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1 Wetlands: an overview

All life contains water. From distant space, Earth appears as a mosaic of blue and green, blue for water, green for plants. This book is about the ecological communities that occur where green meets blue: wetlands. Wetlands are intimately associated with water. They are one of the most productive habitats on Earth, and they support many kinds of life. This book explores the general principles that control the distribution and composition of wetlands around the world. The cover (Figure 1.1, artwork by Howard Coneybeare) illustrates a typical temperate zone wetland. Common wetland plants shown include floating-leaved water lilies (*Nymphaea odorata*), emergent pickerelweed (*Pontederia cordata*), and shoreline reed canary grass (*Phalaris arundinacea*). The food web is largely composed of invertebrates that feed upon decaying plants. Near the top of the food web are vertebrates such as fish (yellow perch), reptiles (snapping turtle), and birds (great egret). The surrounding forests interact with the wetland. Amphibians, such as tree frogs, over-winter in the forest, while nutrients and runoff from the forest enter the wetland.

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Wetlands have always influenced humans. Early civilizations first arose along the edges of rivers in the fertile soils of floodplains. Wetlands continue to produce many benefits for humans – along with fertile soils for agriculture, they provide food such as fish and waterbirds. Additionally, wetlands have other vital roles that are less obvious – they produce oxygen, store carbon, and process nitrogen. Of course, wetlands have also been a cause of human suffering, such as providing habitat for mosquitoes that carry malaria. And, for thousands of years, human cities in low areas have flooded during periods of high water. Philosophers and theologians may enquire how it is that one system can be both life-giving and death-dealing. Our more confined task as scientists is

- to explore the basic patterns that occur in wetlands,
- to uncover the causes of these patterns, and
- to guide society in wise coexistence with wetlands.

I intend to take you through these three steps in this book. Along the way, we will encounter not only hard science, but some entertaining natural history – fish that breathe air, mosses that drown trees, plants that eat insects, and frogs that climb trees. We shall also meet the world's largest wetlands, wetlands that perch on hillsides, wetlands that burn, and of course, wetlands that flood.

1.1 Definitions and distribution

Wetlands form at the interface of terrestrial and aquatic ecosystems and have features of both. While they may be highly variable in appearance and species composition, inundation by water is a shared characteristic that is, in turn, reflected in soil processes and adaptations of the biota. Thus wetlands are found where there is water, from saline coastal areas to continental interiors, but most are associated with fresh water.

FIGURE 1.1

1.1.1 Definition of wetlands

A wetland is an ecosystem that arises when inundation by water produces soils dominated by anaerobic processes, which, in turn, forces the biota, particularly rooted plants, to adapt to flooding.

This broad definition includes everything from tropical mangrove swamps to subarctic peatlands. This single sentence of definition has a complex structure: there is a cause (inundation by water), a proximate effect (reduction of oxygen levels in the soil), and a secondary effect (the biota must tolerate both the direct effects of flooding and the secondary effects of anaerobic conditions). It is not the only definition, and maybe not even the best, but it shall get us started. Since many biologists and lawyers or agencies and organizations have

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attempted to define wetlands, we shall start with this simple idea. We shall explore other definitions in Section 1.8.1.

Since wetlands require water, the obvious place to begin is the distribution of water on Earth. Table 1.1 shows that a majority of the Earth's available water is in the oceans. A much smaller amount is present as fresh water. Heat from the sun drives a distillery, removing water vapor from the oceans and returning it to the land as precipitation. Some wetlands form along the edges of oceans; these tend to be mangrove swamps in equatorial regions and salt marshes at higher latitudes. A majority of wetlands are, however, freshwater ecosystems. They occur where rainwater accumulates on its way back to the ocean. Some people regard the distinction between freshwater and saltwater wetlands as critical, and you will often run into many documents that refer to "interior wetlands" and "coastal wetlands." Certainly salinity is very important in determining which kinds of plants and animals occur, but in this book we shall do our best to think about wetlands as one group of ecosystems.

Since life began in the oceans, most life, including freshwater life, has a chemical composition more like the ocean than fresh water (Table 1.2). Yet it appears that most life found in fresh water today did not originate in fresh water, but first adapted to land, and then adapted to fresh water. Fish, were, of course, an exception. The bodily fluids of freshwater aquatic animals still show a strong similarity to oceans. Indeed, many studies

Table 1.1 **Mass of water in different forms on Earth**

Form	Mass ($\times 10^{17}$ kg)
Chemically bound in rocks[a]	
Crystalline rocks	250 000
Sedimentary rocks	2100
Free water[b]	
Oceans	13 200
Ice caps and glaciers	292
Ground water to a depth of 4000 m	83.5
Freshwater lakes	1.25
Saline lakes and inland seas	1.04
Soil moisture	0.67
Atmospheric water vapor	0.13
Rivers	0.013

[a] Does not cycle.
[b] Part of hydrological cycle.
Source: From Clapham (1973).

Table 1.2 **Concentrations of some common ions in animals, sea water, and fresh water (concentrations are given as mM/kg water)**

Ions	Standard sea water	Fresh water (soft)	Fresh water (hard)	Crab (*Maia*) blood	Frog (*Rana esculenta*) blood	Crayfish (*Astacus fluviatilis*) blood (mM/l blood)	Rat (*Rattus rattus*) blood
Na^+	478.3	0.24	2.22	487.90	109	212	140
K^+	10.13	0.005	1.46	11.32	2.6	4.1	6.4
Ca^{2+}	10.48	0.067	3.98	13.61	2.1	15.8	3.4
Mg^{2+}	54.5	0.043	1.67	44.14	1.3	1.5	1.6
Cl^-	558.4	0.226	2.54	552.4	78	199	119
SO_4^{2-}	28.77	0.045	3.95	14.38	–	–	–
HCO_3^{2-}	–	–	2.02	–	26.6	15	24.3

Source: Modified from Wilson (1972).

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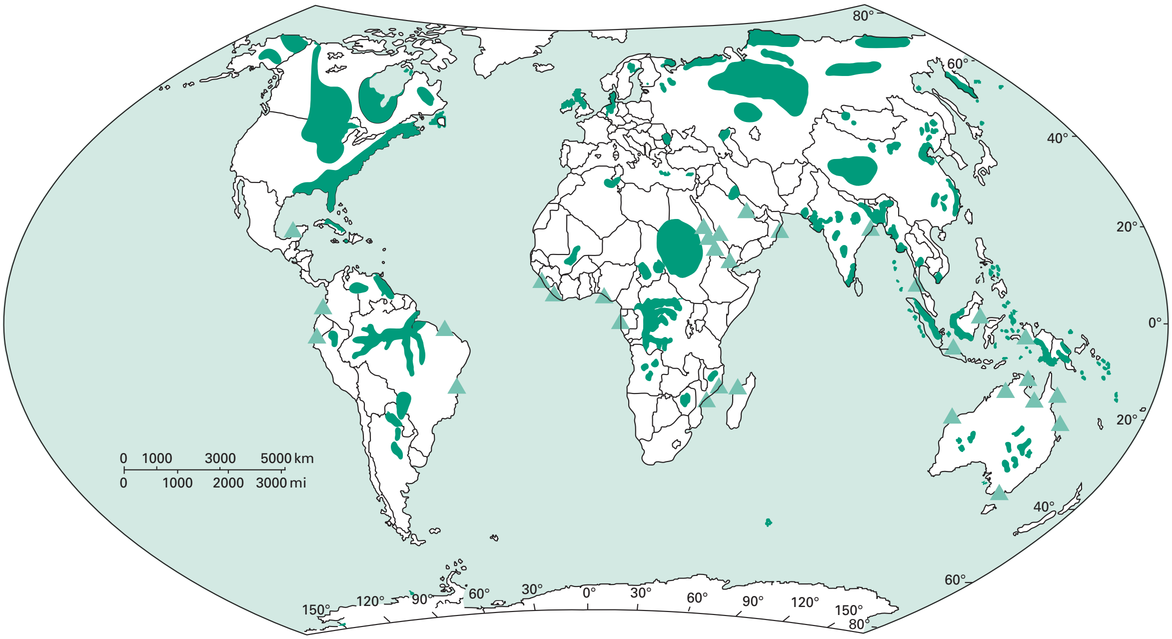

FIGURE 1.2 The major wetland areas on Earth. Mangrove swamps are shown as triangles. (Compiled from Dugan 1993 and Groombridge 1992.)

of ion balance in freshwater organisms show that fish, amphibians, and invertebrates attempt to maintain an inner ocean in spite of surrounding fresh water. They also show that, as with plants, access to oxygen becomes limiting once a site is flooded.

Wetlands have soil, so they are not truly aquatic like planktonic and pelagic communities. But they have standing water, so neither are they truly terrestrial. As a consequence, they are often overlooked. Terrestrial ecologists often assume they will be studied by limnologists, while limnologists may assume the reverse. We will therefore feel free to borrow from both terrestrial ecologists and limnologists in studying wetlands.

