Chapter contents

2 Flooding

Water creates wetlands. The most important causal factor that we need to study is therefore water. The biological composition of the wetland, from its fish to its birds, from its plants to its insects, depends upon the way in which water moves through the wetland. Timing and rate of flow are critical. In most landscapes there tend to be drier periods interrupted by pulses of flooding after rainfall or when snow melts. The more we study wetlands, the more we find that these cycles of flooding, also called flood pulses, are critical to understanding wetlands. There is an entire scientific discipline of hydrology, that addresses the occurrence, distribution, and movement of water (Ward and Trimble 2004; Brutsaert 2005).

Here we shall focus on flooding. The amplitude and frequency of water level fluctuations are probably the most important factors affecting the composition and function of wetlands. Water levels change over many timescales – the annual cycle of flooding is the most obvious, but there is also change from one year to the next. Let us begin, then, by considering these two sources of variation, flooding within and among years.

Within years Pictures of flooding (Figure 2.1) are a vivid reminder that flow rates change with the time of year in rivers around the world (Figure 2.2). High water periods or **pulses** (Middleton 2002) are natural and entirely predictable events. In the temperate zone pulses are produced each spring by the rapid melting of the accumulated precipitation of an entire winter. In tropical and subtropical rivers pulses are usually caused by rainy seasons such as monsoons. The size of pulses is often remarkable – the Amazon River, which carries approximately one-fifth of the Earth's total freshwater runoff, can change level by more than 10 m within a single year!

Among years There are also pronounced differences in water levels from one year to the next in most wetlands. This is caused by factors such as changes in rainfall patterns or timing of spring thaws. In the Great Lakes, historical records show that the yearly mean has ranged across several meters over a century

FIGURE 2.1 Flooding is a natural process in landscapes. When humans build cities in or adjacent to wetlands, flooding can be expected. This example shows Cedar Rapids in the United States in 2008 (*The Gazette*), but incidences of flood damage to cities go far back in history to early cities such as Nineveh mentioned in *The Epic of Gilgamesh* (Sanders 1972). (See also color plate.)

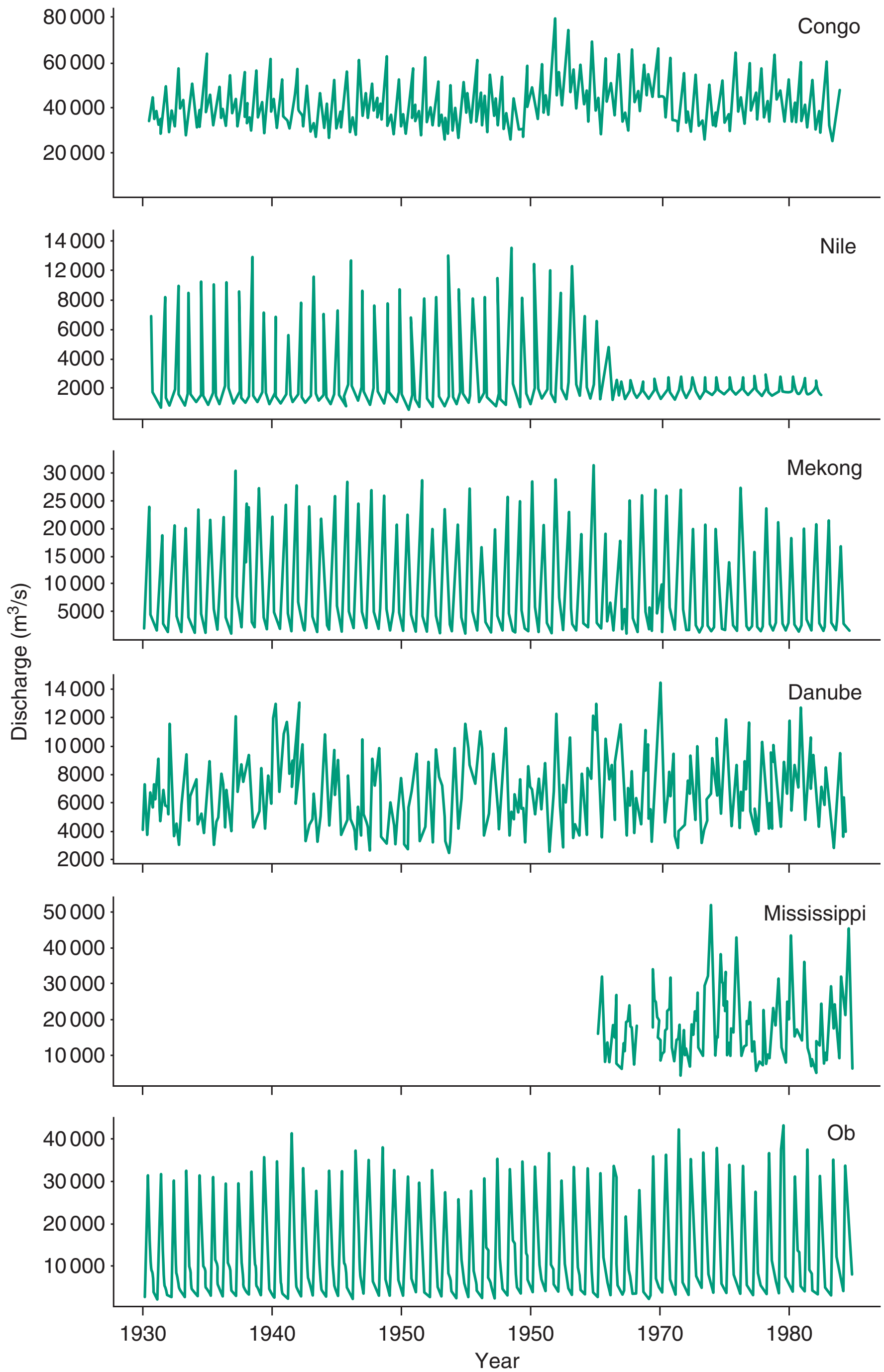

FIGURE 2.2 Annual high water periods, or flood pulses, create extensive areas of wetland along rivers. These rivers illustrate the variability of water level fluctuation patterns. The sampling stations are as follows: Congo (Kinshasa, Democratic Republic of the Congo), Nile (Aswan Dam, Egypt; note the effect of the dam on flood amplitude after 1965), Mekong (Mukdahan, Thailand), Danube (Ceatal Izmail, Romania), Mississippi (Vicksburg, U.S.A.), and Ob (Salekhard, Russia). (From Vörösmarty *et al.* 1996.)

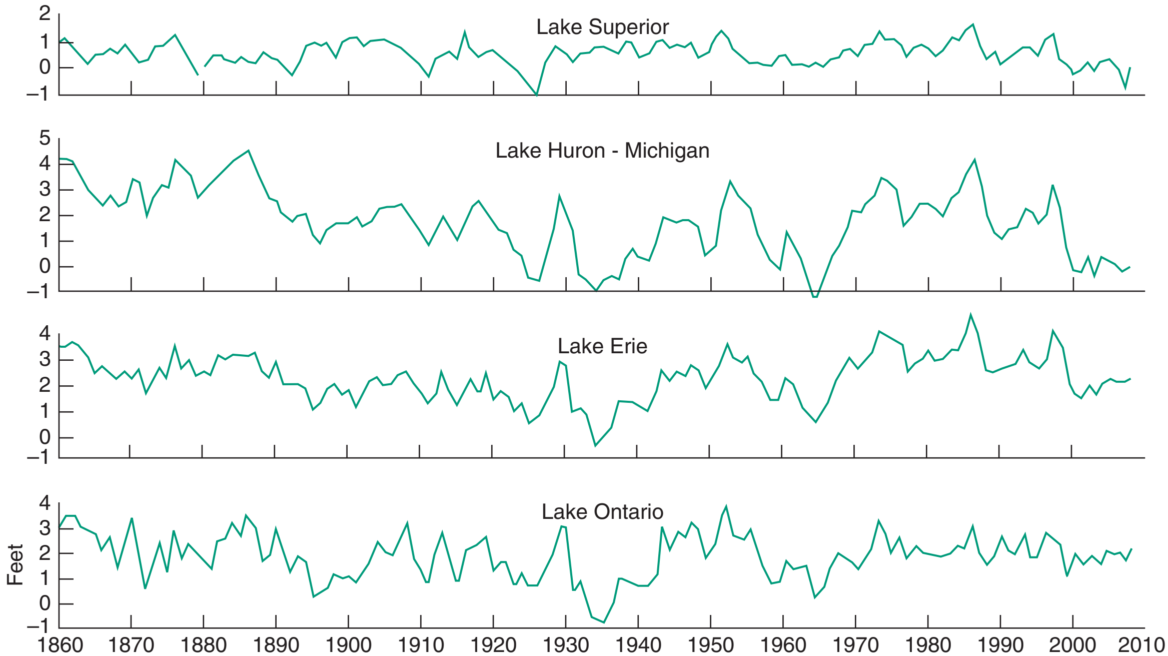

FIGURE 2.3 Water levels in the Great Lakes illustrate longer-term changes in water level. These changes too are part of natural processes that create wetlands. (From Environment Canada 1976 and Canadian Hydrographic Service 2009.)

(Figure 2.3). Cores that have been extracted from old sand deposits and dune systems in Lake Michigan track such water level changes back for more than 4000 years (Baedke and Thompson 2000; Johnston *et al.* 2007); peat deposits, shells, and pollen document early low-water stages in Lake Erie (Pengelly *et al.* 1997); old shorelines far inland document major changes in elevation and drainage since the departure of the ice sheets (Teller 2003). Such evidence, when compiled, shows that wetlands – and entire lakes – have come and gone over the past 10 000 years (Figure 2.4).

In this chapter we shall look at some effects of water level fluctuations across a broad array of wetland types, and a broad array of plants and animals. We will also consider how human activities change these natural patterns, and examine attempts to predict the consequences for wetlands. But first a little bit of history.

2.1 Flooding and humans: an old story

Floods have been a part of human experience ever since the first settlements were built on floodplains. Stories of floods go back at least to the book of Genesis, which recounts how it rained 40 days and nights, how Noah built an ark which floated on the floodwaters, how “the waters prevailed exceedingly upon the earth; and all the high hills, that were under the whole heaven were covered” (7:19).

Archeologists have found even earlier flood stories. In the 1830s, a young Englishman, Austen Henry Layard, spent some years excavating archeological sites in Mesopotamia (Sanders 1972).

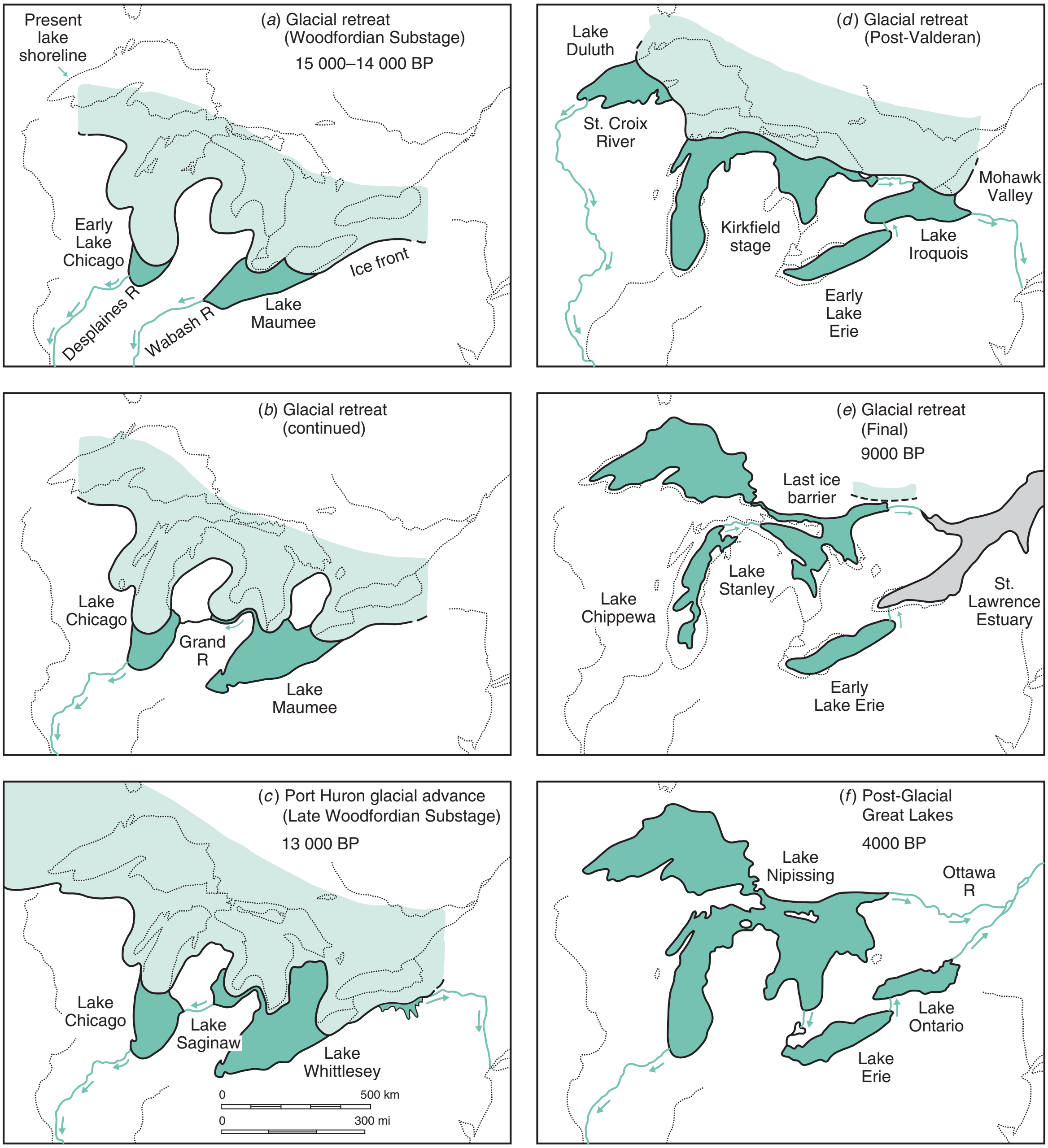

FIGURE 2.4 Water levels can change over even longer periods of time as the climate changes. Here are changes in the water levels of the Great Lakes over the past 20 000 years. (From Strahler 1971.)

