperate areas, and 30% in boreal regions. These estimates do not include large lakes or deepwater coastal systems.

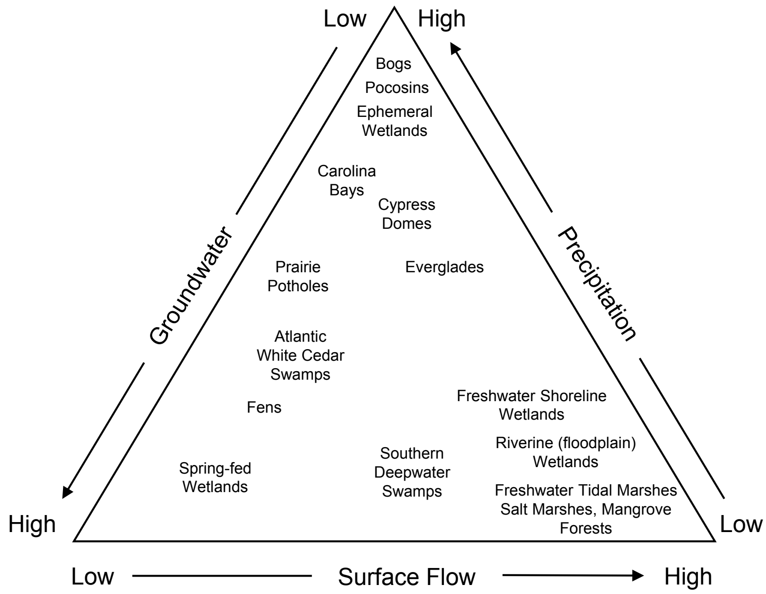

FIGURE 1.2. The relative contribution of three water sources (precipitation, groundwater discharge, and surface inflow) to wetlands. As there may be much variation in the relative importance of different water sources within many of the wetland types, their locations are approximations and often overlap. Modified from Brinson (1993b).

The classification and naming of wetland types is often confusing because names have evolved over centuries in different parts of the world and often reflect regional or continental differences. The wetlands described here reflect a North American perspective and are chosen to be representative of the variety of wetland types rather than totally inclusive of the range of wetland plant and animal communities that occur on this continent. We have grouped them ecologically, according to major sources of water (Fig. 1.2)—(1) precipitation, (2) groundwater, and (3) surface water—with the understanding that sources and amount of water may vary considerably within a wetland type and that most wetlands receive water from more than one source. A more detailed treatment of many North American wetland habitats is available in a companion volume by Batzer and Baldwin (2012).

Wetlands with Predominantly Precipitation Inputs

NORTHERN BOGS

Bogs are freshwater wetlands that occur on acid peat deposits throughout much of the boreal zone of the world (Fig. 1.3). They are frequently part of a larger complex of peatlands that includes fens, with readily apparent gradients of plant species distributions, biogeochemistry, and hydrology (Bridgham et al. 1996; Rochefort et al. 2012; Fens and Related Peatlands below). Bogs are distinguished from fens, however, because they receive water and nutrients exclusively from precipitation (ombrogeneous). Precipitation inputs are greater than evapotranspiration losses, and the slow decomposition of organic material under cold temperatures results in peat accumulation. Bog soils are organic, waterlogged, low in pH, and extremely low in available nutrients for plant growth (Chapter 2). In addition, growing seasons are short. Thus, a specialized and unique flora occurs in this wetland habitat.

Mosses, primarily *Sphagnum*, are the most important peat-building plants in bogs. Bogs can be open *Sphagnum* moss peatlands, *Sphagnum*-sedge peatlands, *Sphagnum*-shrub peatlands, or bog forests; these bogs often form a mosaic across the landscape with other peatlands such as fens, which are more influenced by groundwater. Plants often associated with *Sphagnum* in bogs include various sedges (*Carex* spp.); cottongrass *(Eriophorum vaginatum)*; and a variety of ericaceous shrubs such as heather *(Calluna vulgaris)*, leatherleaf *(Chamaedaphne calyculata)*, cranberry and blueberry (species of *Vaccinium*), and Laborador tea *(Ledum groenlandicum)*. Trees such as spruce (*Picea* spp.) and tamarack *(Larix larcina)* may occur in bogs, often stunted in growth to reach only a meter or two tall. Many northern peatlands show a considerable overlap of species along the hydrologic and chemical gradients from nutrient-poor bogs to more mineral rich fens (see Fens and Related Peatlands below).

Vegetation development in many bogs may follow the model of hydrarch succession, or terrestrialization, at least to some degree (see Chapter 5). Through the buildup of soil organic matter, vegetation in these peatlands has significant control over habitat development (Moore and Bellamy 1974). Primary production exceeds decomposition of the peat substrates (Clymo et al. 1998), and the accumula-

FIGURE 1.3. Bog and lake with ericaceous shrubs and conifer trees in northern Michigan. Courtesy of K.E. Francl.

tion of peat affects hydrologic conditions, chemistry, and plant community composition (Damman1986; Bridgham et al. 1996; Bauer et al. 2003). As peat builds up, it is often colonized first by shrubs and then by trees. Paleo-ecological evidence from several studies suggests a sequence of plant associations from wet marshes to a *Sphagnum* bog or wet forest (Walker 1970). Other processes, such as paludification (which occurs when bogs exceed the basin boundaries and encroach on formerly dry land) (e.g., Moore and Bellamy 1974; Bauer et al. 2003; Yu et al. 2003) and fires (Kuhry 1994), complicate the patterns of bog successional development.

Sphagnum has the ability to acidify its environment, probably through the production of organic acids located on its cell walls (Clymo and Hayward 1982). The acid environment retards bacterial action and reduces decomposition rates, enabling peat accumulation. *Sphagnum* also maintains waterlogging in the substrate. Its compact growth habit and overlapping, rolled leaves form a wick that draws up water by capillarity. Many bog plants are adapted to waterlogged anaerobic (low oxygen) environments by aerenchyma production, reduced oxygen consumption, and a leakage of oxygen from the roots to the rhizosphere. Many bog plants also have adaptations to the low available nutrient supply; these include evergreenness, sclerophylly (thickening of the plant epidermis to minimize grazing), the uptake of amino acids as a nitrogen source, and high root biomass (Bridgham et al. 1996). In addition, carnivorous plants such as pitcher plants (*Sarracenia* spp.) and sundews (*Drosera* spp.) have the ability to trap and digest insects. Some bog plants, such as the sweet gale *(Myrica gale)* and alders (*Alnus* spp.) also carry out symbiotic bacterial nitrogen fixation in nodules on their roots.

POCOSINS

Pocosins are evergreen shrub bogs (Fig. 1.4; Richardson 2012) restricted to the southeastern US Atlantic Coastal Plain, chiefly in North Carolina. They occur on waterlogged, acidic, nutrient-poor sandy or peaty soils (Bridgham and Richardson 1993; Richardson 2003) and are located primarily on flat topographic plateaus of the outer Coastal Plain. Their source of water is precipitation, and most of their water loss is through evapotranspiration during the summer and fall, although surface runoff also occurs, especially during winter and spring (Richardson 2012).

Evergreen shrub and tree species dominate in pocosins, and the composition and stature of the vegetation is related to depth of the peat and nutrient availability. On deep peat accumulations (>1 m), roots do not penetrate into the underlying mineral soils, and ombrotrophic shrub bogs develop (Otte 1981). Ericaceous shrubs in these communities, called *short pocosin,* include titi *(Cyrilla racemi?ora),* fetterbush *(Lyonia lucida),* and honeycup *(Zenobia pulverulenta)* as well as vines, particularly greenbriar (*Smilax* spp.). A sparse and often stunted canopy of pond pine *(Pinus serotina)* and loblolly bay *(Gordonia lasianthus)* may be present. Where organic substrates are shallower (approximately 50–100 cm), roots can penetrate into the underlying mineral soil and the vegetation grows somewhat taller. Additional species in these tall pocosins may include red maple *(Acer rubrum),* black gum *(Nyssa sylvatica),* and sweetbay *(Magnolia*

FIGURE 1.4. Short pocosin with ericaceous shrubs and pond pine *(Pinus serotina)* in eastern North Carolina.

virginiana). Fire during drought may also be an important factor in pocosin community development. Shallow peat burns allow the regeneration of pocosin species, although if the depth of the peat is reduced, roots of the recovering plants may be able to reach mineral soils. Severe burns that destroy peat substrates lead to development of a non-pocosin community, such as a marsh. Pocosins temporarily hold water, especially during winter and early spring, and then slowly release it to adjacent wetlands. Since they occur in close proximity to estuaries, this slow release of freshwater may stabilize the salinity of regional estuaries (Daniel 1981). Draining and development activities may greatly change these hydrologic outputs. Richardson and McCarthy (1994) reported that peat mining resulted in an increased runoff of approximately 30%. Furthermore, drainage and agricultural conversion have increased the turbidity and levels of phosphate, nitrate, and ammonia in adjacent estuaries (Sharitz and Gresham 1998).