1.1.2 Distributions

Figure 1.2 presents an approximate distribution of global wetlands. Such a map has many limitations. It is difficult to map wetlands at the global scale for at least three reasons. Firstly, wetlands are frequently a relatively small proportion of the landscape. Secondly, they are distributed in small patches or strips throughout biomes, and therefore cannot be mapped at a scale suitable for reproducing in a textbook. Thirdly, they are very variable, and one biome can therefore contain a wide array of wetland types. Table 1.3 lists the largest wetland areas in the world. These set an important priority list for research and conservation.

1.2 Wetland classification

Now that we have a definition, and some idea of where wetlands occur, the next step is to sort them into similar types. Each type can be visualized as a particular set of plant and animal associations that recur. This recurrence probably means that the same causal factors are at work. Unfortunately, the

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Table 1.3 **The world's largest wetlands (areas rounded to the nearest 1000 km^2)**

Rank	Continent	Wetland	Description	Area (km^2)
1	Eurasia	West Siberian Lowland	Bogs, mires, fens	2 745 000
2	South America	Amazon River basin	Floodplain forest and savanna, marshes, mangal	1 738 000
3	North America	Hudson Bay Lowland	Bogs, fens, swamps, marshes	374 000
4	Africa	Congo River basin	Swamps, riverine forest, wet prairie	189 000
5	North America	Mackenzie River basin	Bogs, fens, swamps, marshes	166 000
6	South America	Pantanal	Savannas, grasslands, riverine forest	138 000
7	North America	Mississippi River basin	Bottomland hardwood forest, swamps, marshes	108 000
8	Africa	Lake Chad basin	Grass and shrub savanna, marshes	106 000
9	Africa	River Nile basin	Swamps, marshes	92 000
10	North America	Prairie potholes	Marshes, meadows	63 000
11	South America	Magellanic moorland	Bogs	44 000

Source: From Fraser and Keddy (2005).

terminology for describing wetlands varies both among human societies, and among their scientific communities. Thus one finds an abundance of words used to describe wetlands – bog, bayou, carr, fen, flark, hochmoore, lagg, marsh, mire, muskeg, swamp, pocosin, pothole, quagmire, savanna, slob, slough, swale, turlough, yazoo – in the English language alone. Many of these words can be traced back centuries to Old Norse, Old Teutonic, or Gaelic origins (Gorham 1953). Now add in other world languages, and the problem is compounded.

Given the global distribution, it is not surprising to find that abundant wetland classification schemes have been developed. They vary, for example, by geographic region, the intended use of the classification results, and the scale at which classification is undertaken. We will start with a simple classification system that distinguishes six wetland types largely on the basis of location and hydrology. After learning more about the environmental factors that control the development of wetlands and their communities, we will return to wetland definition and classification (Section 1.8).

1.2.1 The six basic types

To keep the terminology simple, we will begin with four types of wetland, and then add two to extend the list to six. One of the simplest classification systems recognizes only four types: swamps, marshes, fens, and bogs.

Swamp

A wetland that is dominated by trees that are rooted in hydric soils, but not in peat. Examples would include the tropical mangrove swamps (mangal) of Bangladesh and bottomland forests in floodplains of the Mississippi River valley in the United States (Figure 1.3).

Marsh

A wetland that is dominated by herbaceous plants that are usually emergent through water and rooted in hydric soils, but not in peat. Examples would include cattail (*Typha angustifolia*) marshes around the Great Lakes and reed (*Phragmites australis*) beds around the Baltic Sea (Figure 1.4).

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FIGURE 1.3 Swamps. (*a*) Floodplain swamp (Ottawa River, Canada). (*b*) Mangrove swamp (Caroni wetland, Trinidad). (See also color plate.)

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(*a*)

(*b*)

FIGURE 1.4 Marshes. (*a*) Riverine marsh (Ottawa River, Canada; courtesy B. Shipley). (*b*) Salt marsh (Petpeswick Inlet, Canada). (See also color plate.)

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Bog

A wetland dominated by *Sphagnum* moss, sedges, ericaceous shrubs, or evergreen trees rooted in deep peat with a pH less than 5. Examples would include the blanket bogs which carpet mountainsides in northern Europe, and the vast peatland of the West Siberian Lowland in central Russia (Figure 1.5).

Fen

A wetland that is usually dominated by sedges and grasses rooted in shallow peat, often with considerable groundwater movement, and with pH greater than 6. Many occur on calcareous rocks, and most have brown mosses, in genera including *Scorpidium* or *Drepanocladus*. Examples can be found within the extensive peatlands of northern Canada and Russia, as well as in smaller seepage areas throughout the temperate zone (Figure 1.6).

Other wetland types could be added to these four. Two important ones are the following.

Wet meadow

A wetland dominated by herbaceous plants rooted in occasionally flooded soils. Temporary flooding excludes terrestrial plants and swamp plants, but drier growing seasons then produce plant communities typical of moist soils. Examples would include wet prairies along river floodplains, or herbaceous meadows on the shorelines of large lakes. These wetlands are produced by periodic flooding and may be overlooked if visited during a dry period (Figure 1.7).

Shallow water

A wetland community dominated by truly aquatic plants growing in and covered by at least 25 cm of water. Examples include the littoral zones of lakes, bays in rivers, and the more permanently flooded areas of prairie potholes (Figure 1.8).

Any attempt to sort the diversity of nature into only six categories will have its limitations. The Everglades, for example, have a peat substrate, moving water, and many reeds. So is it a fen or a marsh or wet prairie, a mixture of several of these, or something completely unique? Rather than worry further about this, we should probably admit that wetlands show great variation, and agree to not get stalled or diverted by debates over terminology. As Cowardin and Golet (1995) observe "no single system can accurately portray the diversity of wetland conditions world-wide. Some important ecological information inevitably will be lost through classification."

1.2.2 Some other classification systems

The system I present above has the advantage of simplicity and generality. You should be aware that there are more elaborate systems, and that these vary around the world. Each wetland classification system tries to summarize the major types of wetland vegetation, and then relate them to environmental conditions. Here are a few examples. We shall add several more near the end of the chapter.

A global summary

Figure 1.9 provides a summary that ties different classification systems into a unified whole. It begins with "water regime," from permanently waterlogged on the left to permanent shallow water on the right. Combining these three hydrological regimes with "nutrient supply," one obtains peatlands on the left, swamps in the middle, and lakes on the right. Further, the scheme then goes on to address the main plant forms that will occur. (One other system has been presented by Gopal *et al.* [1990] to summarize world wetland types. It again has two principal axes, hydrology and fertility, but it will be introduced at the end of Chapter 3 after these two factors have been explored in more depth.)

Hydrogeomorphic classifications

The location or setting of a wetland often has important consequences for duration of flooding and water quality. Hence, there are classification systems that emphasize the landscape setting of the wetland, such as the widely used Cowardin classification system (Table 1.4). Setting may be particularly

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(*a*)

(*b*)

FIGURE 1.5 Bogs. (*a*) Lowland continental bog (Algonquin Park, Canada). (*b*) Upland coastal bog (Cape Breton Island, Canada). (See also color plate.)

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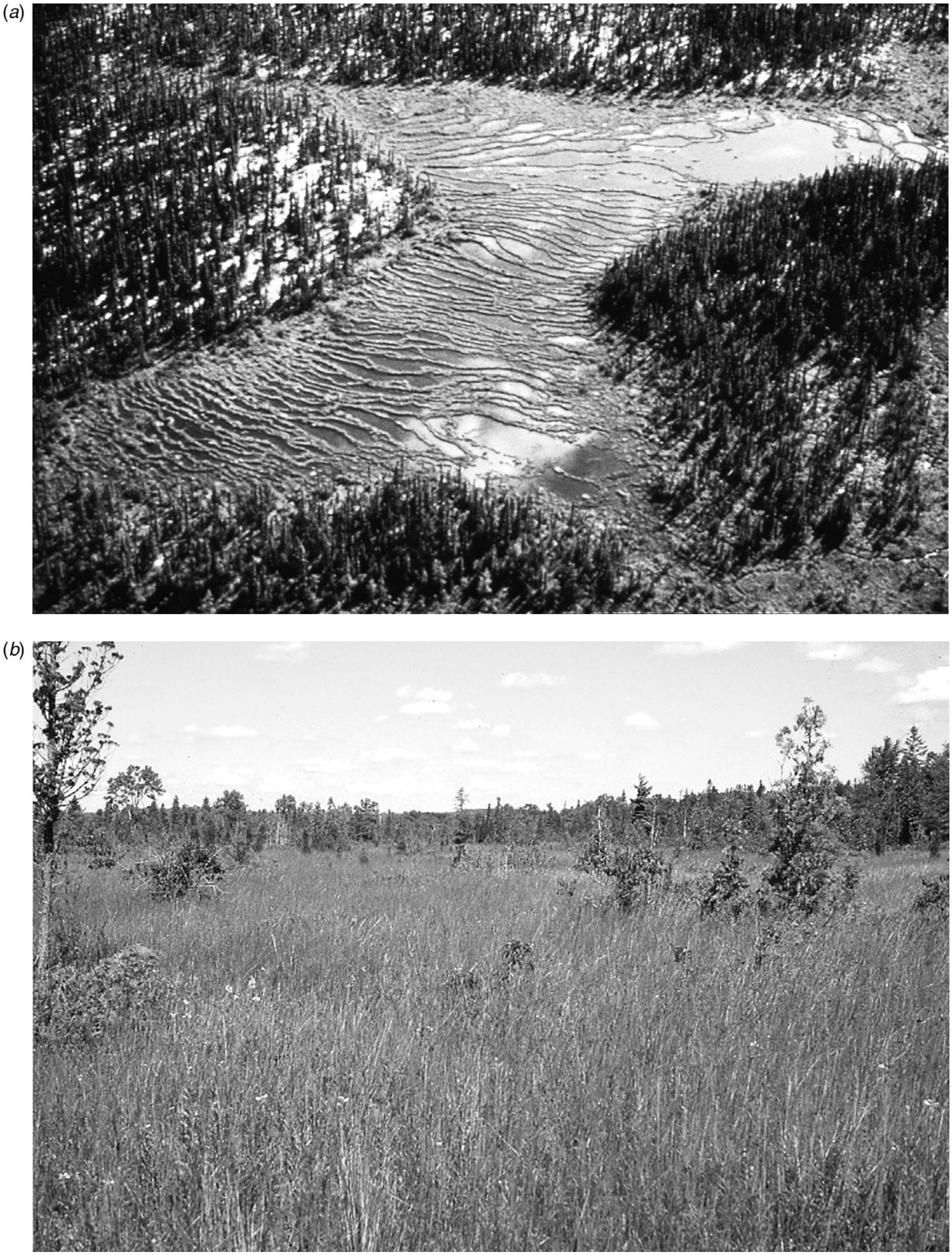