One of the most significant discoveries was thousands of broken tablets from the palace of Nineveh. Nineveh, now in modern Iraq, was then an Assyrian city that fell in 612 BC to a combined army of Medes and Babylonians. The destruction was so complete that the city never rose again. Included in the ruins was the entire library of Assurbanipal "King of the World, King of Assyria." Over 25 000 broken tablets from this library were taken to the British Museum. When deciphered, they revealed a story now known as *The Epic of Gilgamesh*. One section of this epic narrates how there was a flood. "The rider of the storm sent down the rain . . . a black cloud came from the horizon; it thundered within where Adad, lord of the storm, was riding . . . For six days and nights the winds blew, torrent and tempest and flood overwhelmed the world . . ." (pp. 110–11). This epic also has a boat full of survivors who come to rest on a mountain and who release a dove to search for land.

In *The Epic of Gilgamesh*, as now, floods are depicted as tragedies. Says the epic, "Would that famine had wasted the world rather than the flood. Would that pestilence had wasted mankind rather than the flood." (p. 112). This attitude is similar to the accounts of flooding presented by reporters today. One of the objectives of this chapter is to tell the rest of the story and put floods in their proper ecological context.

2.2 Some biological consequences of flooding

Water level fluctuations affect wildlife by creating and maintaining different wetland habitat types. In addition, nearly all species of animals are sensitive to both the depth of water and the timing of floods. Let us look at a few examples.

2.2.1 Wading birds in the Everglades

The Everglades are famous for their great variety of wading birds including great egrets, white ibis (Figure 2.5*a*), wood storks, and roseate spoonbills. Annual low-water periods force small fish to concentrate in the remaining few wet areas, where they become prey for wading birds (Brosnan *et al.* 2007). Nesting is timed to coincide with these low-water periods. Wood storks, for example, are very dependent upon high concentrations of small fish for feeding their nestlings. Gradual and consistent declining water levels throughout the nesting period appear to be critical for such birds to raise their young.

2.2.2 Frogs in temporary ponds

Many species of frogs and salamanders breed in temporary ponds, also known as vernal pools. In the north, these ponds are filled by melting snow. Further south, they may be filled by winter rain. Adult frogs and salamanders often live in adjoining forest areas. As soon as standing water becomes available they must move to the ponds, mate, and lay eggs. The juveniles must then grow rapidly and reach maturity before the water dries up (Pechmann *et al.* 1989; Rowe and Dunson 1995). It is a race against time.

One example is the Mississippi gopher frog (Figure 2.5*b*). Adult gopher frogs spend most of their life in the longleaf pine forests, often living in burrows constructed by gopher tortoises or mammals or even crayfish. They breed in small isolated ponds. The timing and frequency of winter rain is critical; normally rain fills the ponds around December. The ponds dry out during the summer – in nearly half the years, the pond dries before young can emerge (Richter *et al.* 2001, 2003).

Other environmental factors also need to be considered in maintaining habitat for gopher frogs. The ponds must dry up completely, because this kills fish which would otherwise eat the tadpoles. During dry periods, the surrounding longleaf pine forests must burn to maintain habitat for adults. The timing of rain, drought, and fire are all

FIGURE 2.5 Many wetland organisms are dependent upon annual flood pulses. Animals discussed here include (*a*) white ibis (U.S. Fish and Wildlife Service), (*b*) Mississippi gopher frog (courtesy M. Redmer), (*c*) dragonfly (courtesy C. Rubec), and (*d*) tambaqui (courtesy M. Goulding). Plants discussed here include (*e*) furbish lousewort (bottom left; U.S. Fish and Wildlife Service) and (*f*) Plymouth gentian. (See also color plate.)

important. Real estate development, reduced water tables, roads, logging, fire suppression, and fish stocking have all taken their toll on this habitat. Although the Mississippi gopher frog once occurred along the gulf coastal plain from Louisiana to Alabama, there is now only a single population of about 100 individuals (Richter and Seigel 2002).

2.2.3 Birds in salt marshes and deltas

In deltaic marshes, even small pulses of fresh water can change salinity. The Camargue in southern France is one of Europe's largest deltas, and is bracketed by two branches of the Rhone River. The Rhone carries fresh water from the north southward to the Mediterranean Sea and into an area with hot dry summers and moisture deficits. The Camargue is well known for its population of flamingoes. Flamingoes (there are six species in the world) are filter feeders and depend upon populations of aquatic invertebrates such as fairy shrimp, which they separate from the mud with their distinctive bills. The greater flamingo (the species in the Camargue) feeds largely on macroinvertebrates; the composition and abundance of the macroinvertebrates is strongly affected by hydroperiod and salinity (Waterkeyn *et al.* 2008). Rice fields, canals, and other human alterations to hydrology can therefore have a significant effect upon food supplies; we will return to this topic later (Section 8.1.5).

Tidal cycles also affect water levels and salinity. Humans may manipulate both through the construction of ditches and impoundments. The costs and benefits of these structures are controversial. Certainly, they can have major effects on birds. Consider an example from salt marshes on the east coast of North America. One study compared three flooding regimes – typical salt marsh, impounded marsh, and areas that had been partially flooded by plugging drainage ditches (Burger *et al.* 1982). The impoundments had more than five times as many birds as the natural tidal marshes and had many red-winged blackbirds, gulls, terns, shorebirds, and waterfowl. Salt marsh species, such as clapper rails, seaside sparrows, and sharp-tailed sparrows, were, however, absent from impoundments (Figure 2.6). Thus changes in the water level regime not only changed the abundance of birds, they also caused dramatic shifts in composition.

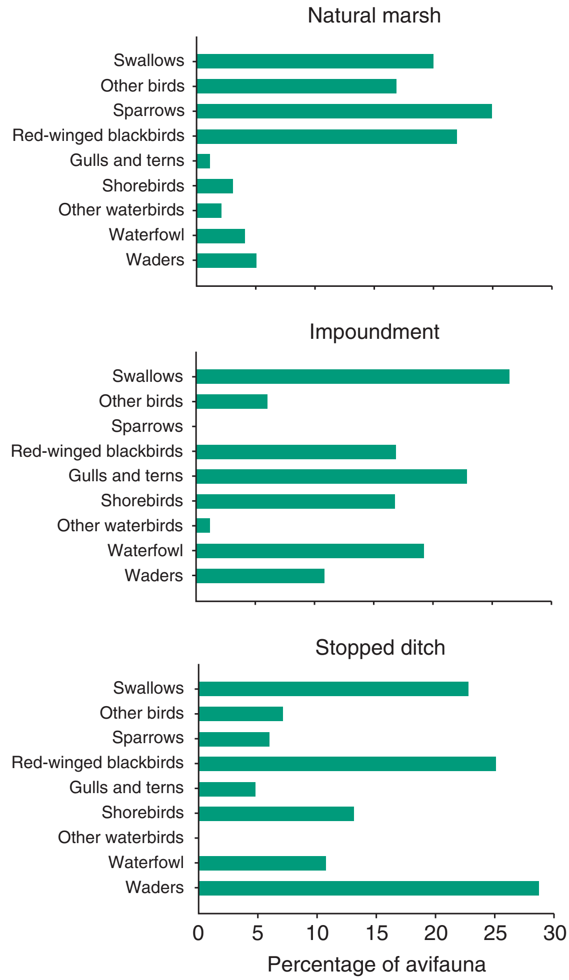

FIGURE 2.6 The composition of birds changes with salinity and flooding. Compare these three different kinds of coastal marsh: natural salt marsh, impounded marsh, and marsh with stopped ditches. (From data in Burger *et al.* 1982.)

2.2.4 Fish in floodplains

Fish (Figure 2.5*d*) behavior and life cycles are also closely tied to periods of inundation. In her monograph on tropical fish, Lowe-McConnell (1975) says "In both Africa and South America where much of the land is very flat peneplain, the rivers inundate immense areas, on a scale unknown in temperate regions. Submerged seasonally and drying out for part of each year, these floodplains are interspersed with creeks, pools and swamps, some of which retain water throughout the year." (p. 90) Although rains occur in the summer, flood peaks occur well after the rains have started; the delay depends upon the origin of the main floodwater and the time taken to travel downstream. As the rising water floods up channels and creeks, it releases fish imprisoned within ponds and swampy areas. Still higher levels then create a vast sheet of water. This water is enriched in nutrients from decaying organic matter, including the droppings of grazing animals, perhaps first baked by sun or fire. "This leads to an explosive growth of bacteria, algae and zooplankton, which in turn supports a rich fauna of aquatic insects and other invertebrates. The aquatic vegetation, both rooted and floating, grows very rapidly." (p. 92) Many fish then migrate upstream and move laterally onto the floodplain to spawn. The eggs hatch within a few days, so the young appear when food is plentiful. The high-water period allows feeding, growing, and fattening. Once water levels fall, the fish move back into the main river. Some fish are killed by being stranded in drying pools. Even ungulates such as peccaries (*Tayassu pecari*) have been observed visiting floodplains to feed upon fish trapped by falling water (Fragoso 1998). This same general sequence of events occurs in rivers throughout the tropics including Africa, South America, and Asia (Figure 2.7).

2.2.5 Macroinvertebrates

Vernal pools which are filled by rainfall or by melting snow, and which then progressively dry during the summer, also provide habitat for many insects. The insect fauna changes with the duration of standing water, often termed **hydroperiod**. Hydroperiod affects nearly all the species in the pond, including plants, amphibians, and fish. Insects (Figure 2.5*c*) often receive less attention. Insects process a large proportion of the biomass in wetlands (Chapter 1), they provide food for species ranging from minnows to flamingoes, and they can also be predators that feed upon amphibian larvae. It was with the latter interest that Tarr *et al.* (2005) used dip nets to sample the predatory macroinvertebrates that occupied vernal, intermediate, and permanent ponds – a gradient from short to long hydroperiod.

Short hydroperiod wetlands (those lasting less than 4 months after spring thaw and drying in May–July) were generally small (ca. 0.05 ha), were covered by a forest canopy, supported shrubs, and contained logs and leaf litter. The long hydroperiod wetlands were larger (ca. 2.5 ha) and had well-developed aquatic plant assemblages including *Sparganium* spp. and *Potamogeton* spp. A total of 6202 aquatic invertebrates representing 47 genera were collected, with a mean of more than 10 genera per wetland. The most widespread genus was predatory diving beetles (*Acilius* spp.) while the most abundant genus was backswimmers (*Notonecta* spp.). Overall, the diving beetles dominated the short hydroperiod wetlands, while backswimmers became more dominant with increased duration of flooding (Figure 2.8).

Invertebrates are generally more common in permanent ponds and marshes, with hundreds or thousands of individuals in a single square meter. These invertebrates provide food for many wetland species including fish, amphibians, and waterbirds. To illustrate their abundance and composition, Table 2.1 shows invertebrate communities in wetlands managed for migrating waterfowl. Note that most invertebrates occur on the bottom, with relatively few in the water column. Where abundance significantly differs with depth, more invertebrates occur in shallow rather than deep water.

2.2.6 Rare plants in wet meadows

Many rare plants also depend upon fluctuating water levels. The endangered furbish lousewort (*Pedicularis furbishiae*) (Figure 2.5*e*) occurs on the banks of the

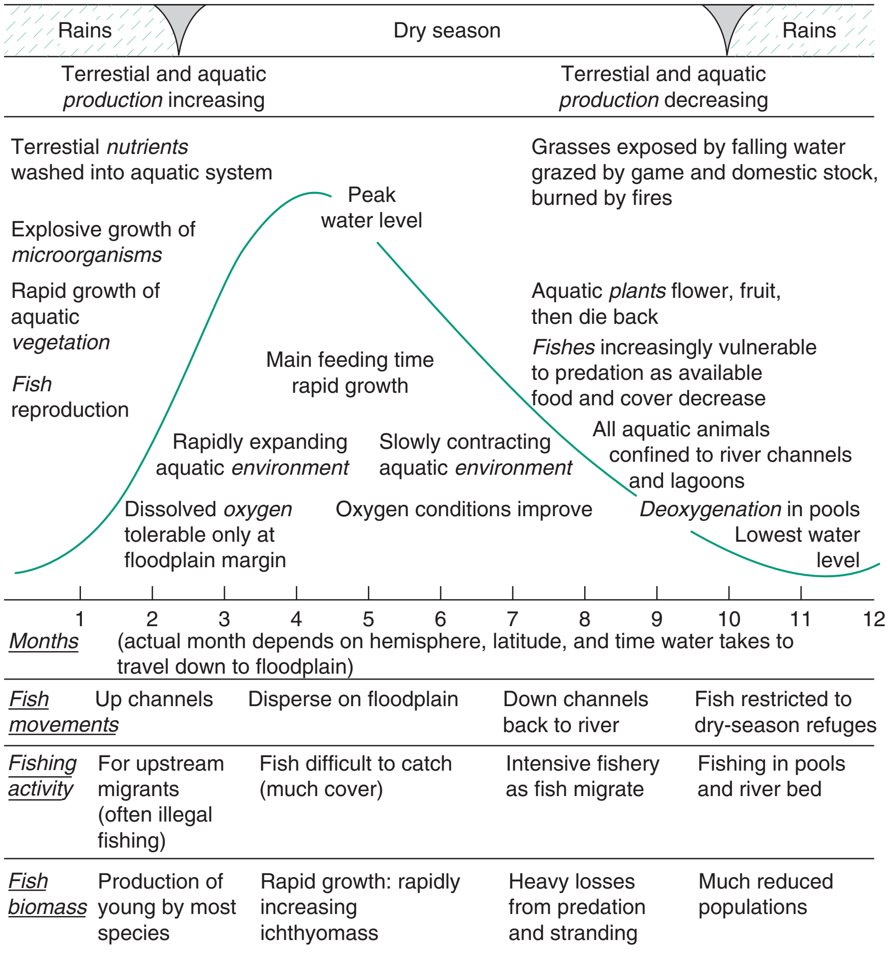

FIGURE 2.7 The life cycles of floodplain fish are closely tied to annual flooding. (From Lowe-McConnell 1975.)