CAROLINA BAYS

Carolina bays are elliptical depressional wetlands (Fig. 1.5) that occur throughout the southeastern US Atlantic Coastal Plain from New Jersey to northern Florida (Kirkman et al. 2012). These wetlands range in size from greater than 3,600 hectares to less than 1 hectare. Early estimates of their number were as high as 500,000 (Prouty 1952), although it is more likely that only 10,000 to 20,000 remain (Richardson and Gibbons 1993). Carolina bays characteristically have no natural drainage, either into them or out of them, and overland water flows are minimal. Precipitation is their predominant source of water, and these shallow basins range from nearly permanently inundated to frequently dry, depending on their depth and local rainfall patterns. Most have highly variable hydroperiods (Sharitz 2003) and tend to be wetter in the winter and drier in the summer. Many small bays typically dry completely during most summers and refill during fall and winter rains. Soils in the basins of Carolina bays range from highly organic to predominantly mineral, and most are underlain with sand and impervious clay layers that retard vertical water movement. This sandy clay hardpan is often assumed to limit interactions between surface and groundwater and result in a perched water table in the basin, although a few studies have shown some connection with shallow groundwater (Lide et al. 1995; Chmielewski 1996; Pyzoha et al. 2008). The water in most bays is nutrient poor and acidic (with a pH range of 3.4 to 6.7) (Newman and Schalles 1990).

Plant communities in Carolina bays are influenced by soils and hydroperiod, and at least 11 vegetation types have been described (Schafale and Weakley 1990; Bennett and Nelson 1991). Pocosin communities, pond cypress *(Taxodium ascendens)* savannas, and pond cypress ponds are more common in bays on the lower Coastal Plain, which tend to have soils that are more organic. Herbaceous depression meadows are found on mineral soils in bays of the upper Coastal Plain, and forested habitats occur throughout. Various submersed and floating-leaved species such as bladderworts (*Utricularia* spp.), water lily *(Nymphaea odorata),* and water shield *(Brasenia schreberi)* are often common in bay ponds. Depression meadows are dominated by graminoids, including grasses such as *Panicum, Leersia,* and *Dichanthelium;* sedges such as *Carex;* and rushes including *Juncus* and *Rhynchospora* as well as a variety of other herbaceous plants. Forested bays may contain pond cypress as well as broad-leaved trees such as swamp tupelo *(Nyssa bi?ora),* red maple, and sweetgum *(Liquidambar styraci?ua).* Pocosin vegetation that occurs in bays is dominated by evergreen shrubs similar to that of the larger regional pocosins. Across this range of plant communities, Carolina bays have high plant

FIGURE 1.5. A 5-hectare Carolina bay showing characteristic elliptical shape. Aquatic herbaceous vegetation in the center is surrounded by bald cypress trees on the rim. Courtesy of L.S. Lee.

species richness and contribute greatly to the regional biodiversity. The seed banks of some Carolina bays, especially depression meadows, are highly species rich (Kirkman and Sharitz 1994; Collins and Battaglia 2001; Mulhouse et al. 2005).

Rich zooplankton communities have been reported from Carolina bays (Mahoney et al. 1990), and a wide variety of aquatic and semiaquatic insects live in these habitats (Taylor et al. 1999). These seasonal wetlands are critical breeding habitat for numerous species of amphibians, some of which are entirely dependent on these ecosystems (Gibbons and Semlitsch 1991) and may be found in huge numbers during the breeding season (Pechmann et al. 1991; Gibbons et al. 2006).

Many Carolina bays, especially the smaller ones, have been drained and converted to agriculture or other uses, and the great majority of those remaining have drainage ditches (Bennett and Nelson 1991). Since 2001, one of their most serious threats has come from US Supreme Court decisions that held that isolated non-navigable waters are not necessarily protected under the Clean Water Act (Downing et al. 2003; Sharitz 2003; see Chapter 8).

CYPRESS DOMES

Cypress swamps found in nearly circular isolated depressions throughout the karst landscape of Florida are called *cypress domes* because of the dome-like appearance of the tree canopy (Fig. 1.6). Trees are usually taller and grow faster in the centers of the depressions than at the edges (Ewel and Wickenheiser 1988). Trees on the perimeters of domes are also more susceptible to fire mortality (Watts et al. 2012). These depressions are formed by the dissolution of underlying limestone, and most are less than 10 hectares in size (Ewel 1998). Most of the water is received from precipitation, although surface inflows may also occur. Water may also move from these depression ponds into shallow groundwater (Heimburg 1984). Pond cypress and swamp tupelo are the dominant species, with slash pine *(Pinus elliottii)* co-dominant in partly drained cypress domes (Mitsch and Ewel 1979).

These wetlands play a major role in maintaining the region's biodiversity. Many are significant amphibian breeding grounds. In addition, since they hold water for long periods, cypress domes help prevent flooding of local areas and aid in groundwater discharge. Nearly all cypress domes in northern Florida have been harvested, although in many the trees have regenerated. The most detrimental human impact is caused by development and conversion to residential and commercial sites. Drainage of cypress domes also causes oxidation of the organic soils, land subsidence, and an increase in fire susceptibility (Ewel 1998).

PRAIRIE POTHOLES

One of the most important areas of freshwater wetlands in the world is the prairie pothole complex of North America (Galatowitsch 2012). These shallow depressional wetlands (Fig. 1.7) are found in Minnesota, Iowa, and the Dakotas in the United States, and in Alberta, Saskatchewan, and Manitoba in Canada. Although individual pothole marshes are usually small, they are regionally abundant. Between 4 and 10 million potholes are estimated to occur in Canada (Adams 1988), and about 2.3 million existed in the 1960s in North and South Dakota (Kantrud et al. 1989), although many had been drained even by that time. Using assumptions from these estimates regarding abundance and size, van der Valk and Pederson (2003) suggested that these wetlands covered approximately 63,000 square kilometers prior to drainage.

FIGURE 1.6. Cypress dome wetland with pond cypress (*Taxodium ascendens* [*T. distichum* var. *imbricarium*]) trees in Florida. Note that the tallest trees are in the center, which is usually the deepest part of the wetland..

FIGURE 1.7. Prairie pothole marsh wetland in the upper Midwest. From Tiner et al. (2002).

Precipitation is the primary source of water for prairie potholes. Annual precipitation can vary significantly from year to year, with periods of severe drought alternating with periods of above-normal precipitation. Because of the small size of their catchments, changes in annual precipitation can result in major changes in these potholes' annual water levels. Almost all prairie potholes also have some connection to groundwater (Winter 1989). They can be groundwater recharge sites, groundwater discharge sites, or groundwater flow-through wetlands. Because of these groundwater connections, prairie potholes are interlinked wetland complexes. In addition, during wet years when the catchments fill, water may overflow on the surface from one basin to another. Such ephemeral surface-water connections may provide opportunity for seed dispersal or movement of aquatic animals among prairie potholes. Herbaceous marshes containing robust perennial plants along with submersed species characterize prairie potholes throughout most of their range. Often, stands of emergent vegetation dominated primarily by one species such as cattail (*Typha* spp.) will have high primary productivity (van der Valk and Davis 1978b). Periodic drawing down and refilling of these shallow basins results in changes in vegetation types and species that can be predicted from a knowledge of the seed bank, the potential dispersal of plant propagules, and the conditions under which different species will germinate and become established (van der Valk 1981). The vegetation cycle results in four distinct stages:

a dry marsh stage, a regenerating marsh stage, a degenerating marsh stage, and a lake stage (van der Valk and Davis 1978b). During droughts when the substrate is exposed, perennial emergent species (e.g., cattails *Typha* spp., perennial sedges *Scirpus* spp., bur-reed *Sparganium eurycarpum*) and annual mud flat species (e.g., smartweed *Polygonum* spp., annual sedges *Cyperus* spp., beggarticks *Bidens cernua*) become established from the seed bank or from propagules dispersed into the basins. This dry marsh stage is followed by a wet marsh community when rainfall returns to normal and basins refill. The annual species that required exposed substrate for germination disappear, leaving the perennial emergents. Submersed species that can germinate under water (e.g., pondweed *Potamogeton* spp., water nymph *Najas ?exilis,* water milfoil *Myriophyllum sibiricum*) also appear. Wet marsh may persist for several years, but eventually the emergent vegetation begins to decline, perhaps because of the failure of some emergent species to continue to reproduce vegetatively (van der Valk and Davis 1978a), or destruction by muskrats. This degenerating marsh may become a pond or shallow lake marsh in which the dominant vegetation is comprised primarily of free-floating and submersed plants. When drought once again exposes the marsh bottom, the cycle repeats (see Chapter 6 for animal responses to this cycle).

Prairie potholes are especially important ecologically and economically because they are the major waterfowl breeding area in North America. An estimated 50% to 80% of North America's game waterfowl species are produced in this region (Batt et al. 1989). Successful breeding requires availability of a variety of wetlands and wetland plants (for food and habitat) because no single wetland basin provides for all their reproductive needs throughout the breeding season (Swanson and Duebbert 1989). The existence of large numbers of small wetlands allows the birds to disperse across the landscape, thereby lowering their vulnerability to predation and diseases and increasing the likelihood of successful reproduction and brood rearing (Kantrud et al. 1989).

About half the original prairie potholes in the Dakotas have been destroyed, mostly by agriculture, and more than 99% of Iowa's original marshes have been lost (Tiner 1984, 2003). Drainage of potholes significantly reduces their water-storage capacity, and destruction of natural vegetation buffers around remaining wetlands has significantly reduced valuable waterfowl nesting and rearing areas (Tiner 2003). Like all depressional wetlands, prairie pothole protection through federal regulations has been weakened as a result of recent Supreme Court decisions (see Chapter 8).