FIGURE 1.6 Fens. (*a*) Patterned fen (northern Canada; courtesy C. Rubec). (*b*) Shoreline fen (Lake Ontario, Canada). (See also color plate.)

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(a)

(b)

FIGURE 1.7 Wet meadows. (*a*) Sand spit (Long Point, Lake Ontario, Canada; courtesy A. Reznicek). (*b*) Gravel lakeshore (Tusket River, Canada; courtesy A. Payne). (See also color plate.)

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(a)

(b)

FIGURE 1.8 Shallow water. (*a*) Bay (Lake Erie, Canada; courtesy A. Reznicek). (*b*) Pond (interdunal pools on Sable Island, Canada). (See also color plate.)

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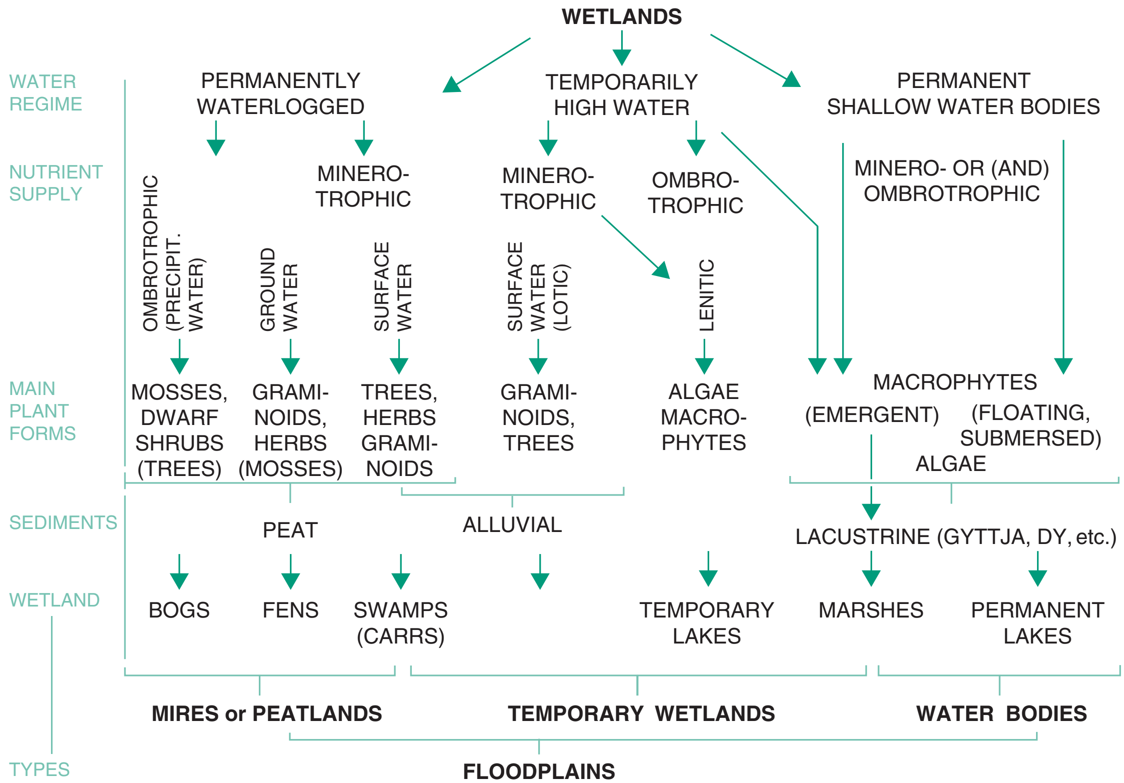

FIGURE 1.9 The principal kinds of wetlands can be related to two sets of environmental factors: water regime and nutrient supply (upper left). The term "water regime" refers to hydrological factors including depth and duration of flooding, while "nutrient supply" refers to chemical factors including available nitrogen, phosphorus, and calcium. (From Gopal *et al.* 1990.)

important for fens, since it affects so many aspects of hydrology and chemistry (Godwin *et al.* 2002). Many countries and regions have developed their own classification systems and procedures (e.g. Russia: Botch and Masing 1983; Zhulidov *et al.* 1997; China: Hou 1983; Lu 1995; Canada: Committee on Ecological Land Classification 1988).

A hydrological perspective

There are three main sources of water for wetlands – precipitation, groundwater, and water moving across the surface (Figure 1.10). Raised bogs are almost completely dependent upon the first, whereas floodplains are largely dependent upon the third. In practice, nutrient levels are often closely correlated with hydrology, since rainfall tends to be low in nutrients, whereas water that flows across the surface or through the ground picks up dissolved nutrients and particulate matter. Wetlands can therefore be classified according to the relative proportions of these three water sources.

1.2.3 Combining classification systems

It is sometimes difficult to fit different classification systems together. Overall, you will likely need to use several classification systems at the same time. There may be international, national, state, and even local systems. Many of you will also inherit a situation in which you have multiple sets of information available, both in reports and on line. Let us walk through how the above information on

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Table 1.4 **Cowardin classification of wetlands and deepwater habitats**

System	Subsystem	Class
Marine	Subtidal	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Reef
	Intertidal	Aquatic Bed
		Reef
		Rocky Shore
		Unconsolidated Shore
Estuarine	Subtidal	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Reef
	Intertidal	Aquatic Bed
		Reef
		Streambed
		Rocky Shore
		Unconsolidated Shore
		Emergent Wetland
		Scrub–Shrub Wetland
		Forested Wetland
Riverine	Tidal	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Rocky Shore
		Unconsolidated Shore
		Emergent Wetland
	Lower Perennial	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Rocky Shore
		Unconsolidated Shore
		Emergent Wetland
	Upper Perennial	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Rocky Shore
		Unconsolidated Shore
	Intermittent	Streambed
Lacustrine	Limnetic	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
	Littoral	Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Rocky Shore
		Unconsolidated Shore
		Emergent Wetland
Palustrine		Rock Bottom
		Unconsolidated Bottom
		Aquatic Bed
		Unconsolidated Shore
		Moss–Lichen Wetland
		Emergent Wetland
		Scrub–Shrub Wetland
		Forested Wetland

Source: From Cowardin *et al.* (1979).

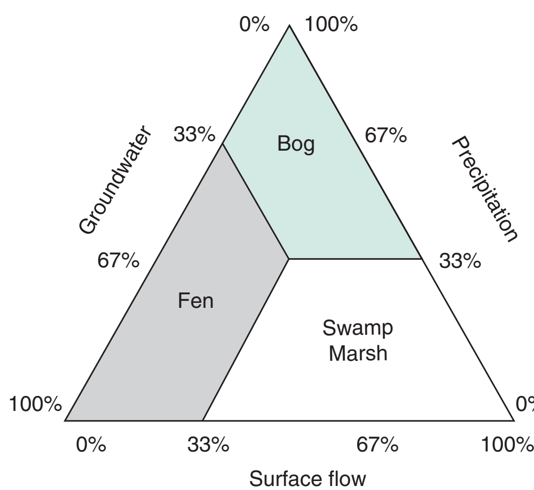

FIGURE 1.10 The principal kinds of wetlands can be related to water source: groundwater, precipitation, and surface flow. The relative importance of these sources varies among types of wetlands. (Modified from Brinson 1993a, b.)

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classification might allow you to sort the work into useful categories.