St. John River that flows along the Canada–United States border. The lousewort establishes in areas that are disturbed by ice scour and slumping of the soil associated with spring flood pulses (Menges and Gawler 1986). These types of shorelines may support entire associations of rare plants. The Plymouth gentian (*Sabatia kennedyana*) (Figure 2.5*f*) grows in seasonally flooded wet meadows along the Tusket River in Nova Scotia. This is the only river north of Cape Cod with rich wet meadows supporting significant Atlantic coastal plain species (including both pink coreopsis and Plymouth gentian) that are considered rare, threatened, or endangered in Canada (Keddy and Wisheu 1989). Some of the flood periods result from melting snow in the spring, but others are caused by occasional severe storms. One thunderstorm in summer 1983 raised water levels 75 cm over two days, completely submerging the wet meadows. In drought years extensive areas of river and lake bottom are exposed. The number of plant species on shorelines is correlated with watershed area across 37 lakes (Hill and Keddy 1992). The mechanism appears to be this: the larger the watershed area, the larger the amplitude of water level fluctuations, the broader the wet meadows, and hence the more species of plants.

Table 2.1 Abundances of the most common macroinvertebrates in relation to water depth (shallow vs. deep) in freshwater marshes

		Density (number/m²)			
		Benthos samples		Water column samples	
Invertebrate taxa		Shallow	Deep	Shallow	Deep
Class Crustacea	Amphipoda	760	531	1	0
	Cladocera	3581	4775	172[a]	19
	Copepoda	1955	1520	–	–
	Eucopepoda	–	–	25[a]	3
Class Gastropoda	Basommatophora (Physidae)	1061	1061	<1	1
Class Insecta	Coleoptera (Dystiscidae)	1061	1061	1	<1
	Diptera (Chironomidae)	3682[a]	796	3[a]	1
	Hemiptera (Corixidae)	1061	1061	2[a]	1
Class Oligochaeta		3797	5128	2	2

[a] Means significantly different between depths.
Source: After Riley and Bookhout (1990).

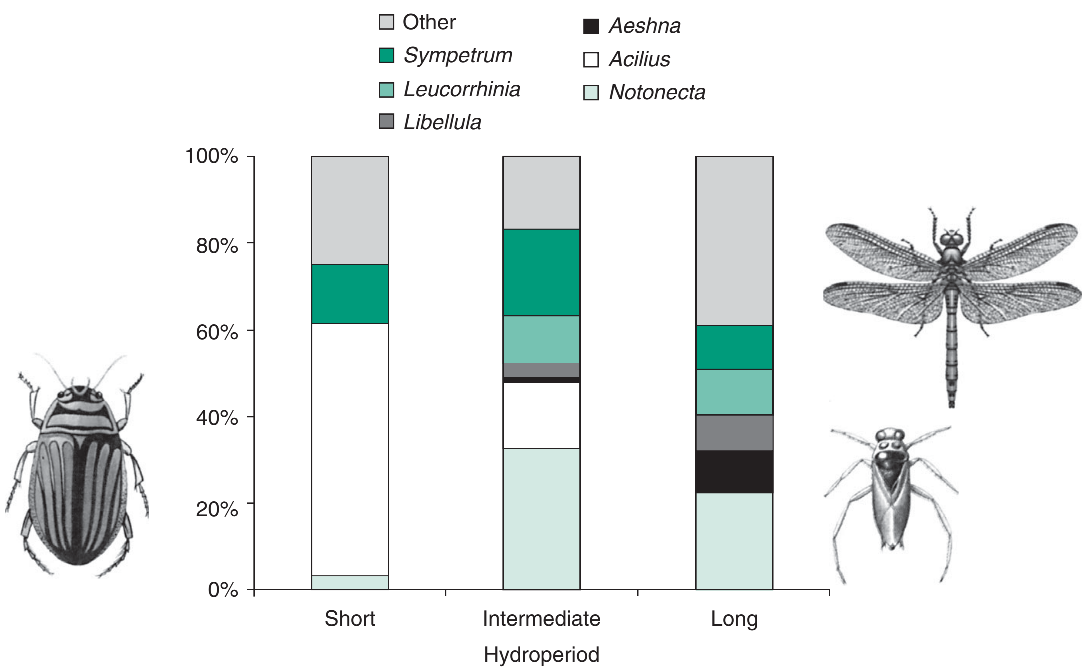

FIGURE 2.8 Predatory macroinvertebrates are affected by hydroperiod, from temporary ponds (left) to permanent ponds (right). *Acilius* (left) are diving beetles, *Notonecta* (bottom, right) are backswimmers, and the other genera are dragonflies (top, right). (After Tarr *et al.* 2005; images from Clegg 1986.)

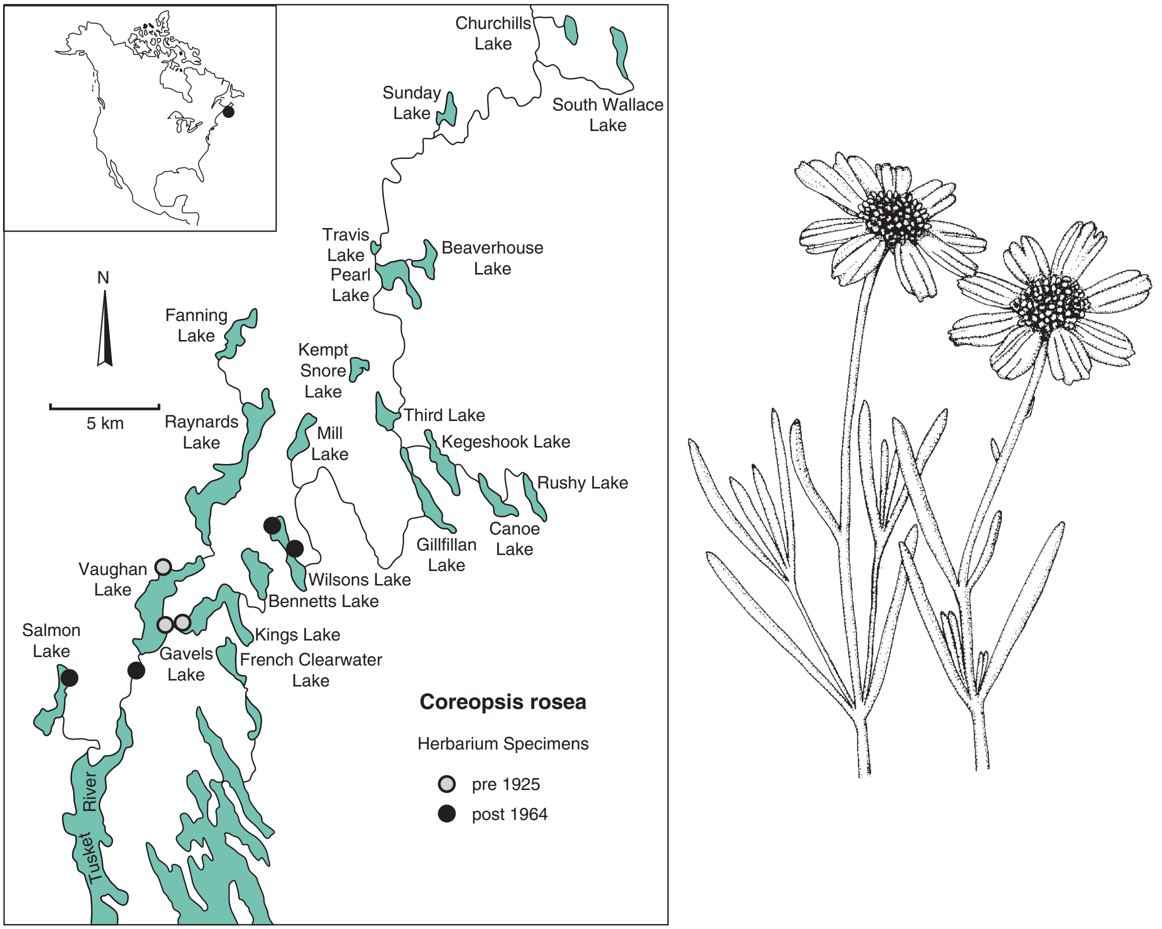

FIGURE 2.9 The endangered pink coreopsis (*Coreopsis rosea*) grows in seasonally flooded wet meadows along the Tusket River, Nova Scotia. The lightly shaded circles show sites from which the species disappeared after the construction of a hydroelectric generating station in 1925. (After Keddy 1985.)

Dams have a negative effect on such plants. Both pink coreopsis and Plymouth gentian once occurred more widely in the lower lakes of the Tusket River watershed (there are pre-1925 specimens from early botanical exploration), but they no longer occur there (Figure 2.9). All three of these lakes were converted to reservoirs for the Tusket Falls generating station in 1925. Pink coreopsis now survives only in those lakes where water level fluctuations are unaffected by reservoirs.

2.3 A survey of water level fluctuations

We have discussed some of the effects of water level fluctuations. Now we will take a closer look at these fluctuations in the different sources of water than can be associated with wetlands.

2.3.1 Rivers

Large fluctuations in water levels are certainly the rule. We have already encountered 10-m changes

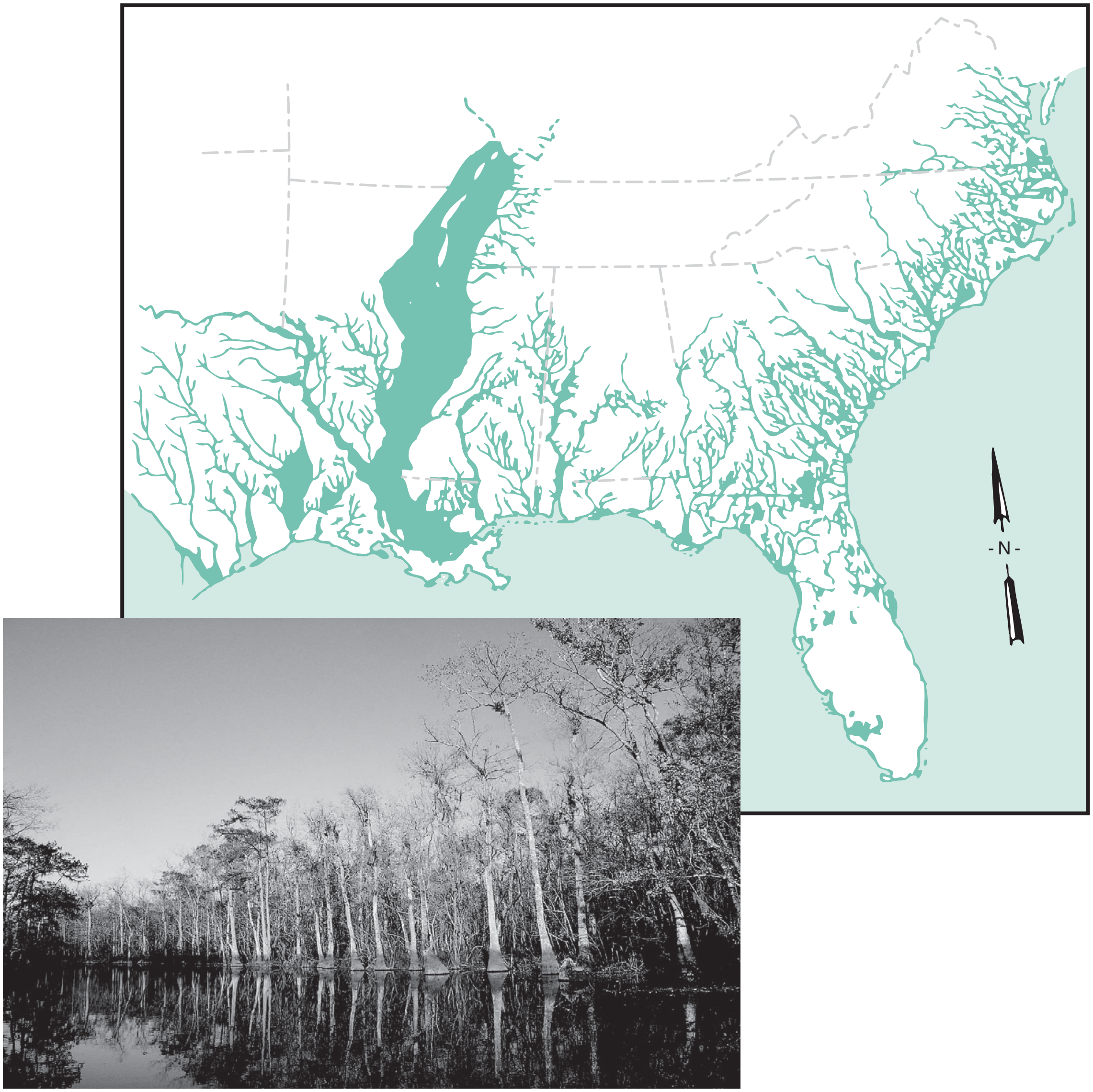

FIGURE 2.10 Spring floods produce the extensive bottomland forests that accompany many large rivers, such as those of the southeastern United States of America. (Map from Mitsch and Gosselink 1986.) (See also color plate.)

in the water levels in the Amazon, and seen the seasonal variation in flow of major rivers (Figure 2.2). These seasonal floods produce the extensive bottomland forests that occur along rivers in Europe (Palczynski 1984; Grubb 1987), central North America (Robertson *et al.* 1978), the Amazon River basin (Duncan 1993), and Africa (Denny 1985; Petr 1986).