PLAYA AND RAINWATER BASIN/SANDHILLS WETLANDS

Playas are shallow recharge wetlands found in semiarid prairie areas of the southern Great Plains (Smith et al. 2012). They range in area from less than 1 hectare to greater than 250 hectares and average 6.3 hectares (Guthery and Bryant 1982). There are probably more than 30,000 of these small circular depressions, which are thought to result from a combination of dissolution of subsurface materials and wind action (Haukos and Smith 2003). Playas receive most of their water from rainfall and local runoff (including irrigation water), and it is rare for them to be connected to groundwater sources (Haukos and Smith 1994). These wetlands are usually dry in late winter, early spring, and late summer; multiple wet-dry cycles during a single growing season are common.

Playas are considered to be keystone ecosystems serving as biological refugia and critical sites of biodiversity in this semiarid and intensive agricultural region (Smith and Haukos 2002). More than 340 plant species have been recorded in playas (Haukos and Smith 1997), although most of these species are also commonly found in other wetland and terrestrial habitats. Because of their rapidly changing environmental conditions, the flora is dominated by annuals and short-lived perennials. In a survey of 224 playa wetlands, Smith and Haukos (2002) found that only 38% of plant species present in the early growing season were still present late in the season. Thus, the vegetation is influenced by the composition of the seed bank and the environmental conditions that regulate germination and seedling growth. Because the land surrounding most playas is cultivated, annual and exotic plant species are common invaders (Smith and Haukos 2002). Playas also support a broad array of bird species and are vital overwintering, migration, and breeding habitats for waterfowl in the region (Haukos and Smith 2003), and are recognized as important for invertebrates and amphibians as well.

All flora and fauna occupying playas must be adapted to the fluctuating environmental conditions, and any alteration of the hydroperiod may have drastic effects on species persistence. Unfortunately, many playas have been affected by sedimentation as a result of cultivation and erosion of the surrounding landscape. This has caused a dramatic decrease in playa hydroperiod and altered floral and faunal communities (Haukos and Smith 1994).

In Nebraska, aeolian forces from winds have created depressional wetlands in the Rainwater Basin in the south-central part of the state and in the Sandhills region of the northern and central areas. The Rainwater Basin wetlands depend on precipitation and overland runoff for their water supply (Frankforter 1996), and most are marshes, wet meadows, or ponds (Tiner 2003). Lakes and marshes in the Sandhills region are interconnected with the regional groundwater (LaBaugh 1986b; Winter 1986). Both Rainwater Basin and Sandhills wetlands have been identified as wetlands of international importance to waterfowl and other wildlife. Millions of waterfowl in the Central Flyway use these wetlands during spring migration (Gersib 1991); an abundance of aquatic invertebrates and fish provide a food source for these migratory birds. Agricultural activities, such as drainage and groundwater pumping, have been major causes of loss or degradation of these wetlands. At least 66% of the original area of Rainwater Basin wetlands has been lost (LaGrange 2001), as have more than 30% of the original Sandhills wetlands (Erickson and Leslie 1987).

VERNAL/SEASONAL POOLS

Vernal pools, broadly defined as ephemeral depressional wetlands that flood during the spring months of the year but that dry during the summer, are distributed throughout the world (Zedler 2003). These wetlands are largely collectors of rainfall and snowmelt water, although groundwater inputs may occur in some. Depending on climate, geology, hydrology, and other factors, vernal pools may be dominated by trees and shrubs, by marsh and wet meadow species, or by aquatic plants, or they may be devoid of vegetation (Tiner 2003). In the United States, "true" vernal pools are particularly abundant on the Pacific Coast. In the glaciated landscapes of the North and Northeast, seasonal woodland pools are very abundant and are often called "vernal" pools, but in fact they can be flooded in seasons other than spring, depending on precipitation patterns for a given year (Calhoun et al. 2012). Both types—west coast vernal pools and eastern woodland vernal pools—have received considerable attention because of their importance as habitats for rare plants and amphibians.

West coast vernal pools fill from winter rains characteristic of the region's Mediterranean climate, and then dry to extreme desiccating soil conditions during the dry summers (Zedler 2003). The isolated nature and unpredictable flooding of these wetlands promote endemism, thereby creating unique flora and fauna and making these vernal pools vital sites for the conservation of biodiversity (Tiner 2003). The flora of vernal pools in California contains numerous federally listed threatened and endangered species as well as state-listed endangered and rare species. In the past, west coast vernal pools were used for grazing and other forms of agriculture. More recently, population growth and corresponding urbanization in California have greatly reduced the extent of these ecosystems, and the largest remaining complexes are found in the open lands of military facilities.

Seasonal woodland pools occur throughout forested regions of the eastern United States and southeastern Canada (Calhoun et al. 2012). These habitats are typically inundated during the spring and early summer and then dry out in late summer or autumn (but, as mentioned, can be flooded longer in wet years). The flora may consist primarily of the surrounding forest trees and shrub species as well as various grasses and shrubs, depending in part on hydroperiod and canopy openness; vegetation characteristics are highly variable (Palik et al. 2001). Because predatory fish are not present, these seasonal wetlands can be extremely productive sites for macroinvertebrate and amphibian reproduction, and several salamander species are entirely dependent on seasonal woodland pools for breeding (Gibbs 1993; Semlitsch and Bodie 1998; Kenney and Burne 2000). While the seasonal pool breeders require such habitats for reproduction and growth of larvae, adult salamanders and frogs spend their lives in the surrounding woodland. Thus the protection of seasonal pools and the surrounding forest is important for the conservation of biodiversity (Semlitsch and Bodie 1998; Kenney and Burne 2000; Calhoun et al. 2012). Unfortunately, since these pools are usually very small, they are often destroyed by development activities.

THE EVERGLADES

The Everglades (Fig. 1.8) is perhaps one of the most well recognized wetlands in the world, its notoriety derived from the wealth of its biotic heritage as well as the magnitude of factors that threaten its resources (Gunderson and Loftus 1993; Gaiser et al. 2012). Occurring in the subtropical southern part of the Florida peninsula, the Everglades historically covered a vast area of about 1.2 million hectares; about half has now been drained for agriculture and development (Davis et al. 1994). The bedrock substrate underlying most of the Everglades is limestone, of marine and freshwater origin. The soil substrate is predominantly peat, formed during the last 5,000 years (Gleason and Stone 1994) and often interspersed with light-colored calcitic soils called marl. It is the largest and most important freshwater subtropical peatland in North America (Koch and Reddy 1992; Gaiser et al. 2012).

Precipitation is the main route by which water enters the Everglades ecosystem (Duever et al. 1994). Thus waters of the historic Everglades were probably very low in dissolved nitrogen and phosphorus (oligotrophic), but relatively high in calcium and bicarbonate (Flora and Rosendahl 1982). Approximately 60% of the rain falls between June and September, produced primarily by localized thunderstorms and, at times, tropical cyclones. The hydroperiod is quite variable, with water levels declining slowly during the winter and droughts common during the dry spring months when evapotranspiration is high. Lake Okeechobee, to the north, is linked hydrologically with the Everglades by groundwater connections and, during high water periods, by overland flow. The topography of this region is very flat, and water moves southward through the Everglades marshes at velocities ranging from approximately 0 to 1 cm/sec (Rosendahl and Rose 1982). This slow southerly flow of water inspired Marjorie Stoneman Douglas (1947) to call the Everglades a "River of Grass."Major freshwater wetland plant communities include marshes and wet prairies, forested communities (tree islands), and ponds and sloughs with little emergent vegetation (Gunderson 1994) (Fig. 1.8). These communities are arrayed in a mosaic influenced by hydrologic and substrate conditions. Sawgrass *(Cladium jamaicense [C. mariscus ssp. jamaicense])* is the most common and widespread species in the Everglades marshes. A robust, rhizomatous, perennial sedge rather than a grass, as

FIGURE 1.8. Everglades freshwater marsh and tree island complex in southern Florida. Courtesy of South Florida Water Management District.

its name implies, sawgrass is well adapted to the low nutrient conditions as well as to flooding and also burning during droughts. Throughout much of the Everglades, sawgrass marshes are interspersed with shallow sloughs that contain spikerush (*Eleocharis* spp.) and floating-leaved aquatic plants such as water lily, yellow pond-lily *(Nuphar lutea),* and submerged aquatics including bladderworts. The submerged portions of most aquatic macrophytes in the Everglades are covered with periphyton (a community of many species of microalgae, including calcareous species), which serves as a food web base, as well as oxygenating the water column and building calcite mud sediment (Browder et al. 1994; Gaiser et al. 2005a, 2005b, 2012).

Wet prairies of graminoid species develop on peat or marl (limestone) substrates, and each soil type has distinct plant communities. Those on peat commonly are dominated by species of spikerush, beakrush, or maidencane *(Panicum hemitomon)*. Prairies on marl substrates are dominated by sawgrass and muhly grass (*Muhlenbergia* spp.). Tree islands are clumps of bayhead/swamp forest taller than the surrounding marsh. Canopy species include redbay *(Persea borbonia)* and sweetbay as well as dahoon holly *(Ilex cassine)* and pond apple *(Annona glabra),* with a dense layer of shrubs underneath. Found throughout many parts of the Everglades marshes, these tree islands are often in the shape of an elongated teardrop with the long axis parallel to the main direction of flow (Gaiser et al. 2012).