- First, there is the identification of a site as wetland, and identification of its spatial boundaries. In the United States this is part of a formal process called "wetland delineation." Many parts of the world have similar procedures that result in maps of wetlands.
- Each wetland can be assigned to one the six basic types, or, perhaps, a combination of them.
- A hydrogeomorphic system puts the wetland into a landscape setting category.
- Depending upon where you work, there are likely to be one or more national or regional systems to apply, quite possibly using languages other than English. You may find yourself in a turlough, *várzea*, *igapó*, *corixos*, or Scirpo-Phragmitetum.
- There are likely to be particular species of interest, depending upon the agency employing you, and upon the type of project in which you are involved. This might be species that are uncommon in your region, indicator species, or species that are threatened at the global scale.

It is not, then, that one system is right and the other is wrong. Each provides useful information for certain purposes. To decide which is best for a particular project requires you to know the purpose of your work, including your audience, and the geographical and political region in which you will be working.

1.2.4 Plants, stress, and wetland types

In spite of all the variation in wetlands, there are still only a small number of causal factors. By looking at simple causes, we can reduce the difficulty of understanding the variation in types of wetlands. Figures 1.9 and 1.10 showed two ways of describing

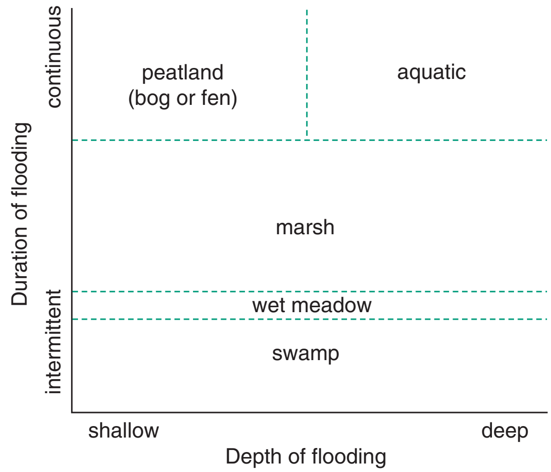

FIGURE 1.11 The principal kinds of wetlands can be related to duration and depth of flooding. These two axes are important because they give rise to the secondary constraints described in Table 1.6. (Modified from Brinson 1993a, b.)

these causes. Let us look at one more, which leads naturally to the idea of primary and secondary constraints. If we set aside other factors such as water chemistry or location, we can use just flood duration and depth as key factors (Figure 1.11). Even these two factors alone will produce five main wetland types. Fen and bog appear as peatland in the upper left, aquatic appears at the upper right, and marsh and swamp appear as broad zones across the bottom. Wet meadows may squeeze in between marsh and swamp depending upon the nature of water level changes.

This lays out the logic for the next few sections. First we will look at the main factor that causes a wetland: flooding. We will briefly examine effects of flooding on soils, plants, and animals. We will then look at some additional, or secondary, effects of flooding, and explore how these produce the different types of wetlands shown in Figures 1.3–1.8.

1.3 Wetland soils

Most soil types arise from chemical and microbial processes that occur in the presence of oxygen. Wetlands are the exception – most lack oxygen – and therefore they have distinctive hydric soils. In this

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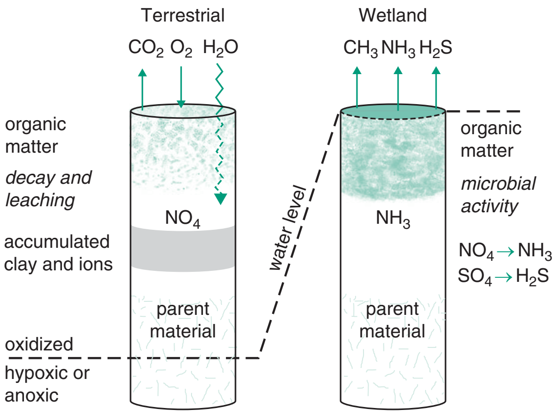

FIGURE 1.12 A typical terrestrial soil profile compared to a typical wetland soil profile. The principal differences arise largely out of the presence or absence of oxygen. Overall, wetland soils tend to store more organic matter, experience less leaching, and contain microorganisms that emit gases such as CH_3 (methane), NH_3 (ammonia), and H_2S (hydrogen sulfide).

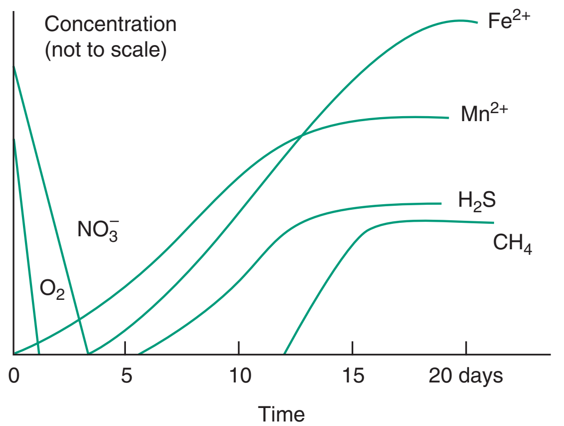

FIGURE 1.13 The chemistry of a soil changes rapidly within days of being flooded. (From Brinkman and Van Diepen 1990 after Patrick and Reddy 1978.)

section, we will discuss the effects of flooding on soil chemistry and the importance of wetland soils in global biogeochemical cycles.

1.3.1 Wetlands have reduced rather than oxidized soils

The general differences between terrestrial and wetland soils are shown in Figure 1.12. Oxidized soils have small amounts of organic matter near the surface, and major ions have been transported deeper into the soil column by leaching. Reduced soils in wetlands have larger amounts of organic matter, and instead of leaching, there is chemical transformation toward reduced elements. The presence of a distinctive soil type is therefore one defining characteristic of wetlands.

Since oxygen is so widely distributed in the atmosphere, wetlands provide one of the few places on Earth for microbial interactions that occur in reduced rather than oxidized conditions. Wetlands are therefore globally important for the chemical transformation of elements in the world's biogeochemical cycles.

One cause of low oxygen (O_2) levels is the low rate of diffusion of oxygen in water, and hence in flooded soils. Oxygen and other gases diffuse about 10^3–10^4 times more rapidly in air than in water. Oxygen is soon depleted from flooded soils by the respiration of soil microorganisms and plant roots. The deficiency of oxygen is termed **hypoxia**, the absence of oxygen is termed **anoxia**. In the absence of oxygen, oxidation of organic matter ceases, and populations of microorganisms begin to change the ionic composition of the rooting zone (Ponnamperuma 1972, 1984; Faulkner and Richardson 1989; Marschner 1995).

1.3.2 The degree of reduction changes with time and depth

The effects of flooding on soil chemistry occur rapidly (Figure 1.13). Not only do O_2 and nitrate (NO_3^-) disappear in only a few days, gases such as methane (CH_4), hydrogen sulfide (H_2S) and ammonia (NH_3) begin to accumulate. As well, ions such as Fe_2^{2+} appear. Hence organisms living in wetland soils have at least three metabolic problems to contend with: not only is there a shortage of oxygen, but there are atypical concentrations of ions, and there are toxic gases.

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The significance of these conditions requires a brief digression. Oxidized conditions are a consequence of life, and more precisely, of photosynthesis. The early atmosphere was anoxic (Day 1984; Levin 1992). The gradual accumulation of oxygen has been termed the "oxygen revolution." I have recently summarized the story of oxygen accumulation in another textbook (Keddy 2007, ch. 1). The main point here is that the hypoxic/anoxic conditions found in wetland soils represent a type of chemistry that was once common on earth. It is now mostly restricted to flooded sites.

The degree of hypoxia not only changes with time, but with depth. In many wetlands, one can identify three regions: standing water with dissolved oxygen, an upper oxidized layer of soil, and a deeper reduced layer of soil. As molecules are transformed in one layer, diffusion gradients arise to transport them to adjoining layers.

1.3.3 The processing of carbon, nitrogen, phosphorus, and sulfur

The chemical states of carbon, nitrogen, phosphorus, sulfur, iron, and other elements are affected by the state of oxidation in soils. Flooded soils are therefore critical in global biogeochemical cycles. Let us briefly consider changes in effects of flooding on four major elements: C, N, P, and S.

Carbon

Carbon arrives as organic matter, either from uplands, or from plants growing in the wetland. If oxygen is available, the organic matter is decomposed to carbon dioxide (CO_2), whereas if oxygen is scarce, it may be decomposed to methane (CH_4). This methane can diffuse into the atmosphere, where it becomes a powerful greenhouse gas. Some microorganisms, including Archea, intercept and consume methane. The organic matter that does not decay becomes stored in the soil in various forms including peat.