Figure 2.10 illustrates the original extent of such floodplain forests in southeastern North America. Floodplain forests often intergrade with other wetland types. For example, in eastern Africa, the Upper Nile swamps at the headwaters of the Nile are enormous – some 16 000 km^2 of permanent swamp, 15 000 km^2 of seasonal swamp, and a further 70 000 km^2 of seasonal

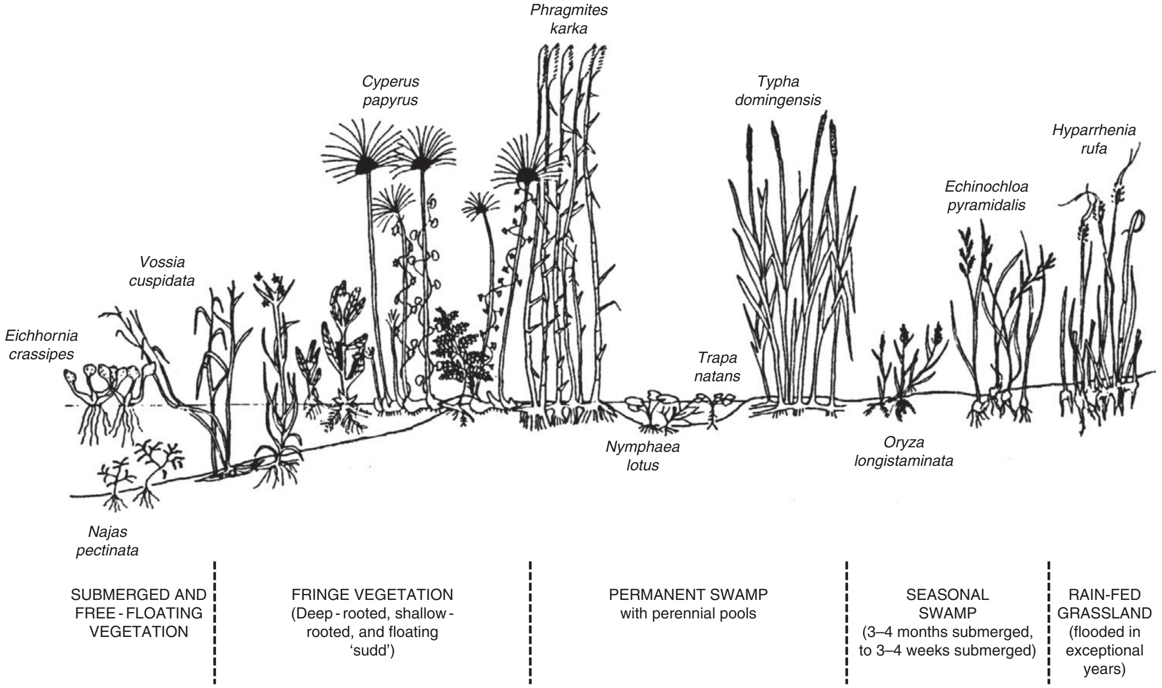

FIGURE 2.11 Flooding produces the characteristic vegetation types in the extensive Upper Nile swamps. (From Thompson 1985.)

floodplain (Denny 1993b). Seven different vegetation types arise (Figure 2.11). The wettest areas (left) have aquatic plants, while the driest (right) have seasonally flooded grasslands. Downstream, the river has cut a floodplain, where the moisture gradient goes from open water (left) to palm and acacia trees on the second terrace (Figure 2.12). Although the species names change, similar types of zonation occur in river systems throughout the world.

Dams and reservoirs are so widespread today that it is often difficult to imagine the enormous expanses of swamp forests and herbaceous wet meadows that once accompanied free-flowing rivers. One of the few free-flowing rivers remaining in Europe is the Torne River in Sweden, and it has wide expanses of herbaceous wetland between the forested floodplain and normal summer water levels (Figure 2.13). Vast wet meadows are also found along undammed rivers in northern North America (Figure 2.14).

These wet meadows along rivers (and, of course, other herbaceous vegetation types such as alvars, wet prairies, and marshes) occur because something removes the trees and keeps them from invading the shoreline. This factor is spring flooding, which in high-latitude rivers is accompanied by large ice floes.

Hence, the critical question for research or management appears to be this: what is the minimum amount of flooding needed to kill trees? This will set the lower limit of the forest and the upper limit of the wet meadow. The answer depends upon the particular tree species, but very few can tolerate permanent flooding (Kozlowski 1984b). Silver maple (*Acer saccharinum*) is one tree species that is widespread in floodplains of northeastern North America. In a study conducted in the Ottawa River on the flood tolerance, and hence lower limits of silver maple, the best predictor of the occurrence of trees combined two hydrological variables: the timing of the end of

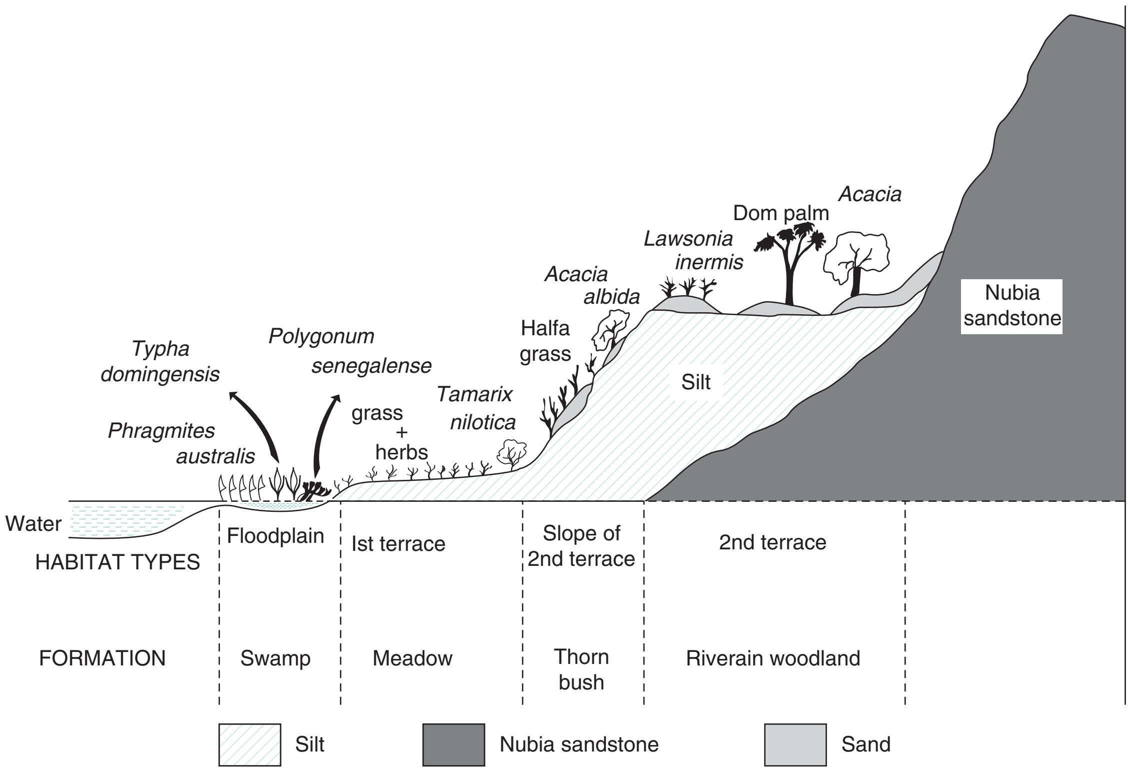

FIGURE 2.12 Flooding, along with sediment erosion and deposition, produces the characteristic vegetation types of the Lower Nile floodplain. (From Springuel 1990.)

the first flood and the beginning of the second flood. The probability of finding a wooded as opposed to herbaceous wetland is a function of these two factors (Figure 2.15). The duration of the first flood is critical. The period of 70 days flooding corresponds to roughly one-third of the average growing season at this latitude. Farther south, woody species such as *Acer saccharum* and *Fraxinus pennsylvanica* can tolerate 100 and 160 days of flooding (Robertson *et al.* 1978). Timing of the second flood is probably important for the following reason: if a second flood follows closely on the first, it represents simply a prolongation of the unfavorable conditions. If, on the other hand, there is a significant gap between floods, there is a period of more favorable conditions; the longer this favorable period, the greater the opportunity for plants to recover enough to withstand a second adverse period. Different predictive models may be needed for different parts of the world, particularly where differences in climate may interact with tolerances to flooding (e.g. Poiana and Johnson 1993; Johnson 1994).

2.3.2 Lakes

Flooding and drying cycles seem typical of many water bodies, ranging from the smallest beaver ponds to some of the largest lakes. Changes in vegetation with falling water level have been frequently observed. The American naturalist and philosopher Thoreau was a keen observer of nature. In 1854 he wrote:

> This rise and fall of Walden [Pond] at long intervals serves this use at least; the water standing at this great height for a year or more though it makes it difficult to walk around it, kills the shrubs and

FIGURE 2.13 Annual spring floods create a broad wet meadow along the unregulated Torne River in Sweden. (Courtesy C. Nilsson.)

FIGURE 2.14 Extensive wet meadows are produced by spring flooding along northern rivers that flow into Hudson Bay. (Courtesy M. Oldham.)

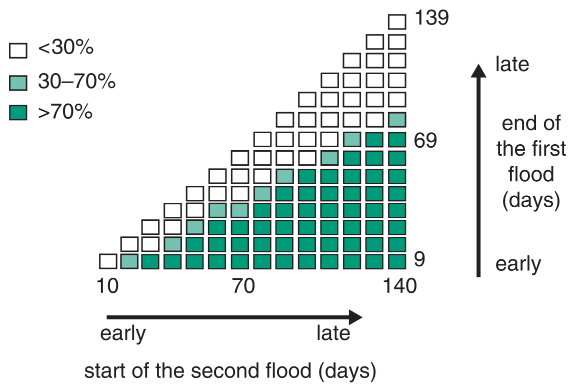

FIGURE 2.15 The probability of finding woody as opposed to herbaceous plants in a wetland can be predicted by knowing when the first flood ends and when the second flood (if any) begins. (From Toner and Keddy 1997.)

trees which have sprung up about its edge since the last rise … and, falling again, leaves an unobstructed shore; for, unlike many ponds and all water which are subject to a daily tide, its shore is cleanest when the water is lowest … By this fluctuation the pond asserts its title to a shore, and thus the shore is shorn, and the trees cannot hold it by right of possession. (H. D. Thoreau 1854)

Beginning our survey with large lakes, Raup (1975) studied the vegetation of the Athabasca–Great Slave Lake region of northwestern Canada during the period 1926 to 1935. He too emphasized the importance of water level fluctuations in producing wet meadow communities and made observations on shoreline succession.

Water levels in the Great Lakes fluctuate over decades and centuries (Figure 2.4). These changes in water level cause dramatic changes in shoreline vegetation (Keddy and Reznicek 1986; Reznicek and Catling 1989). Rich wet meadows, fens, and wet prairies (recall Figures 1.6 and 1.7) are maintained by periodic flooding that kills woody plants. Many of the common genera in these habitats (e.g. *Carex, Cyperus, Juncus, Polygonum*) are known to produce persistent seed banks. In similar marsh vegetation types, seed densities are typically 3000 seeds/m^2, although in one wet meadow, they exceeded 38 000/m^2. Low-water periods allow these seeds to germinate (Figure 2.16). Such dynamic changes in water level and vegetation maintain a rich flora of some 450 plant species. The short-term effects of high water levels can be deleterious; Farney and Bookhout (1982) observed declines in waterfowl nesting, as well as drastic declines in muskrats. However, these long-term fluctuations are necessary to maintain the full array of wetland communities and their associated wildlife (Prince and D'Itri 1985; Reznicek and Catling 1989; Smith *et al.* 1991).

Over the last 15 000 years and the retreat of the Wisconsinan ice sheet, the Great Lakes have changed dramatically in area, distribution, and drainage (Figure 2.4). Lake Agassiz, Lake Algonquin, Lake Minesing, Lake Chicago, Lake Tonawanda, Lake Warren, and the Champlain Sea have come and gone (Karrow and Calkin 1985). Figure 2.4 does not show Lake Agassiz, a 350 000-km^2 body of meltwater that covered much of southern Manitoba and western Ontario about 10 000 BP. This lake was partly created by an ice dam on its eastern outlet. When this ice dam melted, Lake Agassiz drained along the Laurentide ice margin, entered Lake Superior and then discharged through the North Bay outlet of the Great Lakes (Figure 2.4*e*). Calculations of discharge rates yield values of 200 000 m^3/s, which, to put it in context, is 13 times the mean discharge of the Mississippi River at New Orleans today (Teller 1988). At this rate it could have taken only 2 years for the water level of Lake Agassiz to fall 12 m.

On the other side of the world, changes in the water levels of African lakes are caused by the seasons as well as long-term changes in rainfall. The rise in water levels is often rapid from the influx of floodwaters, whereas the subsidence is slower, resulting from evaporation and reduced runoff (Talling 1992). In Lake Chilwa, changes in water elevation of 2.5 m were recorded over one decade. Lake Victoria has a fluctuation in amplitude of about 1.5 m each year (Denny 1993b). As in the Great Lakes of North America, the levels of Lake Victoria have also changed with climate. Before 12 500 BP, Lake

FIGURE 2.16 During a low water year in Lake Erie there was dense regeneration of *Scirpus* and *Sagittaria* plants in Metzger Marsh. (Courtesy D. Wilcox.) (See also color plate.)

Victoria had low levels and lacked an outlet, probably being surrounded by swamps and savanna. There were also periods with much higher water levels, probably within the past 10 000 years, whose presence is documented by old beaches encircling the lake at 3, 12, and 18 m above current levels (Kendall 1969).

Equally dramatic changes occur in small ponds and lakes (Mandossian and McIntosh 1960; Salisbury 1970; Keddy and Reznicek 1982; Schneider 1994). During low-water periods, rich shoreline floras may emerge from reserves of buried seeds (Figure 2.17). Intervening high-water periods kill woody plants. Hence, there is a common process underlying the maintenance of wet meadows along rivers (Figures 2.13, 2.14), those of the Great Lakes (Figures 1.6, 1.7), and those of the smaller lakes and even vernal pools.

2.3.3 Beaver ponds

Beavers construct dams that obstruct water flow, thereby flooding the forest and creating small ponds (Figure 2.18). Before the arrival of Europeans, the beaver population of North America was estimated to be 60 to 400 million, with a range stretching from arctic tundra to the deserts of northern Mexico.

Beavers convert small watercourses to open ponds (Figure 2.19, phases 1–3). Dams may fail during floods, or holes may be punched in them by mammals such as otters, and then wet meadows develop from buried seeds (Figure 2.19, phase 4). Although nearly 40 species of plants are known from beaver pond seed banks, Table 2.2 shows that a few genera of monocotyledons are most common. Dam breaking and repair cycles produce short-lived periods of low water alternating with wet meadows. Hence, the long-term process of converting forest to wetland (phases 1 and 2) can end in a rapidly alternating state between pond and wet meadow (phases 3 and 4).

There is also a longer-term cycle. Abandonment of the dam will result in a short-lived mud flat and then a beaver meadow. Eventually, the forest will

FIGURE 2.17 During low-water periods a rich wet meadow flora emerges from buried seeds on the shoreline of Matchedash Lake, Ontario. Typical high water levels are indicated by the tall grasses at left; the canoe marks the summer water level in a low year. (From Keddy and Reznicek 1982.)

reinvade. This longer cycle of beaver ponds alternating with swamp forest probably has a frequency of centuries rather than decades. It may take that long for food trees to re-establish, at which point the process of damming begins again.