Major parts of the Everglades wetlands now have been drained for agriculture and urbanization, and the water flows in the remaining areas are fragmented by canals, large water conservation areas, and roads and drainage ditches and pipes. Today, only 0.62 million hectares of the original Everglades remain (Davis et al. 1994). Increased phosphorus loading from agricultural runoff in the northern parts of the remaining Everglades may be promoting an increase in southern cattail *(Typha domingensis)* and declines in sawgrass and periphyton, which prosper in nutrient-poor waters (Newman et al. 1996; Noe et al. 2001; Childers et al. 2003; Gaiser et al. 2005a). Many exotic invasive plant species also threaten the plant communities of the Everglades. Among the most aggressive and difficult to control are melaleuca *(Melaleuca quinquenervia),* a pioneering Australian tree species; Brazilian peppertree *(Schinus terebinthifolius);* old world climbing fern *(Lygodium microphyllum),* which overtops and smothers Everglades tree islands; and torpedo grass *(Panicum repens),* which has replaced large areas of marsh plants in Lake Okeechobee (White 1994). Beginning in the late 1990s, a major restoration of the Everglades was initiated by the USACE and the state of Florida to try to restore some of the hydrologic integrity of the Everglades (Comprehensive Everglades Restoration Plan 2000; Gaiser et al. 2012).

Wetlands with Predominately Groundwater Inputs

SPRING-FED WETLANDS

Groundwater can emerge to the surface in isolated locations called *springs*. On flat areas or at the base of slopes, small wetlands can develop around these points of discharge (Fig. 1.9). Most water discharge is cold, but if the Earth's magma is in close proximity to the groundwater aquifer, hot springs (>50°C) can develop. While spring-fed wetlands occur in many different landscapes, they are particularly important ecologically in arid and semi-arid areas, such as the Great Basin of the western United States and Canada (Keleher and Sada 2012); they are one of the few wetland habitats occurring in such areas, and the lack of other water sources in these areas make these spring-fed wetlands true "oases" for many animals from the surrounding landscape. Spring-fed wetlands are also common in karstic (limestone) landscapes such as Florida.

The near-constant supply of water for spring-fed wetlands and the thermal and chemical characteristics of

FIGURE 1.9. A cold spring-fed wetland in Utah. Courtesy of M. J. Keleher.

the water make the flora and fauna of spring-fed wetlands unique. In hot springs, unique species of bacteria, algae, plants, and animals tolerant of high temperatures occur. In cold springs, the water becomes flushed with oxygen after it emerges and the water consistently flows, and thus numerous fishes can inhabit these wetlands (Keleher and Sada 2012), and invertebrates more typically occurring in cool streams (e.g., Plecoptera stoneflies) and not in traditional wetlands may thrive (Batzer and Ruhí 2013). The emerging water contains high levels of dissolved minerals, such as calcium and phosphorus, and thus spring-fed wetlands may support a diversity of emergent (e.g., *Ranunculus*) and submersed plants (e.g., *Potamogeton*), as well as copious growth of filamentous algae (e.g., *Chara*) (Fig. 1.8) characteristic of nutrient-rich waters. Because of ample calcium, various snails, which need calcium for shell development, can reach very high densities in spring-fed wetlands. Spring-fed wetlands are typically geographically isolated from other types of wetland and from each other, and thus the flora and fauna of the habitats show a high degree of endemism (i.e., species that only occur in a restricted area). Because endemic species are so prevalent, an inordinate number of threatened or endangered species occur in spring-fed wetlands. For example, several species of fish and snails in the Great Basin are associated with a small number (sometimes only one) of spring-fed wetlands (Keleher and Sada 2012). In Florida, endangered manatees *(Trichechus manatus)* often migrate to spring-fed wetlands in winter as a thermal refuge (Laist et al. 2013). Because of their reliance on groundwater, one of the biggest human threats to spring-fed wetlands is excessive groundwater extraction that could decrease or even eliminate natural discharge into these wetlands.

FENS AND RELATED PEATLANDS

Peatlands are wetland ecosystems that accumulate carbon because primary plant productivity exceeds decomposition and dead organic material builds up as peat. Most of the global peatland area is found in boreal and subarctic zones of the Northern Hemisphere (Gorham 1990; Rochefort et al. 2012), although peatlands also exist in southern locations (pocosins, southern Appalachian fens). The terminology applied to peatlands is often confusing. Throughout the world, they have been known by many different names, such as bog, fen, moor, mire, marsh, swamp, and heath (Bedford and Godwin 2003).

Peatlands are generally classified into ombrogenous (rain fed) and geogenous (receiving water from the regional water table or other outside sources). Ombrogenous peatlands vegetated largely with *Sphagnum* mosses and geogenous peatlands vegetated mostly with graminoid species (such as grasses, sedges, and rushes) are commonly called *bogs* and *fens,* respectively. Geogenous fens may be further divided into (1) limnogeneous peatlands, which develop along lakes and slow-flowing streams; (2) topogeneous peatlands, which develop in topographic depressions, with a portion of their water derived from the regional ground water table; and (3) soligeneous peatlands, which are affected by water from outside sources percolating through or over surface peat (Bridgham et al. 1996). There is strong overlap among all these peatland categories in environmental conditions, such as soil or water pH, and in plant species. Thus, Bridgham et al. (1996) recommend that the term *peatland* be used for all these systems to reduce confusion. They suggested that the terms *bog* and *fen* be used only in a broad sense, with bogs referring to acidic low alkalinity peatlands

FIGURE 1.10. Fen peatland in Canada. Courtesy of K. E. Francl.

that are typically dominated by *Sphagnum* mosses, various species of ericaceous shrubs, and/or conifers such as spruces or pines. Similarly, fens should refer broadly to somewhat less acidic, more alkaline peatlands dominated by graminoid species, brown mosses, taller shrubs, and coniferous and/or deciduous trees.

The defining characteristic of all types of fens is the importance of groundwater inputs in determining their hydrology, chemistry, and vegetation (Bedford and Godwin 2003). Thus, fens occur where climate and the hydrologic and geologic setting sustains flows of mineral-rich groundwater to the plant rooting zone. They may develop on slopes, in depressions, or on flats. The relatively constant supply of groundwater maintains saturated conditions most of the time, and the water chemistry reflects the mineralogy of the surrounding and underlying substrates. Fens may be slightly acidic (poor fens), circumneutral (rich fens), or strongly alkaline (extremely rich fens). In an extensive survey of North American fens, Bedford and Godwin (2003) reported pH ranging from 3.5 to 8.4.

Peatland development is a dynamic process (e.g., Heinselman 1970; Kuhry 1994; Wheeler and Proctor 2000; Yu et al. 2001, 2003; Bauer et al. 2003; Rochefort et al. 2012) that is controlled by multiple biotic and abiotic factors. Climate, physiography, and peat accumulation all play a role. Terrestrialization (filling in of shallow lakes) and paludification (encroachment of bogs over formerly dry land) are the major processes in peatland development.

The vegetation of fens (Fig. 1.10) is generally dominated by bryophytes, sedges, grasses, dicotyledonous herbs, and coniferous trees. Vegetation of poor fens resembles that of bogs, with *Sphagnum* mosses and ericaceous shrubs. Rich fens, however, are dominated by sedges and brown mosses (mostly of the Amblestegiaceae family), with many distinctive species of dicotyledonous herbs (Bedford and Godwin 2003). Tussock cottongrass, sedges (genera of the Cyperaceae, especially *Carex*) and shrubs such as heather, leatherleaf, Laborador tea, and cranberry and blueberry may occur. In forested peatlands, trees such as spruce and tamarack may be found, often in stunted condition. Individually and collectively, fens are among the most floristically diverse of all wetland types, supporting rare and uncommon bryophytes and vascular plant species (Bedford and Godwin 2003).

In a description of the Lake Agassiz peatlands of northern Minnesota, Heinselman (1970) described seven vegetation associations: (1) a rich swamp forest dominated by northern red cedar *(Thuja occidentalis)* with a shrub layer of alder *(Alnus incana)* and hummocks of *Sphagnum*, (2) a poor swamp forest dominated by tamarack with an understory of bog birch *(Betula pumila)* and *Sphagnum* hummocks, (3) a cedar string bog-and-fen complex with ridges of northern red cedar and treeless hollows of sedges (mostly *Carex* spp.) between them, (4) a larch string bog-and-fen complex in which tamarack dominated the ridges, (5) a black spruce *(Picea marina)* forest with a carpet of feathermoss *(Pleurozium)* and other mosses, (6) a *Sphagnum*-black spruce-leatherleaf bog forest of stunted black spruce and a heavy evergreen shrub layer over *Sphagnum* mosses, and (7) a *Sphagnum*-leatherleaf-laurel-spruce heath in which a low shrub layer including laurel (*Kalmia* spp.) and stunted spruce grow over a continuous blanket of *Sphagnum* mosses.

Peatlands are important wetland ecosystems for several reasons, including their vast extent across northern boreal regions. They are one of the largest “terrestrial” carbon reservoirs. Northern peatlands have accumulated about 400 to 500 Gt (1 Gt = 10^{15} g) of carbon during the Holocene (Gorham 1991; Clymo et al. 1998; Roulet 2000; Vitt et al. 2000; see Chapter 7). Their extent, high-latitude location, and the large size of their carbon pool raise concerns that they may become significant sources for atmospheric carbon under a changing climate (Moore et al. 1998; Schindler 1998; see Chapter 10).

ATLANTIC WHITE CEDAR SWAMPS

These forests, dominated by *Chamaecyparis thyoides*, occur within a wide climatic range along the Atlantic and Gulf of Mexico coastline areas of the United States from Maine to Mississippi. Throughout their range, however, they are uncommon, having decreased historically in area and in biological diversity (Laderman 1989). They are most abundant in the southeastern New Jersey Pine Barrens, in the Dismal Swamp of Virginia and North Carolina, and along several river systems in northwest Florida (Sheffield et al. 1998).