Nitrogen

Nitrogen arrives in wetlands in organic matter or in runoff as nitrate, NO_3^-. When the organic matter partially decays in the absence of oxygen, ammonia (NH_4) is produced, a process called ammonification. If oxygen is available (usually near the soil surface), this NH_4 is oxidized to NO_3^- by chemoautotrophic bacteria. This result is often a concentration gradient with nitrogen as NH_4 diffusing upward from deeper anoxic regions, while nitrogen in the form of NO_3^- diffuses downward. Other complex microbial transformations are superimposed. Most terrestrial ecosystems are sources of organic nitrogen and nitrate, whereas most wetlands are sinks, that is areas where nitrogen and other elements accumulate. Figure 1.14 shows the basic stages and locations

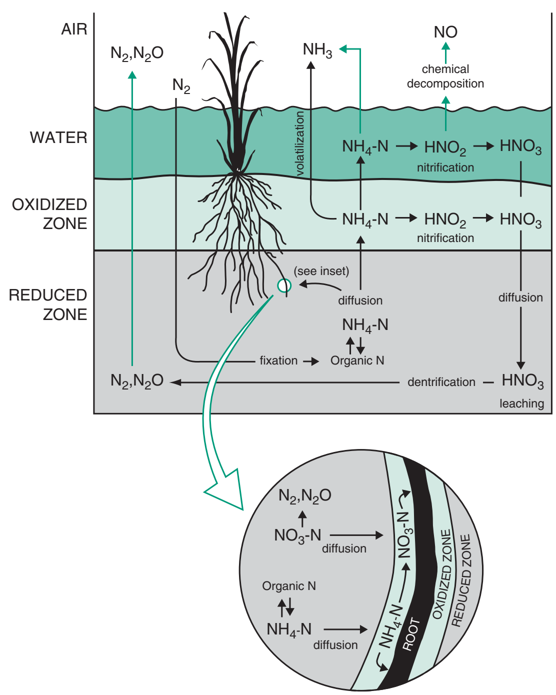

FIGURE 1.14 The transformation in the chemical state of nitrogen is driven by gradients of oxygen availability. These oxidation/reduction gradients occur at two scales. At the larger scale, oxidation decreases with water depth. At the small scale (inset) oxidation decreases with the distance from plant roots. (Illustration by B. Brigham.)

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of nitrogen transformation, a topic to which we will return in the section on wetland services (Section 1.6).

Phosphorus

Nearly all of the phosphorus arrives in sediment and plant litter. Unlike nitrogen, there is no gaseous phase, and no valency changes occur during microbial processing. Wetlands again appear to act as sinks for phosphorus eroded from surrounding terrestrial ecosystems.

Sulfur

The sulfur cycle is more similar to the nitrogen cycle with multiple transformations by microorganisms. Sulfur arrives as organic debris, or in rainfall. If oxygen is available, the decomposition of organic matter can yield SO_4^{2-}. In the absence of oxygen, the product is H_2S. A concentration gradient can therefore arise, with the SO_4^{2-} diffusing downward to be transformed to H_2S by anaerobic bacteria, while H_2S diffuses upward to be oxidized. The H_2S can also diffuse into the atmosphere or react with organic matter. The diffusion of H_2S into the atmosphere explains the rotten egg smell sometimes noticed in wetlands. Most terrestrial ecosystems are sulfur sources, most wetlands appear to be sulfur sinks.

The above information illustrates how wetlands are important in maintaining the quality of flowing water. Some of the nutrients that arrive in wetlands remain stored in organic matter or sediment. Others are transformed to gases – in the case of nitrogen, to N_2, and in the case of sulfur, to H_2S. Artificially constructed wetlands are therefore sometimes used to treat nutrient-laden waters produced by human activities (Hammer 1989; Knight and Kadlec 2004). More background on the chemistry of flooded soils can be found in sources such Good *et al.* (1978), Ponnamperuma (1972, 1984), Mitsch and Gosselink (1986), Faulkner and Richardson (1989), Gopal (1990), Armentano and Verhoeven (1990), and Marschner (1995).

Finally, other factors can complicate the above processes, particularly the biota themselves. Here are two examples. Vascular plants can transport oxygen downward in their stems (Section 1.6), sometimes in sufficient quantities to oxidize the soil around their roots (Figure 1.14). This can obviously change the depth at which the above chemical transformations occur. It can also lead to deposits of metals like iron oxide in the rooting zone. Cyanobacteria, which are photosynthetic, can also fix atmosphere nitrogen, converting N_2 to protein, and therefore increasing nitrogen levels in a wetland. This is an important input of nitrogen for rice paddies.

1.4 Flood tolerance: the primary constraint

The presence of hydric plants, like hydric soils, is another attribute used to define wetlands. These plants, adapted to low levels of oxygen in the soil, provide the habitat template for all the animals, so we must spend some time with the plants first in order to understand the animals later.

1.4.1 Aerenchyma allows plants to cope with hypoxic soils

Since the roots of actively growing plants require oxygen to respire, there has been strong selective pressure to address the problems posed by hypoxia. Many plants have spongy tissue to allow air to reach buried roots. Others have metabolic adaptations to allow at least temporary growth in the absence of oxygen. Added detail can be found in Sculthorpe (1967), Hutchinson (1975), Kozlowski (1984a), and Crawford and Braendle (1996).

The principal adaptation to hypoxia has been the evolution of air spaces or lacunae, which may extend from the leaf parenchyma through the petiole into the stem and into the buried rhizome or root. These spaces are formed either from splits between cells,

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or by the disintegration of cells. The continuity of the air spaces though the plant were, according to Hutchinson (1975), illustrated by Barthelemy in 1874, who found that, when a leaf was placed under reduced pressure, air could be drawn upward from the rhizome. The system of lacunae is frequently called, in spite of Hutchinson's objections, aerenchyma. The transport of oxygen through aerenchyma is sufficiently efficient that roots may be able to oxidize their surroundings (Hook 1984; Moorhead and Reddy 1988) and even provide oxygen for the respiration of roots by neighboring plants (Bertness and Ellison 1987; Bertness 1991; Callaway and King 1996). The lacunae also provide a route for methane produced in the soil to escape into the atmosphere; genera including *Scheuzeria*, *Carex*, *Peltandra*, and *Typha* are known to transport methane (Cicerone and Ormland 1988). The presence of aerenchyma is one of the most obvious characteristics of wetland plants, being particularly well developed in marsh and aquatic plants.

How does air move through aerenchyma? The simplest and most obvious mechanism is diffusion. In addition to the passive diffusion of oxygen, there can be bulk flow of air through aerenchyma if an internal pressure gradient exists. Such bulk flow (also called convective through flow [Armstrong *et al.* 1991] or pressurized ventilation [Grosse *et al.* 1991]), has now been reported in wetland plants including *Phragmites australis, Carex gracilis,* and *Egeria elegans* (Armstrong *et al.* 1991) as well as *Hydrocleys nymphoides, Nelumbo nucifera, Victoria amazonica,* and *Alnus glutinosa* (Grosse *et al.* 1991). Typically, it was first documented by a German botanist in the late 1800s (Pfeffer 1897 in Grosse *et al.* 1991), but then overlooked for decades. In water lilies pressurized gases in young leaves flow down through the petiole into the rhizome. The air then moves back up the old petioles and escapes through the pores in older leaves (Figure 1.15). As much as 22 litres of air a day can enter a single floating leaf and flow to the rhizome (Dacey 1980; Dacey in Salisbury and Ross 1988, pp. 68–70). Most trees do not show obvious morphological features to withstand flooding, but there is one conspicuous exception. Both major groups of woody plants, gymnosperms (e.g. *Taxodium*) and angiosperms (e.g. *Avicennia),* produce above-ground extensions of their roots called pneumatophores (Figure 1.16) that may allow roots direct access to atmospheric gases. The wind flowing across dead stems of some reeds also generates another type of transport called venturi flow (Armstrong *et al.* 1992), in which case it appears that the dead stalks continue to function in conduction of oxygen. This may explain why some species are so resistant to prolonged flooding, and why mowing before flooding increases their sensitivity.

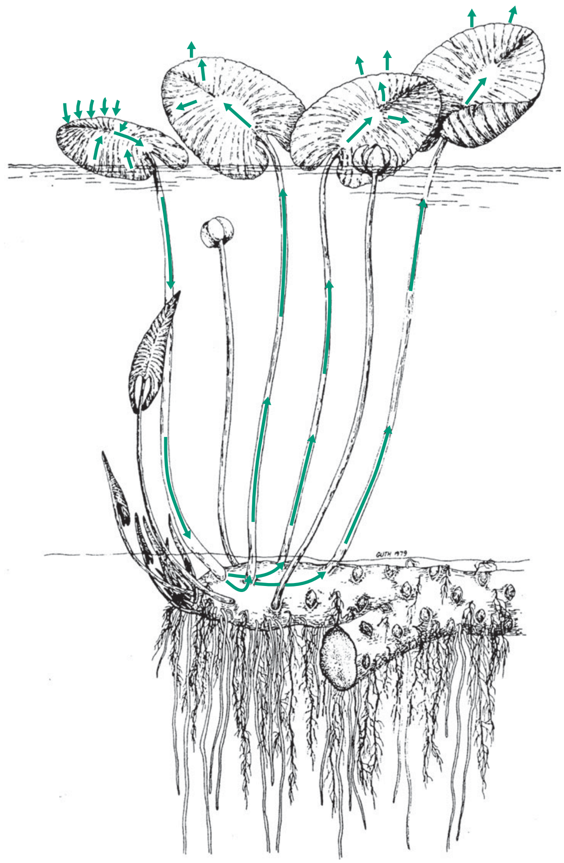

FIGURE 1.15 In water lilies, air enters through young leaves and exits through older leaves. Many other wetland plants have similar processes for transporting oxygen to rhizomes and roots. (From Dacey 1981.)