Much of North America is recovering from a period of low beaver activity – populations were very low at the turn of the century as a result of heavy trapping. They then expanded rapidly after 1940. As a typical example, in Voyageurs National Park in northern Minnesota, aerial photographs from 1940 through 1986 show an increase in pond sites from 71 to 835 (Johnston and Naiman 1990). During the first half of the period (1940 to 1961) ponds were created at the rate of 25/yr but later (from 1961 to 1986) the rate declined to 10/yr.

Beaver ponds provide important habitat for amphibians, mammals, and birds. In one sample of 70 wetlands with beaver activity, a total of 106 species of spring birds was found, with 9 to 39 species per wetland (Grover and Baldassarre 1995). Larger wetlands had more species, as did wetlands with active beaver colonies. Active ponds had more open water, more standing dead trees, more flooded emergents, and a higher habitat diversity index. There were 19 obligate wetland species in active ponds compared with 12 in inactive ones, and there were 18 facultative wetland species that used cavities in the standing dead trees. Beaver ponds provided habitat for more than half of the regional avifauna.

Beavers are only one of many organisms that create, modify, or maintain natural habitats, a type of organism we could call an ecosystem engineer (Jones *et al.* 1994). In wetlands, other examples would be alligators excavating wallows (Section 4.3.5) or *Sphagnum* mosses building peat bogs (Section 7.1.6).

FIGURE 2.18 Beavers can produce water level fluctuations by building dams that periodically break or are abandoned. (Courtesy Friends of Algonquin Park.)

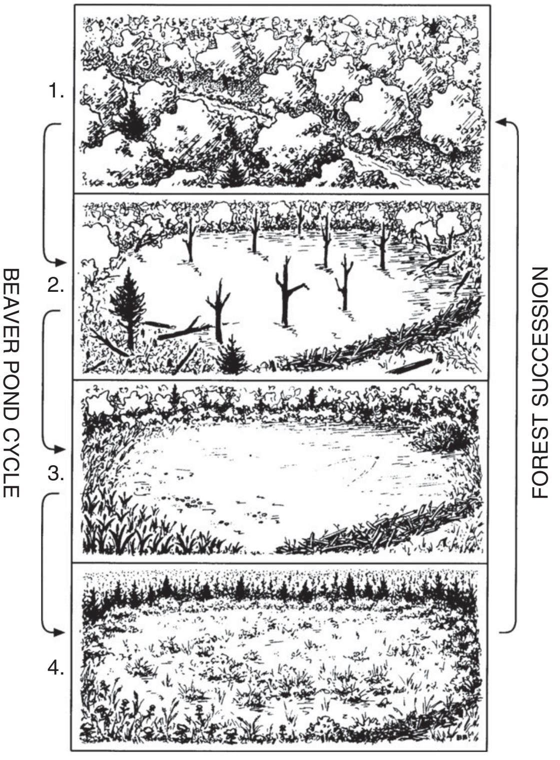

FIGURE 2.19 The beaver pond cycle going from forest with stream (1), to new pond with dead trees (2), to established pond with aquatic plants (3). When the food supply diminishes, indicated by the presence of conifers, the dam fails and a beaver meadow forms (4). Eventually, forest succession can reverse the process. (Illustration by B. Brigham.)

2.3.4 Potholes and related wet depressions

Some wetlands with seasonal flooding are not connected to large rivers or lakes, being dependent instead upon local sources of water such as rain and snow. These include a wide array of wetland types with local names including potholes, vernal pools, and playas. Let us survey them, roughly north to south.

Prairie potholes were formed by the glaciers that covered and then retreated from the continent of North America, leaving behind millions of depressions across over half a million square kilometers of prairie stretching from Alberta south eastward to Iowa. These depressions are filled by melting snow and, depending upon depth, the water table, and summer rainfall, they range from ephemeral to permanent wetlands. An early explorer on an expedition under General Sully against the "hostile Sioux" wrote in 1870: "The entire face of the country is covered with these shallow lakes, ponds and puddles . . ." (in Kantrud *et al.* 1989). More than 20 million ducks representing 12 common species breed in this region. Common species are mallard, blue-winged teal, northern pintail, northern shoveler, and American widgeon (Batt *et al.* 1989). The dominant herbivores are muskrats and waterfowl (Murkin 1989).

Pothole vegetation includes wet prairie, wet meadows, marshes, and submersed aquatics, controlled by three main environmental gradients: water regime, salinity, and disturbance (Walker and

Table 2.2 **The ten most common species that germinated from the mud in a series of beaver ponds in Canada**

Species	Number of seedlings
Juncus effusus	388
Leersia oryzoides	355
Scirpus cyperinus	224
Juncus brevicaudatus	155
Ludwiga palustris	89
Hypericum boreale	87
Unknown dicot	66
Elocharis obtusa	57
Galium palustre	56
Hypericum majus	49

Source: From Le Page and Keddy (1998).

Wehrhahn 1971; Shay and Shay 1986; Adams 1988). The first is flooded for a few weeks each spring, whereas the last is permanently flooded except during severe drought (Kantrud *et al.* 1989). Buried seeds allow plant species to survive inhospitable periods and then re-emerge after prolonged flooding or drought (van der Valk and Davis 1978; van der Valk 1981). Dominant plants include *Phragmites communis, Typha latifolia,* and *Scirpus* spp. (Shay and Shay 1986). The major water input is from melting snow, while the major loss is from evaporation. Since below-ground flow is relatively slow (0.025–2.5 m/yr), the ponds are hydrologically isolated from one another in the short term (Winter and Rosenberry 1995). Potholes also vary in salinity, ranging from fresh (<500 µS/cm) through brackish (500 to 15 000 µS/cm) to saline (>45 000 µS/cm) and values exceeding 10 000 µS/cm are common (LaBaugh 1989). One classification scheme for potholes has the four vegetation zones mentioned above combined with three other features: low prairie immediately adjacent to the wetland, fens where groundwater seeps into the pothole, and an "alkali zone" with saline water (Figure 2.20). There are four hydrological types: ephemeral, intermittent, semi-permanent, and permanent (Woo *et al.* 1993).

Half of these potholes have already been drained and ploughed. Further risks arise from a gradual decline in the water table. In the Nebraska sand hills, for example, irrigation from wells is increasing in extent; by 1985 there were over 70 000 irrigation wells registered, with an estimated volume of water removal approaching 10^8 m^3/yr (Novacek 1989). Wet meadows are most at risk.

Playas occur further to the south in North America, in the arid high plains, in large circular depressions filled during the spring rainy season (Bolen *et al.* 1989; Smith 2003). Some 22 000 playas occur in Texas and New Mexico. The dominant species are perennial grasses. The dominant environmental factors are elevation and unpredictable wet–dry cycles, with fire and grazing thought to be of secondary importance. Playas were once used as wallows by herds of bison and antelope in a manner reminiscent of the African megafauna. Seed banks again allow plants to tolerate fluctuating water levels (Haukos and Smith 1993, 1994).

Vernal pools can be found further west, in an area extending from southern Oregon though central California into northern Baja California, Mexico (Bauder 1989). Winter rains fill small depressions for periods of 3 to 5 months, producing pools ranging from 20 to 250 m^2 in area and up to 30 cm deep. These pools have a unique flora termed vernal pool ephemerals, many of which are annuals endemic to the California floristic province. This flora is absent when water stands for more than 6 months.

In some semidesert regions of Russia, shallow undrained basins are called firths, padinas, or saladas depending upon the depth and duration of flooding (Zhulidov *et al.* 1997). Many of these are found in the loess deposits northeast of the Black Sea. Firths are shallow (2–4 m) undrained basins which maintain lush meadow vegetation during summer droughts. Padinas, shallower than firths, but 0.2–5 km in diameter, are filled by melting snow, whereas saladas are associated with salt domes and contain saline water. In the adjoining steppe zone, reed thickets (plavni) form in continuously flooded lowlands, particularly those associated with river deltas (Zhulidov *et al.* 1997).

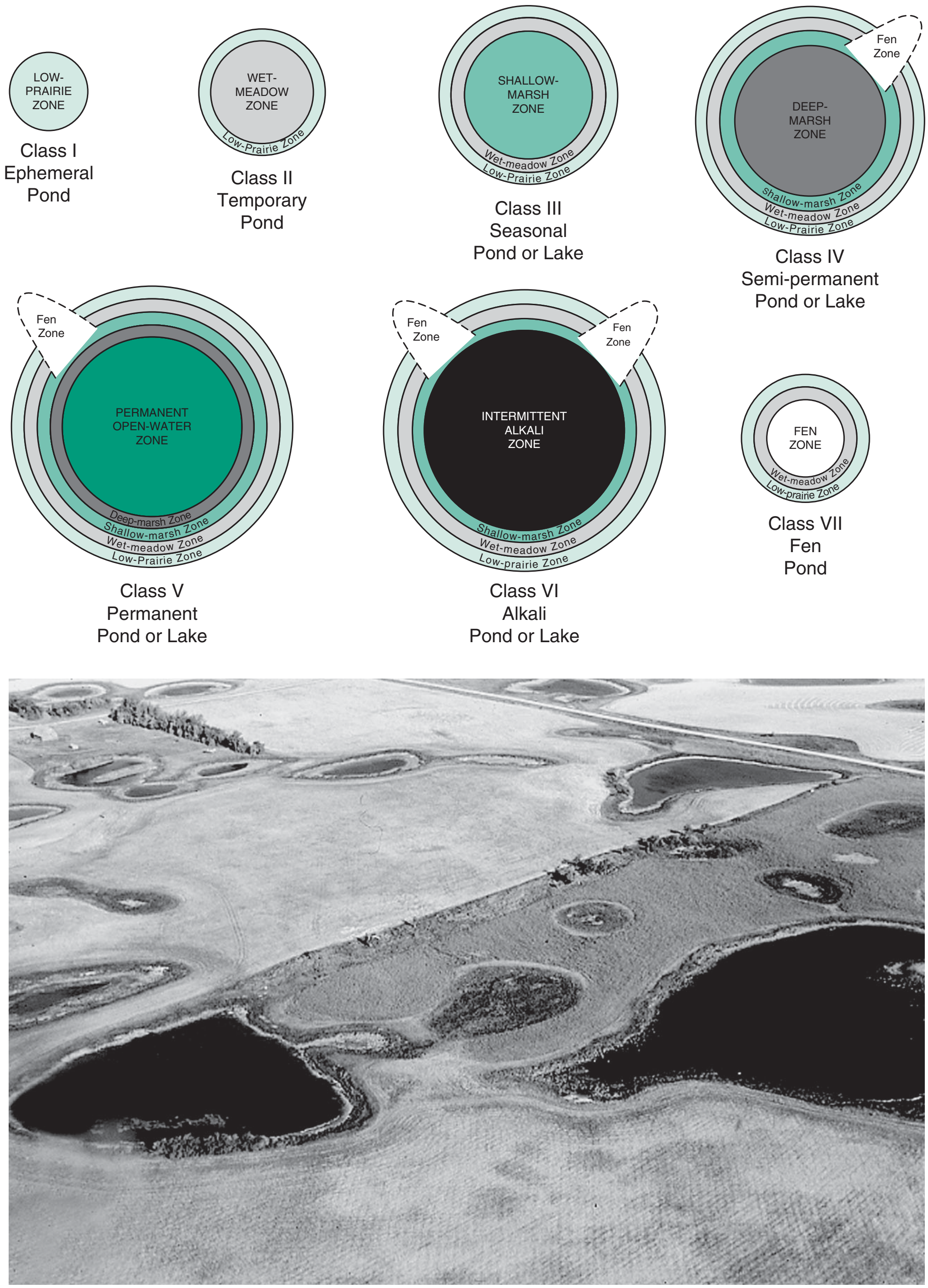

FIGURE 2.20 The vegetation patterns in prairie potholes are controlled by flooding. Here is a classification system showing vegetation zones for seven types of prairie potholes (from Stewart and Kantrud 1971 in van der Valk 1989) and an aerial view of potholes of differing classes near Minnedosa, Manitoba (Courtesy C. Rubec). (See also color plate.)

Wet savannas

Depressions can also support a wide array of wet savannas and prairies, particularly in the subtropics and tropics. Although these could be added as yet another wetland type, they share many of the characteristics of wet meadows, having species that tolerate only short periods of flooding and having high plant diversity. In cases where the soil remains waterlogged, fen species may also occur. Three examples follow: the North American gulf coast savannas, the Orinoco River savannas, and the Cape Peninsula of southwest Africa.

In flat coastal plain areas of southeastern North America, there are large areas of longleaf pine (*Pinus palustris*), often interspersed with savannas and wet depressions. These infertile wet depressions support an array of unusual wetland types with extremely rich floras. Sedges in the genus *Rhynchospora* and species of pitcher plants in the genus *Sarracenia* are characteristic (Peet and Allard 1993; Christensen 1999). Water level fluctuations, infertile soils, and fire are three of the main natural factors responsible for this high diversity. These wetlands also provide habitat for many amphibian species including the Mississippi gopher frog (Figure 2.5*b*).

Savannas extend southward along the Gulf of Mexico and Caribbean Sea into northern South America. One vast savanna (>500 000 km^2) stretches between the Andes Mountains in the west and the Guyana Highlands in the east, being drained by the Orinoco River. In Venezuela, Huber (1982) has described how savannas develop on white sand soils "characterized by marked fluctuations in the water content . . . Shortly after the beginning of the rainy season these soils readily become water-saturated in consequence of the first heavy rainfalls; for the rest of the rainy season, the water accumulates above the soil for a short time after each rainfall, then it eventually drains away superficially towards the small creeks and rivulets" (p. 224). These infertile seasonally wet savannas support a great variety of plant species. Some like the Eriocaulaceae, Xyridaceae, and Haemodoraceae extend north along the Gulf Coast. A few grasses occur, but they "never form a dense cover" (p. 236).

Of course, similar types of habitats occur elsewhere in the world. The arid Cape Peninsula in southwest Africa has some of the highest levels of plant diversity and endemism recorded in the world (Cowling *et al.* 1996a, b). There is high topographical heterogeneity, long and steep rainfall gradients, a variety of infertile soils, and frequent fire. The predominant vegetation is a fire-prone shrubland called fynbos containing thousands of species of southern hemisphere plant groups (including distinctive families like the Restionaceae and Proteaceae); but where rainfall and topography permit, wetlands occur. Seasonally waterlogged sites have distinctive floras (Table 2.3).