Atlantic white cedar swamps may occur in isolated basins, along lake shorelines, shoreward of coastal tidal marshes, on river floodplains, or on slopes (Laderman 1989). Hydrologic conditions can vary considerably among these forests, although flooding typically occurs in late winter and early spring, sometimes for extended periods. White cedar swamps occurring in basins, with precipitation as the major source of water, are usually oligotrophic. Those in other locations, however, may receive significant groundwater and are more nutrient rich (Laderman 1989). Most occur on peat soils of relatively low pH (2.5–6.7) (Day 1984; Whigham and Richardson 1988; Laderman 1989; Ehrenfeld and Schneider 1991). Under these conditions, *C. thyoides* may grow in dense, almost monospecific stands. Other canopy species commonly associated with Atlantic white cedar are red maple, black gum, and sweetbay, and pines such as loblolly *(Pinus taeda),* white *(P. strobus),* or pitch *(P. rigida).*

Relatively open conditions are necessary for the healthy growth of *Chamaecyparis* seedlings (Laderman 1989), and several studies have indicated poor seedling recruitment under the closed canopy in dense stands (Motzkin et al. 1993; Stoltzfus and Good 1998). This suggests that natural biotic processes in which *Chamaecyparis* seedlings are replaced by more shade-tolerant species such as red maple may play a role in the decline of these forests. From age structure analyses and paleo-ecological investigations of an old-growth Atlantic white cedar swamp, Motzkin et al. (1993) determined that extensive *Chamaecyparis* establishment occurred during distinct episodes following disturbance events. Prior to European settlement, fires frequently destroyed existing Atlantic white cedar stands but allowed for subsequent regeneration from seed stored in the upper soil horizon or from surviving trees. Thus abiotic factors associated with disturbances have also been important in influencing the development of Atlantic white cedar swamps (Motzkin et al. 1993).

Much of the historic decrease in *C. thyoides* stands is attributable to selective logging for their valuable lumber, however, and to conversion to agricultural, industrial, or commercial uses (Motzkin et al. 1993). Up to 50% of the Atlantic white cedar area of North Carolina was cut between 1870 and 1890, for example (Frost 1987). Herbivory of seedlings and saplings by deer often has an impact on stand regeneration, and deer browse can destroy young stands (Laderman 1989). Swamps that have frequent, low-level disturbances such as suburban runoff and the presence of roads generally have few *Chamaecyparis* seedlings and lack soil conditions conducive to their growth (Ehrenfeld and Schneider 1991). It is likely, however, that adjacent land uses are more important than regional land-use patterns in affecting the runoff of sediments and contaminants into these swamps (Laidig and Zampella 1999).

Wetlands with Predominately Surface Water Inputs

SOUTHERN DEEPWATER SWAMPS

Deepwater swamps, primarily baldcypress-water tupelo *(Taxodium distichum–Nyssa aquatica)* forests (Fig. 1.11), are freshwater ecosystems that have standing water for most or all of the year (Penfound 1952). They are generally found along rivers and streams of the Atlantic Coastal Plain from Delaware to Florida, along the Gulf Coastal Plain to southeastern Texas, and up the Mississippi River to southern Illinois (Conner and Buford 1998). Other southern deepwater swamps include cypress domes (see the Cypress Domes section). On river floodplains, these baldcypress-water tupelo swamps are found in meander scrolls created as the rivers change course (ridge and swale topography), oxbow lakes created as meanders become separated from the main river channel, and sloughs that are areas of ponded water in meanders and backwater swamps (Brinson et al. 1981).

The major hydrologic inputs to these deepwater swamps are overflow from flooding rivers and runoff from surrounding uplands. In addition, larger and deeper topographic features may impound water from rainfall and may be connected with the regional groundwater. Even though deepwater swamps are usually flooded, water levels may vary seasonally and annually. High water levels typically coincide with winter-spring rains and melting snow runoff. Low levels occur in the summer from high evapotranspiration and low rainfall (Wharton and Brinson 1979). During extreme droughts, even deepwater swamp forests may lack surface water for extended periods (Mancil 1969). Some peat development is characteristic of these deepwater ecosystems because of slow decomposition rates (Conner and Buford 1998). Since many deepwater swamps are found along the floodplains of rivers, their soils generally have adequate nutrients, and these forests are relatively productive. However, anaerobic conditions associated with continuous flooding may limit the availability of several nutrients to plants and reduce their productivity (Wharton et al. 1982; Megonigal et al. 1997). Southern deepwater swamps have unique plant communities that either depend on or adapt to the almost continuously wet conditions (Fig. 1.11).

FIGURE 1.11. Southern deepwater swamp with baldcypress *(Taxodium distichum)* trees in Congaree National Park, South Carolina.

Dominant canopy species include baldcypress, water tupelo, and swamp tupelo. These species grow together or in pure stands. Other species that may occur include red maple, black willow *(Salix nigra),* swamp cottonwood *(Populus heterophylla),* and green and pumpkin ash (*Fraxinus pennsylvanica* and *F. profunda*) in the overstory and buttonbush *(Cephalanthus occidentalis),* water elm *(Planera aquatica),* Carolina ash *(Fraxinus caroliniana),* and Virginia sweetspire *(Itea virginica)* in the understory (Sharitz and Mitsch 1993).

The great majority of cypress-tupelo swamps were logged during the late 1800s and early 1900s, and there has been a general decline in area of this forest type since then (Dahl et al. 1991). In coastal areas, especially in Louisiana and Mississippi, eustatic sea level rise and land subsidence, coupled with coastal levee construction, are causing a significant increase in water levels in deepwater cypress swamps (Gosselink 1984). Most of this coastal area is experiencing an apparent water level rise of about 1 meter per century (Salinas et al. 1986). This inhibits the natural regeneration of baldcypress and limits opportunities for planting and long-term maintenance of coastal deepwater swamps. In addition, saltwater intrusion into these coastal wetland forests reduces their productivity and may cause mortality (Pezeshki et al. 1990; Conner 1994; Allen et al. 1996).

RIVERINE FLOODPLAIN WETLANDS

Floodplain wetlands are riparian ecosystems in which the soil moisture is influenced by the adjacent river or stream (King et al. 2012; Stromberg et al. 2012). These wetlands may be narrow and relatively steep along small headwater streams in mountainous or hilly regions, or broad and nearly flat as along the floodplains of large rivers on coastal plains. Floodplain wetlands connect the river or stream to the adjacent upland. They receive water from over-bank flooding of the river or stream as well groundwater in some instances, as well as surface runoff and groundwater flows from the upland side. Local precipitation also contributes but is usually less important as a water or nutrient source. Typically, floodplain wetlands are long corridors that are functionally connected through the movement of water and materials such as nutrients and organic matter between upstream and downstream sites and between the adjacent upland and aquatic ecosystems (Vannote et al. 1980; Brinson et al. 1981; Junk et al. 1989). Since they receive nutrient-rich waters, floodplain wetlands are often very productive (see Chapter 5).

The greatest expanses of floodplain wetlands in the United States are in the South Central, Southeast, and North Central regions; along large river systems such as the Mississippi and its tributaries, the Atchafalaya (a major distributary of the Mississippi), and other rivers that drain into the Gulf of Mexico; and major rivers of the southern Atlantic Coastal Plain such as the Roanoke, Savannah, and Altamaha (King et al. 2012). Climatic conditions and regional topography influence the stream and floodplain characteristics in different regions of the country. In the eastern United States, for example, precipitation exceeds evapotranspiration, and streams and rivers flow continuously and are seasonally pulsed. In upstream reaches, gradients of slope may be steep to moderate and floodplains relatively narrow, but in the downstream reaches, slope gradients are flat and the floodplains are broad (Putnam et al. 1960; Wharton et al. 1982; Cronk and Fennessy 2001). In the Northwest, evapotranspiration is equal to or slightly higher than precipitation; streams in this region are often somewhat flashy, with temporally unpredictable peak flows. Stream gradients are steep upstream and more moderate downstream, and floodplain widths range from very narrow to relatively wide (Vannote et al. 1980). In the South-west, however, the climate is arid, and evapotranspiration greatly exceeds precipitation. Streams in this environment tend to be very flashy, with temporally unpredictable floods and low mean flows. Along a single southwestern river, conditions may shift from wet to mesic to xeric, and floodplains are often dry downstream (Graf 1988).

Plant communities on floodplains are influenced by riverine processes such as timing, depth, and duration of overbank flooding as well as by regional climate conditions. Northeastern floodplain forests are usually hardwood. Species composition changes from east to west across the region and varies depending on specific site characteristics. Common dominant canopy species include maples such as red maple and silver maple *(Acer saccharinum),* along with American elm *(Ulmus americana),* American beech *(Fagus grandifolia),* green ash, sycamore *(Platanus occidentalis),* and box elder *(Acer negundo)*. Cottonwood *(Populus deltoides)* and willow (*Salix* spp.) are often found in low elevations (Lindsey et al. 1961; Dunn and Stearns 1987; Brinson 1990).