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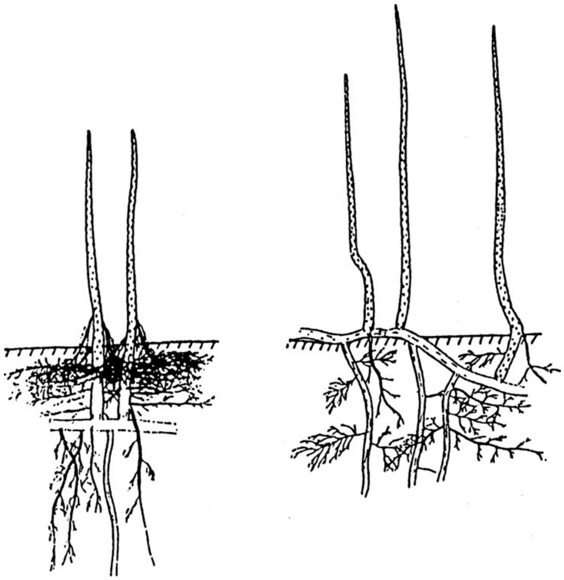

FIGURE 1.16 Pneumatophores, which grow vertically into the atmosphere from the roots of the mangrove, *Avicennia nitida,* may assist with aeration of those roots in flooded soils.

1.4.2 Metabolic adaptations in aquatic plants

In the absence of adaptations such as aerenchyma, wetland plants must cope using other means. They must deal simultaneously with the lack of oxygen and its many other consequences. Once flooded, the soil's oxygen is consumed, and toxic compounds such as ammonia, ethylene, hydrogen sulfide, acetone, and acetic acid are formed from the anaerobic decomposition of organic matter (Ponnamperuma 1984). From the plants' perspective, this "usually sets in motion a sequential and complicated series of metabolic disturbances" (Kozlowski and Pallardy 1984).

The first problem is survival. The second problem is to maintain growth in these unfavorable circumstances. One physiological mechanism may involve the capacity to avoid production of potentially toxic ethanol at the end of the glycolytic pathway. It has long been known, says Hutchinson (1975), that some water plants contain ethanol, and that rhizomes of water plants such as *Nymphaea tuberosa, Sagittaria latifolia*, and *Typha latifolia* can live anaerobically for long periods of time. This remarkable tolerance of rhizomes to anaerobic conditions was demonstrated by Laing (1940, 1941) who grew rhizomes from genera including *Acorus*, *Nuphar, Peltandra*, and *Scirpus* in water through which nitrogen was bubbled. The rhizomes were able to respire anaerobically, producing ethanol in 3% or less of oxygen. Both *Peltandra* and *Typha* showed long persistence even in pure nitrogen. More recent work has expanded the list of species with growth apparently unimpeded by lack of oxygen (Spencer and Ksander 1997). Sulfides are also associated with anoxia, and it is possible that sulfides themselves could be having direct toxic effects upon roots, or interfering with the uptake of ammonium (Mendelssohn and McKee 1988).

1.4.3 Animals must also cope with hypoxia

In this chapter we are focusing upon plants, since they create the main wetland types and provide habitat for the wetland fauna. Yet note in passing that it is not only plants that are affected by hypoxia. Fish are too. When rivers flood, fish migrate into the floodplain to feed and reproduce; when the water recedes, fish can be trapped in shrinking pools. These pools quickly become hypoxic (Graham 1997; Matthews 1998). As they become warmer, oxygen levels fall. Algal mats begin to fill the water column; while providing some shelter for small fish, they increase hypoxia during hours of darkness. Oxygen levels become critical and direct mortality from hypoxia begins …

Some fish tolerate hypoxic conditions by gulping air. Air-breathing fish are thought to have evolved more than 400 million years ago, long before amphibians appeared (Graham 1997). There are 347 species in 49 families known to be air-breathing, and in nearly all, air-breathing is an adaptation to hypoxia. One well-known example is the lungfish (six species, including *Neoceratodus forsteri* in

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Australia). Other examples are the bichar (*Polypterus* spp. in Africa), the gar (*Lepisosteus* spp. in North and Central America), and the bowfin (*Amia calva*), all of which are predators in shallow warm waters.

In addition to breathing air, some can walk away from the shrinking pool. The walking catfish (ten genera and ca. 75 species including *Clarias* spp.) are native to Asia and Africa, where they normally inhabit warm hypoxic water. When stranded, they can move across land, partly by wriggling, partly aided by their pectoral fins. When the Asian species was accidentally introduced to Florida in the 1960s, it spread to 20 counties in just ten years (Robins n.d.).

An alternative to walking away from a drying pool is to bury in the mud and wait for the next flood. Lungfish, which occur in South America, Africa, and Australia, will construct mucus-lined burrows and breathe through their modifed swim bladder until the site is re-flooded (Graham 1997). Fossil burrows containing lungfish have been found as far back as the Permian era. Some types of walking catfish can also walk on land, while others are known to dredge pools to make the water deeper.

Other fish also make burrows. Here is an historical account (Neill 1950) regarding the bowfin:

An Estivating Bowfin

On one occasion I was hunting squirrels in the Savannah River swamp near McBean, Richmond County, Georgia. While sitting quietly on a log, I was suddenly surprised to hear a thumping noise apparently emanating from the ground almost at my feet. Locating the sound, I dug into the ground to disclose, at a depth of about 4 inches, a roughly spherical chamber approximately 8 inches in diameter. In this chamber was a living bowfin, *Amia calva*. The fish was writhing about the chamber; the striking of its head against the chamber walls produced the sounds that had first attracted my attention. The surface soil was a hard, dried mud, but the walls of the chamber were soft and moist; they had been almost polished by the writhing of the fish. The river was nearly a quarter-mile distant, but the presence of yellowish silt on the nearby tree boles attested to previous flooding.

The situation immediately calls to mind the estivation of certain tropical lung-fishes. I suspect that *A. calva*, a species remarkably tenacious of life, could survive in a moist mud-chamber for considerable periods of time. (**Wilfred T. Neill**, Research Division, Ross Allen's Reptile Institute, Silver Springs, Florida)

Let us consider one more fish example – the Amazon River, which has more kinds of fish than any other river in the world. In one small floodplain lake in the Amazon, Junk (1984) found 120 fish species, of which 40 were regularly found under pronounced hypoxic conditions. Of these, ten could gulp oxygen from the air, and ten could use the lower lip like a gill. The adaptations of the others were unknown. Other fish avoid hypoxic conditions by diurnal migration from macrophyte stands during the day to open water at night. There are many biochemical means for tolerating anoxic conditions, at least for short periods (Kramer *et al.* 1978; Junk 1984; Junk *et al.* 1997). In the Amazon, many other animals avoid hypoxia by migrating into the river itself during dry periods; these include manatees, turtles, and invertebrates. Other animals survive the dry period with resting-structures such as eggs or turions; these include clams, sponges, and cladocerans.

Hypoxia is equally important in controlling the distribution of amphibians and reptiles (Goin and Goin 1971). Amphibians can exchange gases with the environment by means of gills, lungs, mucosa of the throat, or the skin; the relative importance of these pathways varies with habitat and species. Reptiles have a skin that is relatively impermeable to water; while this has allowed them to colonize land and diversify in terrestrial environments, it has reduced respiration through the skin, placing greater emphasis upon lungs for oxygen uptake. Among the reptiles, turtles seem especially adapted to tolerate hypoxia, and many of the aquatic turtles (e.g. in the genera *Trionyx* and *Sternothaerus*) can gain sufficient oxygen by pumping water in and out

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of the throat to allow long periods of submersion so long as the animal is not physically active. Most snakes, lizards, and even crocodiles are far less tolerant of anoxia (Table 1.5).

The rich diversity of insect life in wetlands provides for a great array of adaptations to hypoxia. One generalization is certainly possible. Many of the insects in wetlands survive hypoxic conditions by finding some way to retain or obtain access to the atmosphere (Merritt and Cummins 1984). The commonest adaptation is to have a tube to provide access to the atmosphere, although this is useful only in shallow water. Some beetle larvae have extended terminal spiracles, respiratory siphons, that provide access to the atmosphere. Some predatory beetles have truly aquatic larvae that breathe using gills, but they still return to the land for the pupal stage. Mosquito larvae and pupae float near the surface and use respiratory siphons to reach the atmosphere. For access to deeper water, bubbles of atmosphere can be carried. Diving beetles carry a bubble of air under the wing covers. Some aquatic bugs carry a film of oxygen on their ventral surface where it adheres to a dense coating of hydrophobic hairs. A few species of Diptera are known to pierce aquatc plants and withdraw air from the plant's aerenchyma. Gills, of course, are also found in many aquatic invertebrates, particularly in groups like the dragonflies and caddis flies, but gills require dissolved oxygen in the water. Insects that carry a film of air or bubble may in fact also be extracting oxygen from the water, since oxygen may diffuse from water into the film or bubble.