The above are only selected examples. Short-lived pools are widespread, and will vary with the source of the water, the type of substrate, and the length of the growing season. When seen during the dry season, it may be hard to appreciate that they are a wetland vegetation type, yet during the wet season, the importance of water becomes self-evident.

2.3.5 Peatlands

Some of the world's largest wetlands are peatlands (Fraser and Keddy 2005). In order for peat to accumulate, primary production must consistently exceed decomposition. For this to occur, water levels must be relatively stable. Otherwise, decomposition and fire during low-water periods would remove the peat. To illustrate, in one series of wetlands in Japan, valley fens (with significant peat accumulation) had some of the lowest changes in summer water level (SD $<$ 10 cm) whereas marshes showed some of the highest fluctuations (SD $>$ 20 cm) (Yabe and Onimaru 1997).

When the peat is thin, groundwater is the key source of moisture. The calcium content of the groundwater controls acidity, while the nitrogen and phosphorus concentrations control fertility. These two gradients produce much of the variation in fen vegetation (Bridgham *et al.* 1996; Godwin

Table 2.3 **Seasonally flooded and/or waterlogged soils in South Africa support an extremely rich flora with families of plants including the Restionaceae, Proteaceae, and Ericaceae; the fynbos flora alone has more than 7000 plant species and seven endemic plant families**

Vegetation	Environment	Common species
Upland fynbos	Shallow seasonally waterlogged sands	*Thamnocortus nutans, Chrondropetalum ebracteatum, Ursinia nudicaulis, Restio bifidus, Ehrharta setacea, Watsonia borbonica, Penae mucronata, Cliffortia ruscifolia, Erica hispidula, Chondropetalum mucronatum*
Wet fynbos	Shallow seasonally waterlogged sands on sandstone at low altitudes	*Ischyrolepis cincinnata, Tertaria cuspidata, Elegia filacea, Thamnochortus lucens, Cliffortia subsetacea, Erica imbricata, Leucadendron laureolam, Pentaschistis curvifolia, Restio quinquefarius, R. bifurcus*
Wetlands	Seepage sites with shallow–medium depth sandy soils with high organic matter over sandstone bedrock	*Penaea mucronata, Berzelia abrotanoides, Platycaulos compressus, Leucadendron laureolum, B. lanuginosa, Pentaschistis curvifolia, Osmitopsis astericoides, Watsonia tabularis, Psoralea pinnata, Restio quinquefarius*

Source: Modified from Cowling *et al.* (1996b).

et al. 2002). As peat accumulates, the influence of groundwater chemistry declines. Hence, peat accumulation can change groundwater controlled fens to ombrotrophic (rainwater controlled) bogs. In cores, this transition can be recognized by changes in the nature of the peat, particularly the appearance of *Sphagnum*. Many peat sequences therefore begin with sedge peat and end with sphagnum peat (Tallis 1983; Kuhry *et al.* 1993). As peat accumulates, the water table can slowly rise. Peatlands can therefore bury previously forested land, grassland, or even bare rock, a process known as **paludification** (van Breeman 1995). In some cases paludification may be attributed to changes in the climate, but in other cases it seems to be driven simply by local factors that control rates of growth and decomposition (Walker 1970; Frenzel 1983). If the water regime of a site is changed by humans, say by removing the tree cover and reducing evapotranspiration, peat accumulation may be triggered.

As peat accumulates, a raised bog with a dome-like shape may form, producing ombrogenous raised bogs, as shown in Figure 1.19. Here, the underlying topography has less impact upon vegetation. Slowly but steadily, as peat accumulates, there is a shift away from control by local hydrological factors toward control by climatic factors (Foster and Glaser 1986).

Melting spring snow can modify this process. In regions where snow accumulates and then melts rapidly in the spring, the flush of oxygenated water can increase rates of oxidation and produce mineral-rich water flows above the anaerobic zone; this maintains fens. In such circumstances, raised bogs become restricted to areas with minimal water flow such as water divides.

In ombrotrophic bogs, the water table is determined by the balance between inputs from rain and losses through evaporation and seepage. To give some feel for the variation in water levels that is possible, during a dry summer at Wicken Fen in England, the water table dropped as much as 48 cm below the peat surface, although declines of 4 to 20 cm were more typical (Ingram 1983). A dry summer in Finland caused the water table of a bog to drop some 25 cm (Kurimo 1984). In Labrador, Canada, pools on the surface of raised bogs may entirely dry out, forming a mud bottom that cracks from desiccation (Foster and Glaser 1986).

Each species will respond to changes in water level. By way of illustration, consider the effects of low water on one bog species, *Carex exilis*, a widespread sedge of eastern North America. In coastal areas it occupies ombrotrophic bogs, whereas inland it occupies soligenous fens. After a series of transplants and greenhouse experiments, Santelmann (1991) concluded that the water table is the critical factor. *Carex exilis* occurs in those peatlands where the water table remains close to the surface, and it is absent from mid-continental bogs, because the water table normally drops 20 cm or more below the moss surface.

Overall, the hydrology of peatlands differs largely from that of other wetlands with respect to the amplitude of fluctuations, frequency of fluctuations, source of water, and mineral content of the water. The ombrotrophic bog, with its somewhat more stable water table, dependent upon local precipitation, may therefore be regarded as being nearly the exact opposite of the many examples of forested floodplain where distant rainfall causes the water levels to fluctuate by many meters.

2.4 General relationships between wetlands and water level fluctuations

In Chapter 1 you saw the six principal types of wetlands: bog, fen, swamp, wet meadow, marsh, and aquatic ecosystems. The last four of these represent a sequence of vegetation types associated with increasing duration of flooding. From the perspective of wetland classification, these are distinctive types of wetlands. From the perspective of flooding, they are merely four regions in a continuum of communities that are ever-changing, short-lived responses to water levels. Let us reintroduce these four wetland types as they relate to flood pulses.

2.4.1 Swamps

The highest elevations in wetlands are only occasionally flooded by the highest flood pulses. This is the zone of woody plants – called swamps, bottomland forests, riparian forests, or floodplain forests. At higher elevations (landward), they grade into upland forests; at the other end (waterward), they are killed by prolonged flooding and replaced by more flood-tolerant herbaceous plants. Large areas of the world fall between these two extremes: flooded enough to exclude terrestrial plants, but not enough to kill trees (Lugo *et al.* 1990). Extensive areas of floodplains along rivers are dominated by riparian forests (e.g. Junk 1983; Denny 1985; Sharitz and Mitsch 1993; Messina and Connor 1998). Only a few types of trees can withstand permanent flooding (Kozlowski 1984b). Table 2.4 shows some typical survival times for trees exposed to permanent flooding.

2.4.2 Wet meadows

At somewhat lower elevations, where the duration of flooding is sufficient to kill woody plants, swamps are often replaced by wet meadows. Wet meadows usually support more plant species than any other vegetation type. In the absence of periodic flooding, this zone is invaded and dominated by woody plants. Occasional flooding, however, kills the woody plants and allows regeneration of wet meadow plants from buried seeds (Keddy and Reznicek 1986; Schneider 1994). The plants here tend to rapidly establish from buried seeds, producing wet meadows that persist until woody plants reinvade the site, or another flood peak occurs. Two other factors are often associated with the formation of wet meadows. Scouring by ice and waves can prevent reinvasion by woody plants (e.g. Raup 1975; Keddy 1989b). Infertile soils may delay reinvasion by woody plants. This may be why infertile wet meadows tend to have particularly rich floras (Moore *et al.* 1989).

Table 2.4 **Relative survival time under inundation of some flood-tolerant trees**

Species	Survival time (yr)
Quercus lyrata	3
Q. nuttalii	3
Q. phellos	2
Q. nigra	2
Q. palustris	2
Q. macrocarpa	2
Acer saccharinum	2
A. rubrum	2
Diospyros virginiana	2
Fraxinus pennsylvanica	2
Gleditsia triacanthos	2
Populus deltoides	2
Carya aquatica	2
Salix interior	2
Cephalanthus occidentalis	2
Nyssa aquatica	2
Taxodium distichum	2
Celtis laevigata	2
Quercus falcata	1
Acer negundo	0.5
Crataegus mollis	0.5
Platanus occidentalis	0.5
Pinus contorta	0.3

Source: From Crawford (1982).

2.4.3 Marshes

Marshes are flooded for longer periods of time than wet meadows. Wet meadows may be inundated only during flood peaks, whereas marsh vegetation is flooded for most of the growing season. As a consequence, marsh plants have traits for flood tolerance such as aerenchyma (recall Figure 1.15). While marsh species can tolerate flooding, most still require occasional dry periods to regenerate from seeds (van der Valk and Davis 1976, 1978; Smith and Kadlec 1983). Thus, while both marshes and wet meadows are produced by flooding, the duration of flooding and its timing differs between them.

2.4.4 Aquatic communities

At the lowest elevations flooding is more or less continuous; the species here are not dependent upon water level fluctuations for their regeneration. Chapter 1 listed a number of features that allow aquatic plants to tolerate prolonged flooding. These included the presence of aerenchyma to transmit oxygen to the roots, reinforced floating leaves, dissected leaves, and greatly modified flowers (Figure 1.20). Many of the studies on this zone are found in the limnology literature (e.g. Sculthorpe 1967; Hutchinson 1975; Wetzel 1975).

If we look at shoreline wetlands as dynamic features that result from flood pulses, there are two important lessons. (1) The greater the long-term amplitude of water level fluctuations in a landscape, the greater the area of wetland. (2) The relative abundance of these four wetland types in a landscape will depend upon the frequency and duration of flooding. Overall, in the absence of water level fluctuations, we can predict that wet meadows and marshes either shrink or disappear entirely (Figure 2.9).

2.5 Reservoirs, dams, and floodplains

Humans are far more effective at constructing dams than are beavers. The world is now covered with reservoirs created by *Homo sapiens*. As a result, natural water level fluctuations are being disrupted around the globe. Alteration of hydrology is believed to be one of the three major causes of damage to aquatic animals; in the United States of America alone, there are now more than 75 000 large dams (higher than 8 m) and 2.5 million small ones (Richter *et al.* 1997). The giant Three Gorges Dam has recently been built on the Yangtze River in China (Figure 2.21); it will flood more than 1000 km^2

FIGURE 2.21 Dams built by humans, such as the Three Gorges Dam recently constructed on the Yangtze River, increasingly disrupt natural flood pulses in the world's great rivers. (Courtesy ChinaFotoPress/Li Ming.) (See also color plate.)

(Wu *et al.* 2004) while changes in sediment transport will affect areas far downstream along the coast to Shanghai. Many more dams are being proposed for other large rivers.

The nature of the alteration to natural flood patterns will depend upon the purpose of each dam. The effects will also differ between the reservoir upstream from the dam and the river downstream. The list of negative impacts from the construction of dams includes destruction by flooding, mercury contamination, release of greenhouse gases (CO_2, CH_4), and damage to migratory fish species (Rosenburg *et al.* 1995). A nearly universal effect of dams is the reduction in spring flooding and a consequent reduction in wetland area in the remaining floodplain, along with conversion of wet meadows to swamps.

There are four main effects of dams upon hydrology (Klimas 1988).

Water levels stabilized The near-permanent inundation or saturation of substrates that were formerly periodically exposed.

Shifted flood timing Flooding can be delayed by months, sometimes until well into the growing season of vegetation.

Increased flooding Embankments and artificial levees act like linear dams and increase flood peaks by constraining the flow of water onto adjacent floodplains.

Decreased flooding By holding back runoff during normal flood periods, the duration and area of flooding are reduced.

2.5.1 Upstream effects: the reservoir

The pattern of fluctuations in a reservoir depends upon its purpose. The frequency of water level fluctuations may decrease if the reservoir is intended to stabilize water levels for recreation or shipping. Or, the frequency of fluctuations may increase if the reservoir is being used to provide pulses of water for daily peaks in power demand. Similarly, the amplitude may be reduced if the dam stores water during low-water periods, or it may be increased if the dam is used to

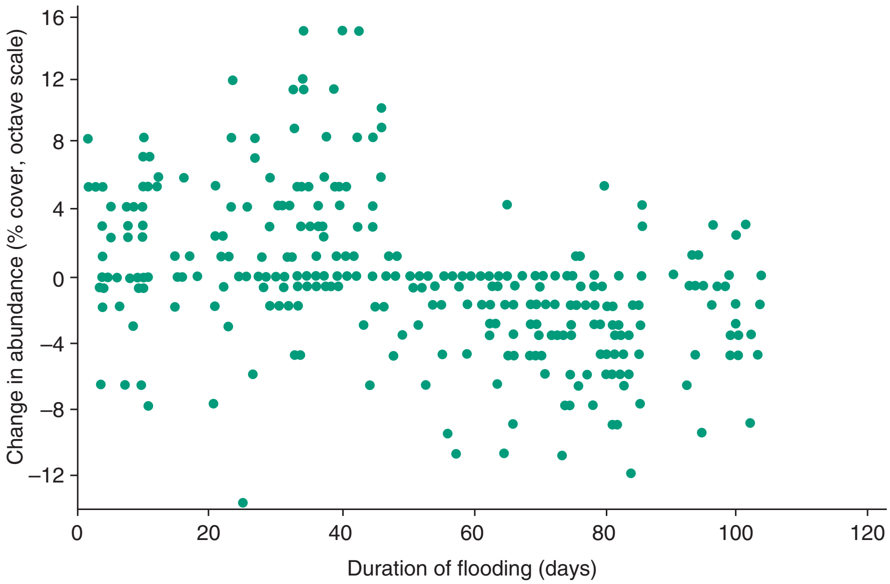

FIGURE 2.22 The effects of duration of flooding on the change in abundance of plants in a northern European reservoir. (From Nilsson and Keddy 1988.)

regulate water levels in headstock ponds for power generation. Every reservoir may be considered to have its own water level personality, determined in part by the purpose of its construction, and in part by the personalities of the people who maintain it.