Southern US river floodplains support vast bottomland hardwood forests (Fig. 1.12) that contain a diverse mixture of hardwood and conifer species (Kellison et al. 1998; Conner and Sharitz 2005; King et al. 2012). The most important condition determining species composition on these broad floodplains is the moisture gradient, or the gradient in anaerobic conditions (Wharton et al. 1982), which varies in time and space across the floodplain. These bottomland forests are extremely heterogeneous with very high species richness (Conner and Sharitz 2005). The lowest parts of the floodplain, such as oxbows formed from previous river channels that are nearly always flooded, support baldcypress-water tupelo *(Taxodium distichum–Nyssa aquatica)* swamps (discussed in the Southern Deepwater Swamps section). At slightly higher elevations, the soils usually are semipermanently saturated or inundated. Species such as overcup oak *(Quercus lyrata)* and water hickory *(Carya aquatica)* occur in back swamp depressions, and willow, cottonwood, silver maple, and river birch *(Betula nigra)* are found on river levees. Only about half of the original southern bottomland forests remained by the 1930s (Fredrickson 2005). In recent years, there has been a modest attempt to reestablish hardwood forests on lands formerly used by agriculture (Allen and Kennedy 1989; King and Keeland 1999).

In the arid southwestern United States, riverine areas are often the only sites moist enough to provide suitable habitat for tree and shrub species (Stromberg et al. 2012). Typical trees of riparian zones are species of cottonwood, willow, and ash as well as the invasive Russian olive *(Elaeagnus angustifolia)* and saltcedar (*Tamarix ramisissima* and *T. chinensis*). In the more montane and mesic areas of the West and Northwest, alder (*Alnus* spp.), cottonwood, and aspen (*Populus* spp.) occur, as well as spruce (*Picea* spp.) at higher elevations (Brinson 1990).

Several important ecological concepts have arisen from studies of the relationships of streams or rivers and their floodplains. Two of these—the river continuum concept and the flood pulse concept—are of special significance. The *river continuum concept* (Vannote et al. 1980) is focused mostly on the processing of organic material and productivity within the stream or river itself. It suggests that most organic matter introduced into streams from terrestrial sources (e.g., leaf litter) is in headwater regions where the stream is narrow, and biodiversity is limited by low light and low temperatures. Invertebrate collectors and shredders in the stream reduce the organic matter in size as it travels downstream. In river midreaches, more light is available, phytoplankton thrive, and primary productivity in the stream increases. Invertebrate filter feeders process the fine organic matter from upstream, and coarse woody debris inputs from the floodplain increase food diversity and the variety of habitats. Downstream, as the river size increases, litter inputs from the floodplain are minor and turbidity reduces primary productivity. Thus there is a continuum of inputs of organic materials from the floodplain and of in-stream productivity and the processing of organic materials as well as a continuum of in-stream plankton communities and invertebrate consumers.

FIGURE 1.12. Bottomland hardwood forest with large cherrybark oak *(Quercus pagoda)* and sweetgum *(Liquidambar styraciflua)* trees on a river floodplain in Congaree National Park, South Carolina.

The river continuum concept addresses mostly in-stream processes and does not adequately take into account the importance of floodplains to river systems, and vice versa. The *?ood pulse concept* (Junk et al. 1989) alternatively proposes that the pulsing of the river discharge is the major force controlling the biota in the river floodplain, and that the river-floodplain exchange during periods of floodplain inundation is of enormous importance in determining the productivity of both the river and the adjacent riparian zone. Flood pulses deliver water and nutrients to sites across the floodplain, creating suitable conditions for biotic processes such as seed dispersal and seedling establishment (Schneider and Sharitz 1988; Jones and Sharitz 1998) and the occurrence of benthic invertebrates (Reese and Batzer 2006) and fish spawning (Lambou 1990). Furthermore, the floodplain provides nutrients, organic matter, and food to stream organisms as flood waters move back into the river (Knight and Bottorff 1984). The flood pulse concept may better describe the ecological situation in many of the vast southern floodplain forests, but both concepts provide valuable insights into the relationships between floodplains and their adjacent water bodies.

FRESHWATER SHORELINE WETLANDS

Lakeshore, or lacustrine, marshes are located along the edges of small and large lakes. Most of the world's lakes are small, with a high ratio of lacustrine marsh area to open water (Wetzel and Hough 1973). In the United States, many of the small isolated wetlands—such as prairie potholes, Carolina bays, and playas—act essentially as very small lakes and contain marshes dominated by herbaceous graminoids (grasses, sedges, rushes), other emergent wetland herbs, and floating leaved and submersed aquatics when periods of inundation are long enough to support these species (see earlier sections on these wetlands). Many of these small wetland marshes receive much of their water from precipitation and are relatively nutrient poor.

Along larger lakes with seiches (wind-driven "tides"), such as the Great Lakes of the United States and Canada, wetlands occur in coastal lagoons behind natural barrier beaches or levees thrown up by wave action on the shore, or in the deltas of tributary rivers (Herdendorf 1987; Wilcox 2012). Since shorelines have been stabilized along the Great Lakes, many of the remaining marshes are now managed and protected by artificial dikes (Herdendorf 1987; Wilcox and Whillans 1999). These wetlands receive much of their water as surface flows from the lakes themselves, in addition to surface runoff and groundwater from adjacent upland areas. As a consequence, they tend to be much more nutrient rich than most marshes in small lakes.

Plant species composition in lakeshore marshes varies greatly, but common species include graminoids such as reeds *(Phragmites australis)*, cattails, wild rice *(Zizania aquatica),* bur-reed, maidencane *(Panicum hemitomun),* sedges (species of *Carex* and *Scirpus*), and spike rush (*Eleocharis* spp.). Other typical herbaceous species are pickerelweed *(Pontederia cordata),* arrowhead (*Sagittaria* spp.), and smartweed (*Polygonum* spp.), and floating-leaved or submersed species such as water lilies (*Nymphaea* spp.), water shield *(Brasenia schreberi),* water milfoil (*Myriophyllum* spp.), and pondweed (*Potamogeton* spp.) (Wilcox 2012). In these wetlands, plant communities typically show a zonation pattern according to depth, from wet meadows to more flooded marshes to aquatic beds (Glooschenko et al. 1993).

SALT MARSHES

Salt marshes occur along coastlines where wave action is moderate enough to allow the accumulation of sediments and growth of macrophytes (Chapman 1960). In the United States, salt marshes dominate the Atlantic (Baldwin et al. 2012; Pennings et al. 2012; Wigand and Roman 2012) and Gulf (Battaglia et al. 2012) coasts, but are rarer on the Pacific Coast (Callaway et al. 2012) because of its steeply sloping shores and heavy wave action. Worldwide, salt marshes occur at almost all latitudes but are largely replaced by mangroves (see the Mangroves section below) in the tropics. Coastal salt marshes receive most of their water input from the ocean, with some contribution from precipitation and groundwater. The hydroperiod varies according to the nature of the local tidal regime, ranging from large-amplitude tides driven primarily by the moon (e.g., the Atlantic Coast) to small-amplitude tides driven primarily by local weather conditions (e.g., the Gulf Coast). Soils vary from highly mineral to highly organic, depending on sediment input and decomposition rates, and the development of soil is promoted by the marsh vegetation, which traps sediment and produces organic matter belowground (Fagherazzi et al. 2012). Salt marsh plant communities worldwide are dominated by a relatively small suite of plant species. Most common are plants from the genera *Spartina* and *Distichlis* (Poaceae), *Juncus* (Juncaceae), *Arthrocnemum*, *Atriplex*, *Salicornia*, *Sarcocornia* and *Suaeda* (Chenopodiaceae), and *Limonium* (Plumbaginaceae). At any one geographic location total plant diversity is low, typically 10 to 20 species, with the dominant plants often arranged in striking zonation patterns parallel to the shoreline (Fig. 1.13).

Salt marsh plants must cope with the dual physical stresses of flooding and salinity (see Chapter 3). Flooding stress increases with decreasing elevation, but decreases again at creek banks because of increased pore water exchange with tidal water. Salinity stress may be greatest at low marsh elevations or may rise to a peak in middle marsh elevations if evapotranspiration concentrates salts in the pore water (Pennings and Bertness 1999). In low-latitude salt marshes, unvegetated "salt pans" are a common feature of the high marsh landscape in areas where pore water salinities exceed levels that plants can tolerate. Within vegetated areas, plants respond to variation across the marsh in flooding and salinity with marked intraspecific variation in

FIGURE 1.13. Salt marsh along a tidal creek with saltmarsh cordgrass *(Spartina alterniflora)* at a creek's edge on Sapelo Island, Georgia. Courtesy of S.C. Pennings.

height, morphology, and palatability to herbivores (Valiela et al. 1978; Seliskar 1985a, 1985b; Goranson et al. 2004; Richards et al. 2005).

Salt marsh plants are commonly arrayed in distinct zones parallel to the shoreline. In New England, competitively superior plant species occupy the higher marsh zones, which are less stressful, and displace poor competitors to lower marsh elevations (Bertness and Ellison 1987; Bertness 1991a, 1991b; Bertness et al. 1992b; Bertness and Hacker 1994; Wigand and Roman 2012). The mechanisms producing zonation patterns in low-latitude salt marshes are more complex. In hotter South Atlantic climates, high evapotranspiration commonly leads to hypersaline conditions at intermediate marsh elevations (Pennings and Bertness 1999; Pennings et al. 2012). Consequently, low marsh zones may be occupied by species tolerant of flooding, intermediate marsh zones by species tolerant of high salinities, and the high marsh by competitive dominants (Pennings and Callaway 1992; Pennings et al. 2005).