Table 1.5 **Tolerance of anoxia in various families of reptiles**

Order and family	No. species tested	Mean survival time (minutes)
Testudinata		
Chelydridae	1	1050
Testudinidae	14	945
Pelomedusidae	2	980
Kinosternidae	5	876
Trionychidae	1	546
Chelidae	2	465
Cheloniidae	2	120
Squamata		
Lacertilia		
Iguanidae	6	57
Gekkonidae	1	31
Anguinidae	1	29
Scincidae	4	25
Teiidae	1	22
Serpentes		
Viperidae	3	95
Boidae	3	59
Elapidae	1	33
Colubridae	22	42
Crocodilia		
Crocodylidae	1	33

Source: Data from Belkin (1963).

Overall, however, the more hypoxic the water, the more likely that the invertebrates are using atmospheric oxygen.

1.5 Secondary constraints produce different types of wetlands

We have seen that the primary constraint caused by flooding is reduced availability of oxygen. Now let us consider some additional consequences of flooding.

1.5.1 Secondary constraints in peatlands

Some wetlands are flooded more or less permanently, but the water table is near the soil surface (Figure 1.11, upper left). Under these conditions decomposition is reduced but since there are no waves, flowing water, or tides to carry away debris, the organic matter accumulates. The setting of the wetland can control chemistry of the water. Of particular importance are elements that control the acidity of the water – such as calcium ions – and elements that control plant growth, such as nitrogen

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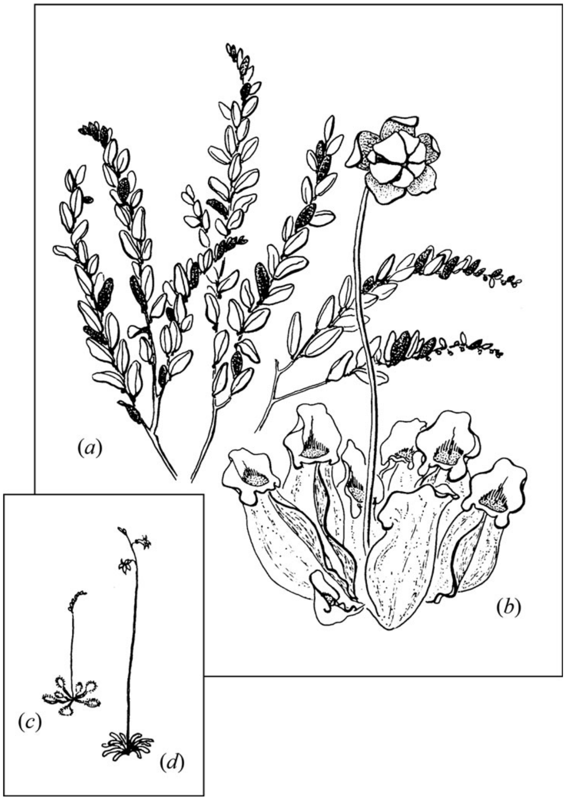

FIGURE 1.17 Peatlands are simultaneously wet and infertile and therefore the plants are often evergreen (e.g. *Chamaedaphne calyculata*, *a*). Others, like pitcher plants (*Sarracenia purpurea*, *b*), are carnivorous. Many other wetland and shoreline plants have the same adaptations, the sundew (*Drosera rotundifolia*, *c*) being carnivorous and water lobelia (*Lobelia dortmanna*, *d*) being evergreen.

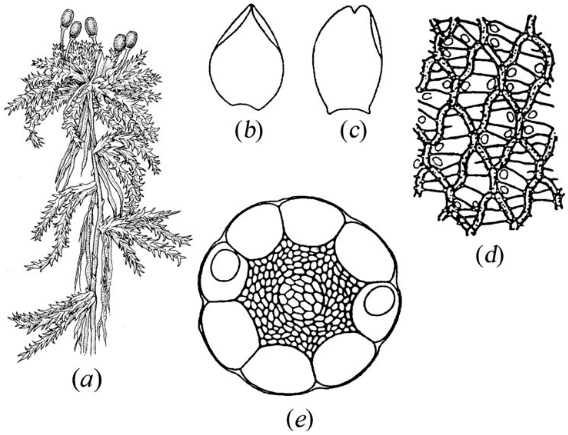

FIGURE 1.18 *Sphagnum* mosses often dominate peatlands. Their morphology and anatomy promote the storage of water and can raise the water table in these wetlands. Of particular significance are hyaline cells, which are dead at maturity and often have pores. (*a*) Shoot with attached sporophytes (*S. squarrosum*; from Kenrick and Crane 1997), (*b*) branch leaf, (*c*) stem leaf, (*d*) network of chlorophyllous cells in leaves surrounding the larger hyaline cells, (*e*) cross-section of stem showing hyaline cells in outer wall (*S. papillosum*; adapted from Scagel *et al.* 1996 and van Breeman 1995).

and phosphorus. If the organic matter accumulates to a depth of about 10 cm, roots can become isolated from the mineral soils beneath the peat, and therefore become increasingly dependent upon dilute nutrients deposited in rainwater (Gorham 1957; Godwin 1981; van Breeman 1995). Therefore, in peatlands, the chemistry of the water – particularly acidity and nutrient status – become two critical factors (e.g. Gore 1983; Glaser *et al.* 1990; Vitt and Chee 1990).

Let us concentrate on nutrient status here. Adaptation to infertile conditions requires a variety of unusual plant traits (Figure 1.17). An obvious one is leathery and evergreen (sclerophyllous) leaves – which is peculiar because these types of leaves are also found in desert plants. A deciduous plant must continually replace the nitrogen and phosphorus lost in falling leaves – so evergreen leaves are generally thought to be an adaptation to cope with low soil fertility (Grime 1977, 1979; Chapin 1980; Vitousek 1982). Hence, evergreen shrubs (often in the Ericaceae) and evergreen trees (many in the Pinaceae) often dominate peatlands (Richardson 1991). A further consequence of sclerophyllous leaves is the fuel they provide for fires (Christensen *et al.* 1981).

Peatlands also exhibit a distinctive abundance of bryophytes. In bogs, one genus, *Sphagnum* (Figure 1.18), tends to be dominant, while in fens brown mosses such as *Scorpidium* or *Drepanocladus* are common (Vitt 1990; Vitt *et al.* 1995; Wheeler and Proctor 2000). Carnivorous plants are also found in peatlands, since the invertebrates trapped by the

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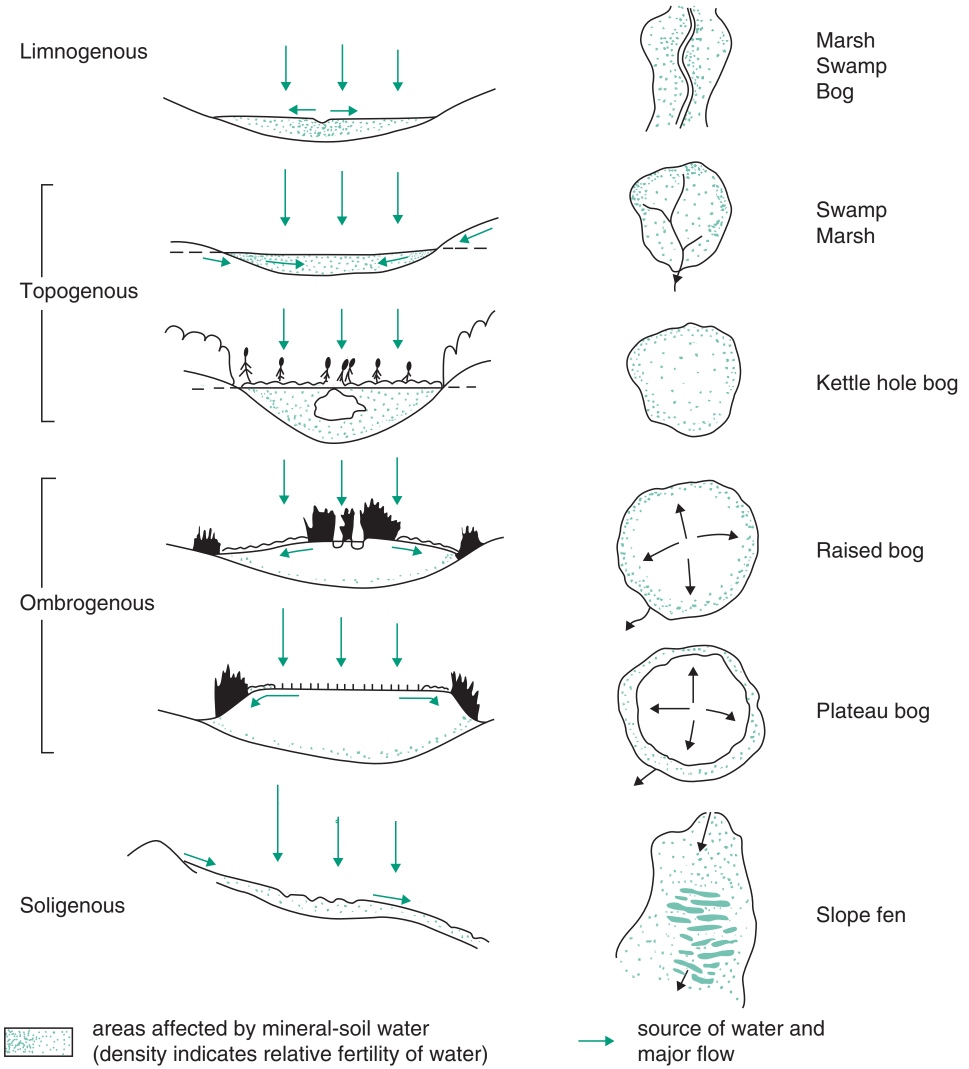

FIGURE 1.19 Peatlands (bogs and fens) are strongly affected by their position in the landscape. This determines the relative importance of rainfall and groundwater, as well as nutrient levels and pH of the groundwater. (From Bridgham *et al.* 1996, from Damman 1986.)

plant provide an alternative source of nitrogen and phosphorus (Givnish 1988). Orchids are also often found in peatlands, particularly in fens, perhaps because their associate mycorrhizae assist with nutrient uptake. Many peatland plants are organized along gradients of peat depth and water chemistry (Slack *et al.* 1980; Glaser *et al.* 1990; Yabe and Onimaru 1997).