Consider one extreme example: the Gardiken Reservoir in northern Sweden covers an area of 84 km^2 (Nilsson 1981). Water levels may fall as much as 20 m, exposing approximately 56 km^2 of shoreline. This reservoir is of particular interest because it represents some sort of biological limit to how much one can alter water levels in wetlands, since the water levels are almost exactly the reverse of natural cycles. It is lowest in spring (in order to provide storage for melting snow) and it is highest in the autumn. It is then progressively lowered during the winter in order to generate hydroelectric power, which, in Sweden, is needed most during the winter. You might predict that reversing the entire water level cycle would have dramatic effects upon vegetation. You would be right. Most of the reservoir shore is barren, except for a 1–2 m-wide strip of sparse vegetation close to the high water level. That is, this combination of conditions is so extreme that no plants can tolerate the conditions over most of the reservoir. If the duration of flooding was around 60 days, the vegetation remained more or less unchanged. If the duration of flooding was less than this, the abundance of plants increased, and if it was greater than this, the abundance of plants decreased (Figure 2.22). Hence, 60 days was the threshold that managers needed to consider to maintain shoreline plants. Studies in Norway indicate that as amplitude increases, plants can grow at lower elevations (Rørslett 1984, 1985).

2.5.2 Downstream effects: altered hydrology

The impacts downstream from the reservoir may affect an even larger area of landscape than the reservoir itself. Downstream from the dam, water levels are usually stabilized, particularly if the dam has been constructed to hold back spring flow and release water later in the year. By reducing spring floods, dams eliminate immense areas of wetland in a watershed. Almost every watershed in the world has been altered by the construction of dams. Hence, there has been a global trend to reduce river pulses during spring runoff (Dynesius and Nilsson 1994).

This also means that any remaining rivers without dams have high conservation value.

Some of the severe negative consequences of altered hydrology are shown by the Peace–Athabasca delta in Alberta, Canada (Gill 1973; Rosenberg and Barton 1986; Rosenberg *et al.* 1995). It is part of the larger Mackenzie River system, discharging into the Arctic Ocean. The Peace–Athabasca delta is "probably the most important northern delta in North America for nesting and is used by hundreds of thousands of birds" (Rosenberg and Barton 1986). The delta consists of 39 000 km^2 of wetlands formed where the Peace River flows into Lake Athabasca (Figure 2.23).

In 1968 the Bennett Dam was completed 1200 km upstream on the Peace River. One effect was the end of the annual June pulse of floodwaters (Figure 2.23, bottom). This led to rapid changes in the vegetation of the delta, with many of the herbaceous wetlands becoming woody vegetation (Figure 2.24). The rate of change was remarkable: within two years (by 1970) the total area of the nine largest water bodies had decreased by 28%, and the numerous perched lakes and ponds of the delta were drying up at the rate of 12% per year. Large grasses and willows spread rapidly. Because of its importance, the problems of the delta were studied by the Peace–Athabasca Delta Implementation Committee (1987), which recommended constructing weirs to hold back floodwaters and re-create flood pulses. Although this could not repair all the damage caused by the Bennett Dam, it made the best of a bad situation.

The Peace–Athabasca situation can be considered a well-studied example of what is now a global problem: dam building and wetland destruction *downstream*. Similar changes can be expected wherever dams are built. A few more examples follow. The Akosombo Dam on the Volta River in Ghana created "Lake Volta" with a surface area of some 8500 km^2 and annual drawdowns of some 3 m (Petr 1986). The dam has stabilized river flow leading to increased plant growth on the river banks, the increased population of a plant-associated snail, and the spread of schistosomiasis. Alteration of vegetation downstream from dams has been observed in many other watersheds, including the Colorado River in Arizona (Turner and Karpiscak 1980), the Milk River in Alberta and Montana (Bradley and Smith 1986), the Platte River in Nebraska (Johnson 1994), the Kissimmee River in Florida (Toth 1993), and streams in the Sierra Nevada (Harris *et al.* 1987). As with the Peace River, floodplains are being invaded by woody vegetation.

When riparian forests are surrounded by arid prairies rather than forested landscapes, the effects of reduced spring floods may be more severe. Poplar forests in river valleys are "thriving oases for wildlife" amidst the dry plains of western North America (Rood and Mahoney 1990). These riparian forests may support a variety of trees, shrubs, and smaller plants absent from the surrounding landscape (Johnson *et al.* 1976): "As the poplars die, so dies the whole riparian forest. Wildlife habitat is lost, the forest canopy is lost, and the forest understorey dies." Reduced water levels may directly stress the older trees, but more importantly, the dams reduce erosion and the movement of sediment, thereby eliminating sites for poplar seedlings to establish. These changes are occurring throughout arid areas of North America (Patten 1998) and, most likely, other arid areas as well.

2.5.3 Dikes are another kind of dam

Dams are not the only way that humans manipulate water level fluctuations in floodplains. Increasingly, rivers are contained within walls to prevent local flooding, particularly in heavily populated areas. Consider just three examples. The Vistula, which drains more than half of Poland, is more than 1000 km long, yet "has side walls on almost its whole length" (Kajak 1993). The Mississippi River is similarly constrained (Figure 2.25). There are also walls along sections of two of the largest rivers in the world, the Ganges and the Brahmaputra, with extensions planned (Pearce 1991). These sorts of walls destroy wetlands. Nearly every delta and floodplain in the world is experiencing these effects.

There is an additional indirect effect of building dams and dikes: the lands temporarily protected from spring flooding are frequently converted to agriculture or urban uses. Because this change is so

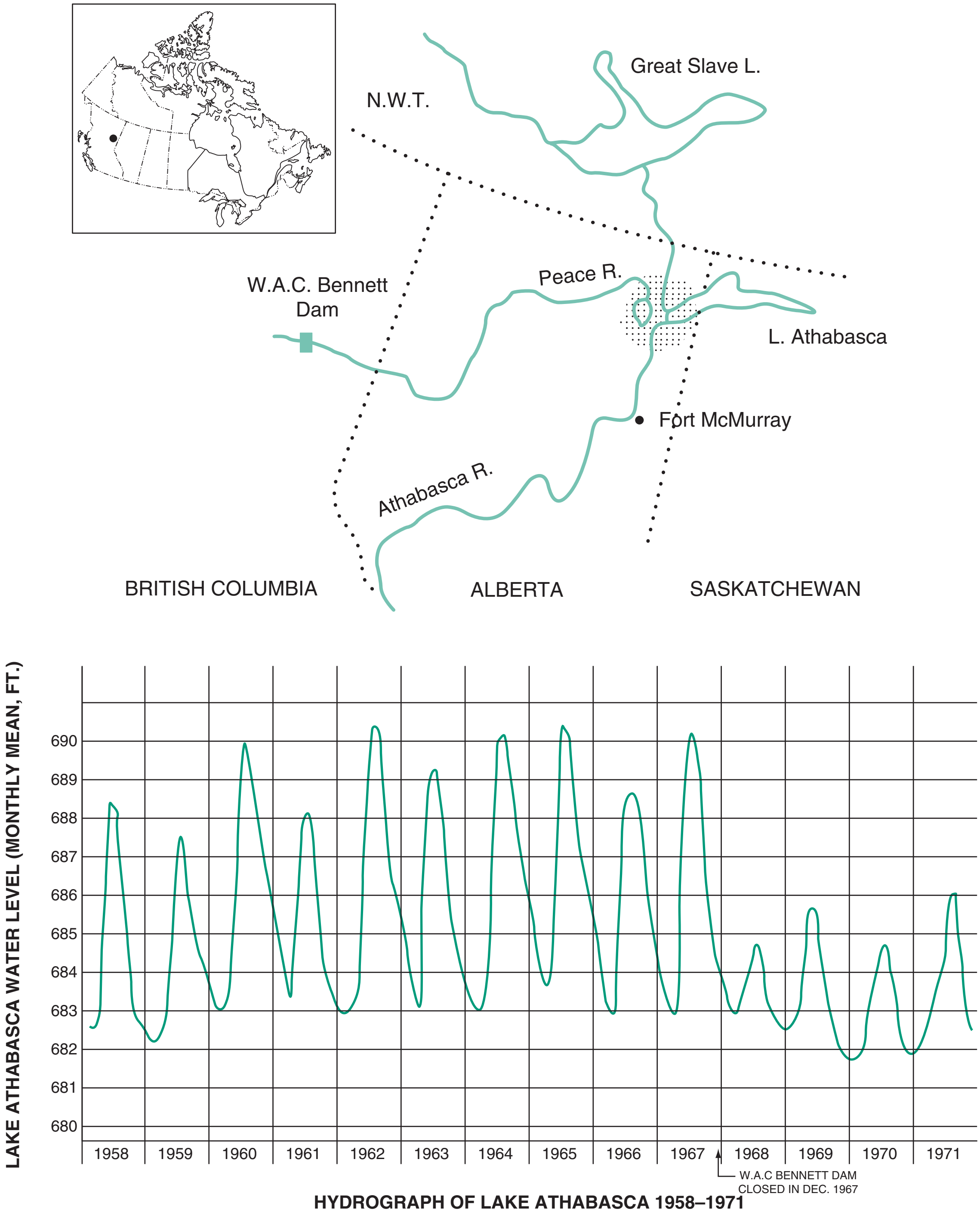

FIGURE 2.23 The location of the Peace–Athabasca delta and the W. A. C. Bennett Dam and changes in the hydrology of Lake Athabasca once the dam was completed. (After Peace–Athabasca Delta Project Group 1972.)

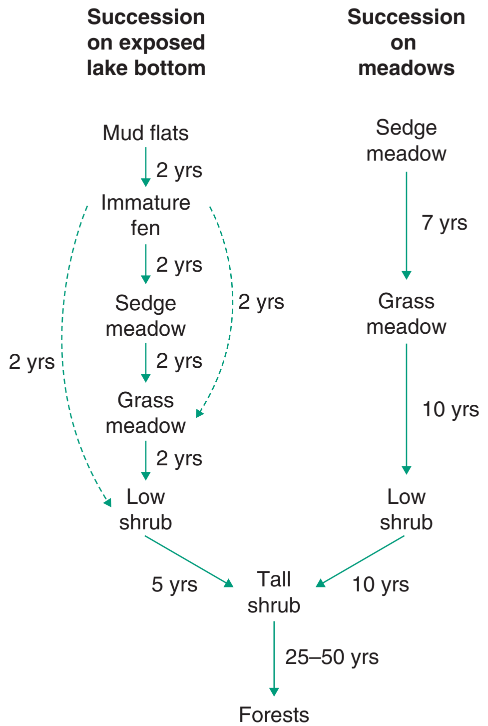

FIGURE 2.24 Changes in the vegetation in the Peace–Athabasca delta after the W. A. C. Bennett Dam (Figure 2.23) reduced spring flooding. (After Peace–Athabasca Delta Project Group 1972.)

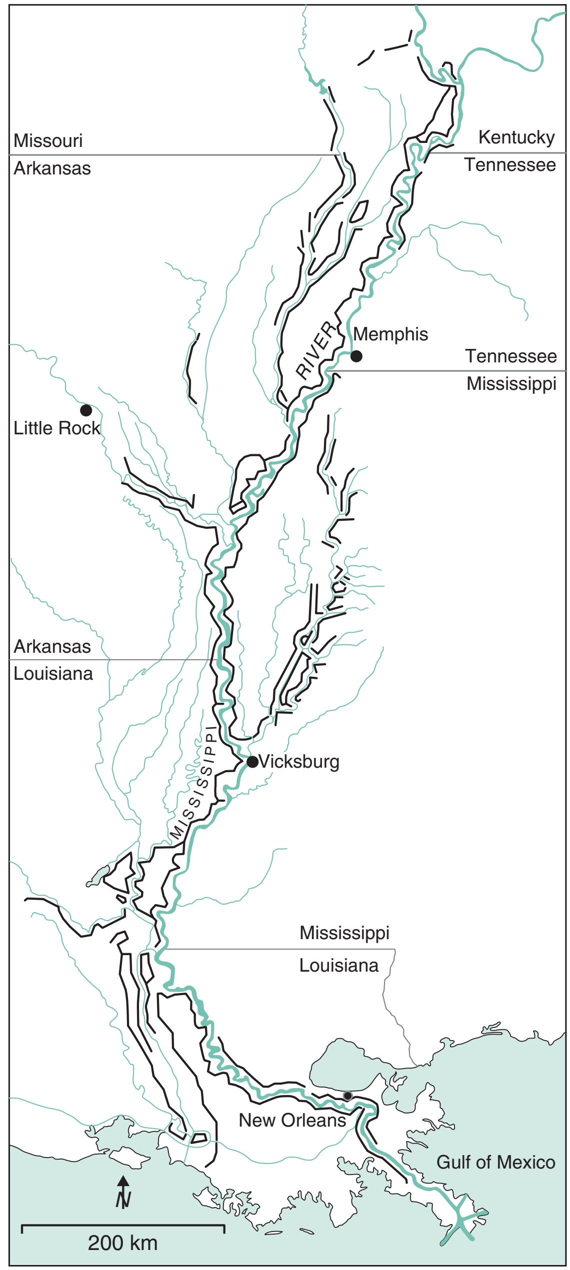

FIGURE 2.25 Rivers are increasingly constrained within walls and dikes. This causes extensive losses of floodplain wetlands, and occasional catastrophe when a big flood breaches the wall. Here are the walls built along the lower Mississippi River as of 1986. (From U.S. Army Corps of Engineers 2004.)

obvious and dramatic, it is sometimes easy to overlook the primary effect of dams, levees, embankments, and dikes – the loss of wetland area and conversion of meadows to swamps or upland. Dams, dikes, and agriculture are a devastating combination for alluvial wetlands. In the Mississippi River floodplain, for example, there were originally an estimated 8.5–9.5 million hectares of wetland forest; by the 1990s, only some 2 million remained (Figure 2.26). When large floods do breach one of these walls, massive flooding and loss of life can result (Barry 1997).

Overall, humans seem to have a fascination with changing natural hydrology, and allowing the return of natural water levels is therefore often one of the simplest yet most powerful ways of restoring a wetland.

2.6 Predicting consequences for wetlands

Having looked at the causes of water level fluctuations and their effect upon wetland species and habitats, we now turn to examining the potential consequences for wetland ecosystems.

2.6.1 Stabilized water levels reduce plant diversity and marsh area

We have seen how many wild species require fluctuating water levels. We could summarize the observations in this way. (1) The greater the long-term amplitude of water level fluctuations in a landscape, the more extensive the area of wetland will be. (2) The relative abundance of wetland types in a landscape will depend upon the frequency and duration of flooding. Figure 2.27 shows what happens when humans reduce flood peaks and augment low-water periods. Natural water level fluctuations (top) result in a shoreline with broad wet meadows and marshes. The bottom portion shows a stabilized shoreline where the woody plants reach the aquatic zone. Increasingly, shorelines like the lower illustration are becoming typical of watersheds. Broad wet meadows such as we saw in Figure 1.7 are becoming increasingly uncommon, with a consequent loss of habitat for the many kinds of plants and animals that occupy meadows and marshes.