Salt marshes are highly productive systems, and there is a long history of ecosystems research in salt marshes that dates back to seminal work by Teal (1962). Most of the primary production enters the detrital food web (Cebrian 1999). The detrital food web has been best studied in the southeastern United States (Newell 1993, 1996, 2003; Silliman and Newell 2003). There, senescing leaves of cordgrass, *Spartina alterni?ora,* undergo initial decay attached to plant stems. Senescent leaves are heavily colonized by fungi, and fungal/leaf complexes are grazed by shredding invertebrates, especially snails and amphipods. Leaf fragments and invertebrate feces fall to the marsh surface, where further decomposition is primarily mediated by bacteria. The resultant detrital fragments comprise part of the diet of a wide variety of other marsh invertebrates (Pennings and Bertness 2001). During periods of sea level rise, salt marshes, tidal freshwater marshes, and mangroves can continually sequester buried carbon in accreting soils, and thus represent an important sink for "blue carbon" (Mcleod et al. 2011).

Depending on their geographic location, salt marshes are subject to a variety of natural disturbances. Ice can severely erode high-latitude marshes (Redfield 1972; Hardwick-Witman 1985). All salt marshes are subject to disturbance by floating mats of dead plant material (wrack), but this is particularly common at higher latitudes where all of the above-ground production dies back each winter (Hartman et al. 1983; Bertness and Ellison 1987; Pennings and Richards 1998). Other sources of disturbance in salt marshes include fire (Turner 1987; Taylor et al. 1994; Baldwin and Mendelssohn 1998b; Bortolus and Iribarne 1999), sedimentation (Rejmanek et al. 1988; Allison 1996), and herbivory (Lynch et al. 1947; Smith and Odum 1981; Jefferies 1988; Silliman and Bertness 2002).

Salt marshes shelter coasts from erosion, filter nutrients and sediments from the water, and provide nursery and feeding grounds for many crustaceans and fishes. The hydrology of many salt marshes has been altered by ditches, culverts, and dikes. Many salt marshes have been filled to allow coastal development. Finally, salt marshes are easily affected by eutrophication and pollution from coastal and up-river sources.

TIDAL FRESHWATER MARSHES

Tidal freshwater marshes occur along rivers upstream of salt marshes, in areas where water column salinities average less

FIGURE 1.14. Mangrove wetland with red mangrove *(Rhizophora mangle)* trees in southern Florida.

than 0.5 parts per thousand (Barendregt et al. 2009). Moving downstream, one encounters oligohaline (0.5–5 ppt), mesohaline (5–18 ppt), and finally salt (18–35 ppt) marshes. This sequence of habitat types occurs along an increasing gradient of sulfur and total dissolved salts whose concentrations are several orders of magnitude higher in the ocean than in river water. For brevity, and because oligohaline and mesohaline marshes have not been extensively studied, we will focus on tidal freshwater marshes. Because tides propagate upstream farther than salt water does, tidal freshwater marshes experience a hydroperiod similar to that of salt marshes downstream but are flooded by river water rather than ocean water. Soils are more organic than those in downstream salt marshes. The plant community is dominated by a different suite of species, including species from the genera *Scirpus* (Cyperaceae), *Typha* (Typhaceae), and *Phragmites* and *Zizaniopsis* (Poaceae).

Although plant zonation patterns are weak within tidal freshwater marshes, they are strong at the scale of the estuary, with a predictable turnover in species composition from tidal freshwater to salt marshes (Wilson et al. 1996). These large-scale zonation patterns are caused by a trade-off between competitive ability and stress tolerance similar to the trade-off that creates zonation patterns within salt marshes (Crain et al. 2004; Guo and Pennings 2012). In general, competitively superior plants dominate the freshwater end of the estuarine gradient, but they cannot survive in salt marshes. Plants that occur in salt marshes can tolerate the stressful conditions found there but are competitively excluded from the freshwater end of the salinity gradient.

Historically, many tidal freshwater marshes along the southeastern coast of the United States were diked for rice cultivation. Although these agricultural efforts have now been abandoned, the systems often remain in a degraded state, with the abandoned dikes altering the hydrologic regime. Some diked areas are actively managed with an altered hydrologic regime intended to benefit waterfowl.

Tidal freshwater marshes have received much less scientific attention than salt marshes. However, the early review by W. E. Odum (1988) and the new book by Barendregt et al. (2009) provide valuable information on these habitats.

MANGROVES

Mangrove forests (Fig. 1.14), also known as *mangal*, are the tropical equivalent of salt marshes. They occur in the same locations—coastal areas with soft sediments and moderate wave action—but in geographic regions that lack hard freezes (Chapman 1976; McKee 2012). With rising global temperatures, mangroves are beginning to expand to higher latitudes, displacing low-latitude salt marshes (Osland et al. 2013). Like salt marshes, mangroves receive most of their water input from the ocean, with the hydroperiod driven by the local tidal regime; they thus face the twin stresses of flooding and salinity. Mangrove forests differ from salt marshes in that, by definition, they are dominated by woody plants—trees and shrubs—rather than by grasses, rushes, and forbs. They are similar in that species diversity is low—there are at most 70 species worldwide, from about 19 families (Tomlinson 1986; Duke 1992). Species richness is high in the Indo-West Pacific and low in the eastern Pacific, Caribbean, and Atlantic (Ellison et al. 1999). Like salt marsh plants, mangrove trees show striking variation in size and morphology across physical gradients, probably as a response to nutrient availability and physical stress (Lugo and Snedaker 1974; Feller 1995). Mangrove plants also display patterns of zonation across tidal elevation, but considerable overlap of zones often occurs, and few studies have experimentally addressed the causes of zonation (Chapman 1976; Smith 1992; Ellison and Farnsworth 2001).

Mangroves are subject to both small- and large-scale natural disturbances (Lugo and Snedaker 1974; Smith et al. 1994; Imbert et al. 1996; Swiadek 1997; Ellison and Farnsworth 2001). Tree falls and lightning strikes create small gaps in the forest canopy. The wind and storm surge that accompany cyclonic storms can kill many trees over large areas. We do not have a general understanding of the process of secondary succession in mangrove forests. Because full recovery of disturbed forests may take decades, however, mangrove forests in areas subject to regular cyclonic storms may always be in early or intermediate stages of secondary succession rather than at equilibrium, “climax” stages.

Like salt marshes, mangrove forests grade into freshwater tidal systems upstream in estuaries. Although the geographical distribution of mangroves is limited by their intolerance to cold (MacMillan 1975), trees occur at higher latitudes in tidal freshwater than in tidal marine wetlands, suggesting that, in the absence of salt stress, trees are better able to deal with cold temperatures (Odum 1988).

Mangrove forests provide many ecosystem services (Ellison and Farnsworth 2001), such as sheltering coasts from erosion and severe storms, filtering nutrients and sediments, and providing nursery and feeding grounds for crustaceans and fishes (McKee 2012). These services have received increasing attention in recent decades, as many mangrove forests have been lost to population growth, forestry, and aquaculture.

Wetland Loss and Degradation

Wetland habitats are dynamic features on the landscape and are constantly being created, altered, and destroyed. Wetlands tend to occur on geologically “young” landscapes (e.g., formerly glaciated areas or coastal plains; see Chapter 2), and over the eons they may disappear from natural erosional or successional processes (see Chapter 5). Natural wetland loss can also occur over shorter time frames. For example, coastal wetlands of the Mississippi River Delta are subject to annual and decadal subsidence from tectonic faulting (Visser et al. 2012). Greatly exacerbated by the loss of compensatory sedimentation from the river because of anthropogenic activities (dams, levees), large areas of wetland in the Mississippi River Delta are disappearing annually because of subsidence. Shifts in beaver activity also cause natural wetland creation and loss over fairly short time periods (Johnston 2012; see Chapter 6). However, compared with natural processes, loss and degradation from human activity is by far the greater impact on our wetland resources.

Patterns and processes of wetland loss from human impacts are probably best understood in the United States. By the 1970s, it was estimated that almost half of the wetlands in the lower 48 states had been filled or drained (Tiner 1984). Productive farmland can be produced by draining wetlands, and hence agriculture was the primary historical threat to US wetlands. For example, Figure 1.15 shows the original extent of wetlands (shaded dark) in the state of Minnesota prior to European settlement (early 1800s) and their extent in the latter 1900s. Although considerable wetland acreage remains in the forested northeastern portions of Minnesota, most of the wetlands in the agricultural south and west were destroyed. A similar pattern of destruction developed throughout the United States (and elsewhere, see the following paragraphs).

More recent wetland loss in the United States is being monitored through a process called the National Wetlands Inventory (NWI) generated by the USFWS (details are available at wetlands.fws.gov; see also Chapter 8). The NWI maps all significant wetlands (mostly those greater than 1 hectare) across the United States, and then resurveys a subset of the land area every decade to determine whether wetlands have been lost or created. In the 1990s, urban and rural development eclipsed agriculture as the major threats to wetlands (Dahl 2000). By the 2000s (Dahl 2011), overall wetland loss in the United States had slowed to the point that no significant areal change was detected. However, certain types of wetlands were still declining; these included forested freshwater wetlands via conversion of forests to other habitats, and coastal salt marsh via losses to subsidence, storms, and sea level rise (Dahl 2011). The acreage of freshwater ponds, mostly farm ponds, has actually increased in recent decades (Dahl 2000, 2011), and wetland restoration and creation projects (see Chapter 9) have compensated for losses of salt marsh, forested wetlands, and other natural wetlands.