2.6.2 A model for predicting how flooding increases wetland area

It is one thing to describe changes in vegetation that occur after a dam is constructed. In some cases, this is the proverbial situation of closing the barn door after the horse has escaped. What we need to be able to do is predict the severity of the changes that will occur before a project is built so that we can fully establish the consequences beforehand. We know the general pattern – illustrated by the Peace River wetlands – that dams reduce flooding, that reduced flooding causes wetlands to shrink, and that herbaceous wetlands are invaded by woody species.

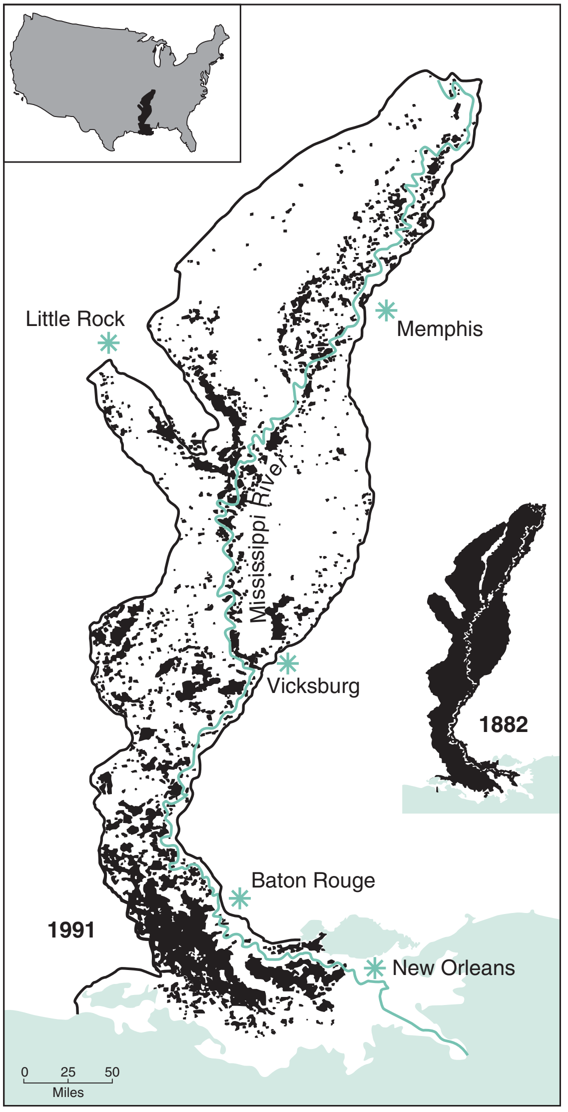

FIGURE 2.26 The remaining bottomland forests of the Mississippi floodplain. Once a river is constrained by dams and dikes, the floodplain is often cleared for agriculture. This can obscure the more widespread but less obvious effects of reduced spring flooding, such as encroachment by terrestrial species, conversion of wet meadow to woody plants, and changes in function and biological diversity. (From Llewellyn *et al.* 1996.)

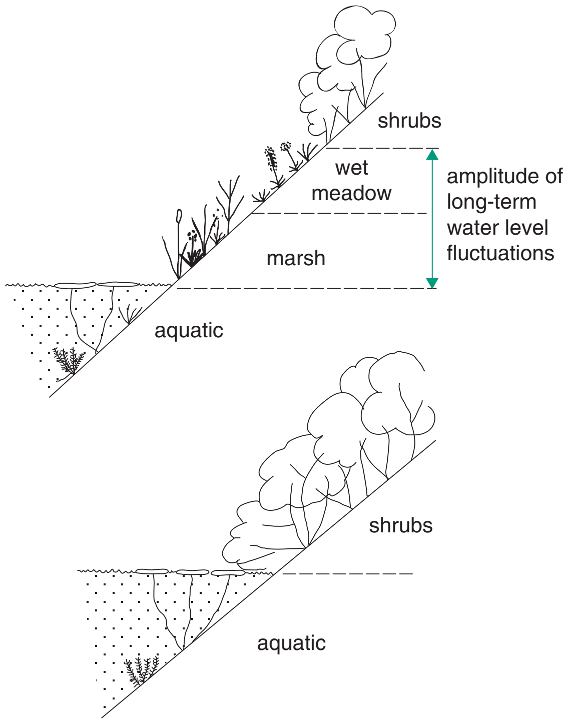

FIGURE 2.27 Stabilizing water levels compresses wetlands from four zones (top) to two zones (bottom). (From Keddy 1991a, b.)

Better predictive models are needed.

One tool, logistic regression, which was used to construct Figure 2.15, may hold considerable promise. This approach attempts to predict the occurrence of woody plants from basic water level patterns.

Another tool uses simple relationships between flooding and vegetation to predict changes in wetland area. This model was developed and tested for the Great Lakes. The Great Lakes contain a rich array of wetland types, including wet meadows, marshes, shoreline fens, and swamps that provide important habitat for fish, waterfowl, and rare plant species (Smith *et al.* 1991). Large areas of these wetlands have been drained. Humans have also reduced the amplitude of water level fluctuations. There is often pressure to control them further to simplify shipping and satisfy cottage owners. The problem was this: how much wetland loss would be caused by further reducing flood peaks?

The model looked at two critical points, the upper and the lower limit of herbaceous wetlands on a shoreline. First consider the upper limit, the landward edge of wet meadows. To model the landward edge of the wet meadow, it was necessary to consider the die-back and recolonization by woody plants. It was first assumed that the die-back of woody plants was caused by the highest water levels during a year. It was next assumed that after dying back, the woody plants reinvade toward the lake. After a lag time (to account for seed dispersal and sapling establishment), the shoreline is reforested using a simple exponential model. This allowed predictions of the lower limit of woody plants from projected water levels. The top line in Figure 2.28 shows occasional periods of death, a lag, and then slow reinvasion. The lag time in this model was 18 years; lag times of 20 or 15 years made little difference.

Now consider the lower limit. The model assumes that the lower boundary of the marsh is set by the yearly low water level, with marshes arising the same year from buried seeds. When the water rises, wetland plants die back over several years. The bottom line in Figure 2.28 shows wetlands forming as lake levels fall, and then decreasing as water levels rise. Lag times of 4 or 2 years as opposed to 3 made little difference. Overall, the lower limit of the wetland tracks much more closely the low water level.

The area between these two lines is then the extent of wet meadow and marsh as a function of time. When the model is applied to water levels between 1910 and 1985, it shows great areas of wetland that occurred during the low water period of the mid-1930s and the mid-1960s.

What about the future? This same model was then used for different future scenarios for water level regulation. If further reductions in amplitude occurred, the model predicted losses approximating 30% of the wetlands in Lake Ontario alone. This approach is particularly valuable because it emphasizes how wetlands are dynamic features that change in response to water levels. Indeed, if larger amplitudes were re-established by changing existing water control structures, even larger areas of wetland might

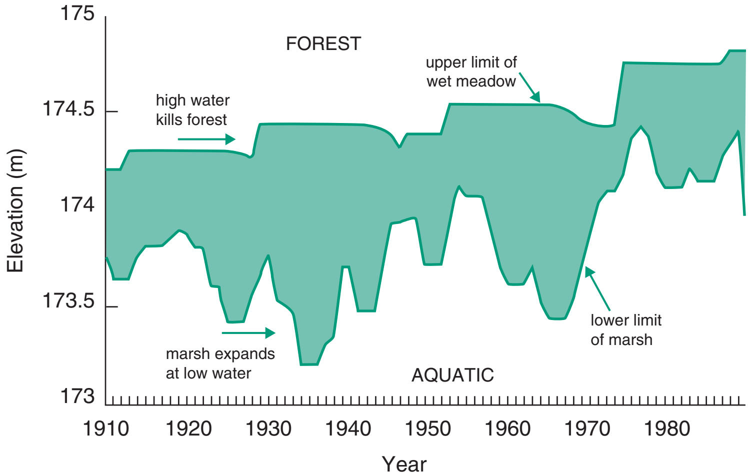

FIGURE 2.28 A simple simulation model showing the response of wetland vegetation to changes in water levels in the Great Lakes. Note that the area of wetland varies with water level history. (After Painter and Keddy 1992.)

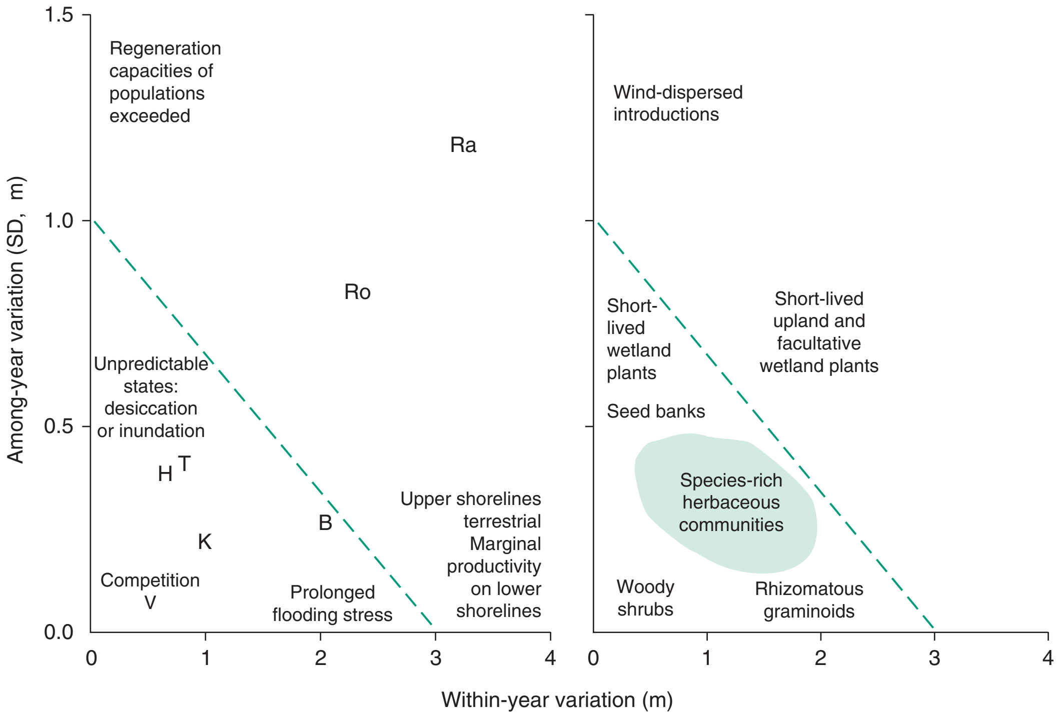

FIGURE 2.29 The effects of water level variation upon shoreline vegetation. The stippled area contains lakes whose hydrological regimes produce rich floras, while hypo- and hypervariable zones represent impoverished systems. Rich floras with many rare species occur in unregulated lakes with high catchment areas such as Kejimkujik (K) and Bennetts (B), both lakes with immediate water level fluctuations (within years and among years). In contrast, hypovariable lakes such as unregulated lakes with small catchment areas and head ponds (e.g. V, Vaughan) lose many species through competitive exclusion by shrubs. Hypervariable lakes such as storage reservoirs (above the dashed line, e.g. Ro, Rossignol and Ra, Raynard) lose species and are subject to invasion by exotic species. The stippled area is therefore the desirable management target. Increased catchment area can push lakes into the region of high richness, but reservoir construction can push lakes into the hypervariable state. (From Hill *et al.* 1998.)

be produced. More elaborate models using GIS data and different types of embayments confirm this story, and extend it to increased habitat availability for waterbirds such as yellow and king rails (Wilcox and Xie 2007). Since similar processes likely occur in most large lakes, natural water level fluctuations are probably critical for wetlands in many of the world's large lakes, providing a powerful tool for restoring wetlands and maintaining biological diversity (Keddy and Fraser 2000).

2.6.3 A summary model: frequency and intensity of flooding

We have seen that two of the most important components of flooding are frequency and amplitude (intensity). These could be assigned to orthogonal axes and the space would represent all possible pair-wise flood combinations. Imagine then plotting biological properties such as plant diversity or numbers of rare species. We could use data from the many reservoirs or wetlands of the world in order to explore patterns. Unfortunately, the required data are scattered through an enormous number of studies that describe individual cases. As a first step in this direction, Figure 2.29 shows a plot for a few lakes, and identifies a probable region of high plant species richness. This is based upon a set of lakes in eastern North America, and there is currently no way to know how well we can extrapolate beyond this geographic region or to other properties. This chapter thus ends with a lament. Here we have possibly the two most important environmental factors influencing wetlands, yet we lack the data to predict the changes in wetlands along these axes. We have our work cut out for us.

CONCLUSION

Fluctuations in water level (e.g. spring flood pulses) are essential for maintaining the diversity and abundance of wildlife species in wetlands. We have seen examples including wading birds, frogs, fish, and rare plants. Species composition and functions of wetlands are determined largely by the frequency and amplitude of flooding. This variation in water level occurs not just within a year but also from year to year. Swamps, wet meadows, marshes, and aquatic ecosystems represent a sequence of vegetation types associated with increasing duration of flooding – four regions in a continuum of communities that are ever-changing, short-lived responses to water levels. Under natural conditions, large water level fluctuations are typical of rivers, the Amazon having an annual fluctuation of 10 m. Among lakes, yearly fluctuations of a few meters generally occur. Plant species richness in lakes is greatest when water level fluctuations are intermediate in magnitude. Low-water periods are important for species that persist as seeds buried in the sediment. High-water periods drown woody vegetation and allow marsh and wet meadow expansion. In peatlands, by contrast, water levels must be relatively stable in order for peat to accumulate.

Stabilization of water levels for uses such as recreation, power generation, transportation, or flood control results in reduced wetland area and lower species diversity. Maintaining natural hydrology is an essential part of wetland conservation and management. Yet dams continue to proliferate, with major new projects in areas including the Amazon River in South America, the Yangtze River in Asia, the Congo River in Africa, and the Tigris and Euphrates Rivers in the Middle East. Although our knowledge about the importance of flood pulses is growing, it seems that wise application of this knowledge is required.