Canada shares a pattern of wetland loss similar to that of the United States. By virtue of extensive boreal peatlands (Rochefort et al. 2012), wetlands occupy 14% of Canada’s land surface (NWWG 1988). Although these peatlands are currently threatened by climate change (see Chapter 10), most historical wetland losses have been in southern Ontario and Quebec and the prairie regions where agricultural activities and urbanization have taken a toll (Environment Canada 2004). In the populated areas of southern Ontario and Quebec, past development has routinely resulted in wetland losses that exceed 80% (NWWG 1988). In the central prairie, it has been estimated that 2% to 4% of wetlands are being lost to drainage every decade (Watmough et al. 2002).

For China, some recent remote sensing studies have documented patterns of wetland loss. Wang et al. (2011) assessed loss and fragmentation of marshes from 1954 to 2005 in the Sanjiang Plain, where some of the most expansive wetland complexes in China occur. Over the 50-year period, 77% of the marshes were lost, primarily related to agricultural “reclamation” activities, mostly drainage. However, more recently (after 1986), losses slowed because of new policies that focused on marsh protection and restoration. Gong et al. (2010) assessed wetland change over the

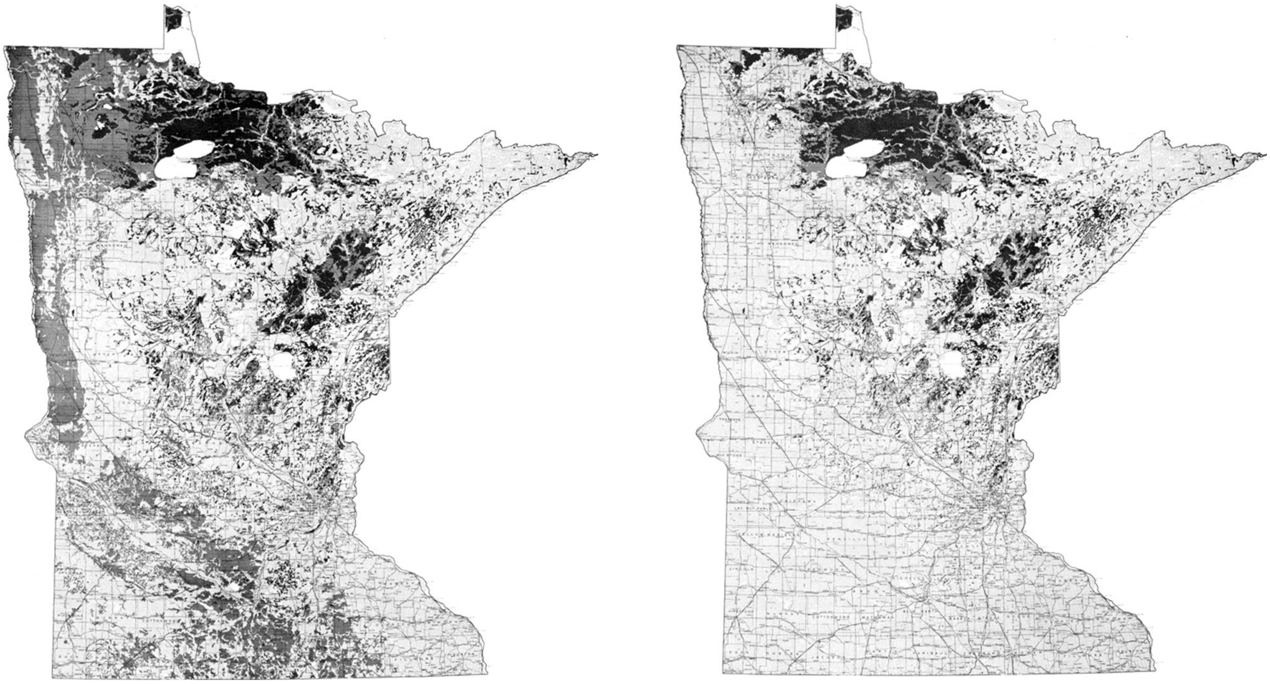

FIGURE 1.15. Wetland occurrence (dark-shaded areas) in the state of Minnesota prior to European settlement (left map) and in the 1970s (right map). From Tiner (1984).

whole of China from 1990 to 2000. Over that short time period, inland wetland area declined by 19% and coastal wetland area declined by 16%. Some new wetlands were created by climate warming melting glaciers and snow fields, and by the creation of artificial wetland around new reservoirs and in fish farms.

One does not need to be an ecologist to recognize the negative impacts of complete wetland loss. However, the more subtle threat of degradation and the loss of specific wetland functions are now being recognized. Brinson and Malvárez (2002) examined the status of freshwater wetlands in the temperate zones of North America, South America, northern Europe and the northern Mediterranean, Asia (Russia, Mongolia, China, Korea, and Japan), and southern Australia and New Zealand. Factors most responsible for wetland loss and degradation included the diversion and damming of river flows; the disconnection of floodplain wetlands from flood flows; eutrophication and other pollution; agriculture and grazing; global warming; invasions by exotic species; and the practices of filling, diking, and draining wetlands (see also Baldwin and Batzer 2012). In Europe, these impacts have been taking place for hundreds of years. In North America, most losses and degradation occurred from the 1950s through the 1970s. In portions of Asia, such as China, very recent expansion of drainage projects and building of impoundments threatens freshwater wetlands. The more industrial countries are more likely to make attempts to restore or conserve wetlands, while nations that are less industrialized may still be experiencing accelerated wetland loss and degradation (Brinson and Malvárez 2002).

Very recently, concerns have developed about the conversion of one wetland type to another. The latest surveys of wetlands in the United States (Dahl 2000, 2011) indicate that many forested wetlands are being converted into scrub/shrub habitats, often from silvicultural practices. While it may be heartening to know that the wetlands have not been eliminated and that scrub/shrub wetlands are themselves valuable, the functional change associated with such conversion needs to be assessed. Similarly, mangroves worldwide are expanding at their high-latitude range boundary and replacing salt marshes because of rising temperatures, with functional consequences that are poorly understood (Osland et al. 2013). In wetland restoration (see Chapter 9), we now recognize that not only does acreage need to be conserved or replaced but also important wetland functions. The common past practice of replacing lost wetlands, regardless of type, with small permanent ponds is being discouraged. Instead, mitigation plans that replace functions actually lost are now required.

What This Book Covers

Wetland ecology incorporates the interactions of biota (microbes, plants, animals) with the unique physical and chemical environment present in wetlands. Wetlands are foremost geologic features, and geomorphology coupled with climate forms the template on which wetland ecology occurs (Fig. 1.16). Hydrology is the factor most influenced by geomorphology and climate, and hydrology is also the primary conduit for the control of the physico-chemical environment and biotic interactions in wetlands. Virtually

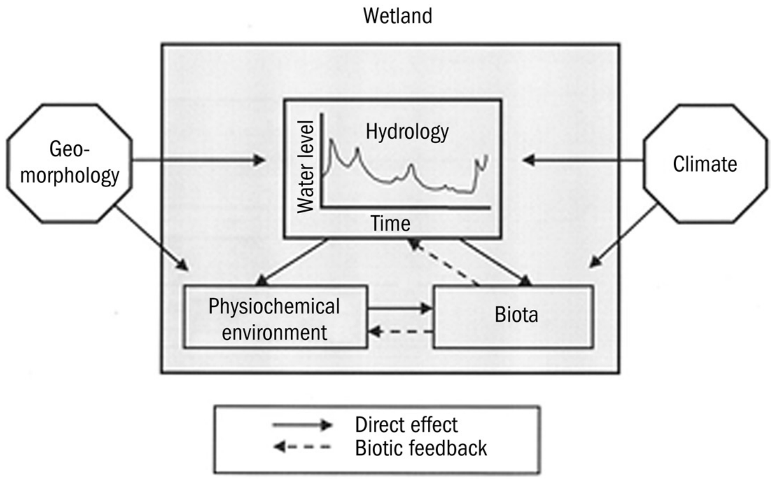

FIGURE 1.16. Schematic indicating the important factors influencing wetland biota. Modified from NRC (1995).

every chapter in this book deals with the impacts of hydrology to some extent, whether it is covering physical factors, biotic interactions, ecosystem ecology, regulation, or the applied ecology of wetlands.

Chapter 2 describes the physical template of wetlands, focusing on the geology, soils, and especially the hydrology of wetlands. Chapter 3 describes the unique adaptations of wetland plants and animals to wetland environments, particularly how they deal with fluctuating wet and dry conditions, low oxygen or acidic conditions, and the saline environments of estuarine wetlands. The middle three chapters deal with major biotic groups: microbes and algae (Chapter 4), higher plants (Chapter 5), and animals (Chapter 6). For all three of these chapters, the focus is on community and ecosystem ecology, and all three will draw on the general background on wetlands provided in Chapters 1, 2, and 3. Chapter 7 focuses on carbon flux in wetlands, and mostly expands on the microbial and plant themes developed in Chapters 4 and 5. Because of the importance of wetlands as sinks and sources of atmospheric carbon, Chapter 7 also provides a useful background for later discussions regarding climate change (Chapter 10). Chapter 8 describes the convoluted history of wetland regulation in the United States, including the most recent judicial decisions, and considers how wetland assessment is currently used in the regulatory process. Chapter 9 covers wetland restoration, focusing on the restoration of natural hydrology, plant communities, ecosystem processes, and functions of wetlands. As mentioned, Chapter 10 covers the influence of a changing global climate on wetland habitats, integrating themes of carbon flux from Chapter 7, and providing an extensive overview of the projected impacts of changing precipitation patterns on inland wetlands and sea level rise on coastal wetlands.

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