The chemical nature of groundwater is a critical factor determining the type of peatland (Bridgham *et al.* 1996; Wheeler and Proctor 2000; Godwin *et al.* 2002). Hence, the location within a landscape is critical. Four general categories can be recognized (Figure 1.19). **Limnogenous** peatlands occur beside lakes and rivers. **Topogenous** peatlands occupy depressions and valleys. **Ombrogenous** peatlands

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occur where peat has accumulated above the land surface. **Soligenous** peatlands occur on sloped land surfaces. Since the depth of peat affects the water chemistry, peat accumulation rates become an important controlling factor. As peat accumulates and absorbs water, the diminutive *Sphagnum* moss can even flood and kill forests, a process known as paludification (van Breeman 1995). Over time, peat can accumulate to a depth of many meters, gradually transforming the landscape (Dansereau and Segadas-Vianna 1952; Gorham 1953), a topic to which we will return in Section 7.2. Disturbances such as fire can reverse this process of peat accumulation (Kuhry 1994; White 1994).

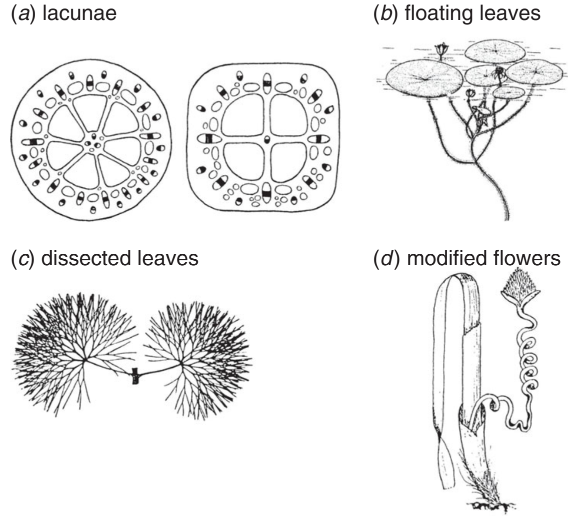

FIGURE 1.20 Four adaptations to standing water: (*a*) lacunae in stems and rhizomes (*Nymphaea* spp.), (*b*) floating leaves (*Brasenia schreberi*; Hellquist and Crow 1984), (*c*) dissected submerged leaves (*Camboba caroliniana*), (*d*) modified flowers that retract below water after pollination (*Enhalus acoroides*). (*a*, *c*, *d* from Sculthorpe 1967.)

1.5.2 Secondary constraints in aquatic wetlands

Standing water (Figure 1.11, upper right) produces a different type of environment. Here, in addition to low oxygen concentrations, the environmental factors are constant submergence, disturbance by waves, reduced availability of carbon dioxide, and the potential access to the atmosphere provided by floating leaves. The traits of aquatic plants therefore include well-developed aerenchyma, floating leaves, heavily dissected submersed leaves, and remarkably modified flowers (Figure 1.20). Aquatic plants have been the subject of two fine monographs (Sculthorpe 1967; Hutchinson 1975).

In aquatic wetlands, however, something more must be said about the problem of carbon acquisition, because this secondary constraint and its solutions are (almost) entirely restricted to aquatic macrophytes. Submersed aquatic plants are isolated from atmospheric supplies of carbon dioxide. In his monograph *Limnological Botany,* Hutchinson (1975) points out that the concentrations of carbon dioxide in water are similar to those in air, and even a little greater at low temperatures, placing aquatic plants in a rather different situation from respiring aquatic animals. If CO_2 concentrations in water are roughly equal to those in the atmosphere, "why should there be a problem at all?" Hutchinson answers that "the assimilating plant is still at a disadvantage in the water, owing to the much lower coefficient of molecular diffusion in a liquid than that in a gaseous medium. Submerging a land plant in water ... may reduce its photosynthetic rate to a negligible value" (p. 145). There are at least three morphological or anatomical responses to increase access to dissolved CO_2: reduction in the waxy epidermis of leaves, reduced thickness of leaves, and most conspicuously, the elaboration of leaves to increase surface to volume ratios (Figure 1.20*c*). These are adaptations that would not be possible in terrestrial plants because of the need for support tissues, and because such changes would also greatly increase rates of water loss. The other main adaptation is a biochemical one, the uptake of bicarbonate ions rather than that of CO_2 directly. Hutchinson concludes that most higher aquatic plants have this capability. One set of exceptions, he says, includes *Lobelia dortmanna* and species of *Isoëtes*; we shall

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return to them shortly. Another exception appears to be the carnivorous *Utricularia purpurea* (Moeller 1978). In such cases carbon uptake is directly related to the concentration of CO_2 in the water. All of these exceptions appear to be restricted to infertile soft water lakes, perhaps in part because these lakes lack the diurnal depletion of CO_2 found in some eutrophic lakes (Moeller 1978).

Those unusual plants that are unable to extract bicarbonate from water appear to be able to absorb CO_2 from their roots rather than from their leaves. Consider the bizarre group of plants in the genus *Isoëtes*, an obscure group of herbaceous plants thought to be evolutionary relicts related to fern-like plants such as *Lycopodium* and *Selaginella. Isoëtes* look rather like a small pincushion, and grow mostly in shallow water in oligotrophic lakes, although some species grow in temporary pools and a few are terrestrial. One member of this group, *Isoëtes andicola*, grows at high altitudes (usually >4000 m) in the Peruvian Andes, and the following account comes from work by Keeley *et al.* (1994). Over half this plant is composed of roots, and only the tips of the leaves emerge above ground and have chlorophyll (4% of total biomass). Most of the carbon for photosynthesis is obtained through the root system – from decaying peat rather than directly from the atmosphere.

In many oligotrophic lakes there is an entire group of plants called, because of their superficial resemblance to *Isoëtes*, "isoetids." These plants are apparently restricted to oligotrophic lakes where there are very low levels of inorganic carbon in the water. Some of these (e.g. *Lobelia dortmanna*) are also known to use their roots to take up CO_2 from sediments (Wium-Anderson 1971), and some have CAM (crassulacean acid metabolism) photosynthetic systems (Boston 1986; Boston and Adams 1986).

1.5.3 Secondary constraints in swamps

Sites that are deeply flooded for shorter periods of time (Figure 1.11, bottom) are generally covered in flood-tolerant trees, and these trees can be ranked in order of their flood tolerance (Kozlowski 1984b; Lugo *et al.* 1990). Hence, flood tolerance is the primary controlling factor in swamp forests, producing a pronounced change in tree species composition with elevation.

Since swamps are heavily forested, light becomes the important secondary factor. Low light levels inhibit the germination and growth of tree seedlings (Grubb 1977; Grime 1979). R. H. Jones *et al.* (1994) studied seedling regeneration over 4 years in four floodplain forests, cataloging over 10 000 seedlings – there was high mortality from shading during the first growing season. In all forests they examined, the composition of seedlings differed from the overstory trees, suggesting that composition would change if the adult trees died. They concluded that flooding, shading, and root competition were important environmental factors, but only in the years following establishment. The high rates of mortality and slow growth that they observed may be typical of densely shaded sites, but major disturbance did not occur during their study, so a period of rapid regeneration was not observed. Many tree species require gaps for their seedlings to establish (Grubb 1977; Pickett 1980; Duncan 1993). These gaps can be produced either by the death of individual trees, or when entire sections of forest are swept away by extreme floods or ice. The secondary constraint in this wetland type is therefore shading. Gap dynamics result. The processes of gap creation, seed dispersal to gaps, and establishment in gaps (Pickett and White 1985) therefore become prominent features of the ecology of swamp forests whether freshwater (Nanson and Beach 1977; Salo *et al.* 1986) or mangal (Lugo and Snedaker 1974).

1.5.4 Secondary constraints in marshes

Marshes arises in the region where the above three vegetation types intersect (Figure 1.11, center). Here, plants are exposed to three sets of environmental constraints. (1) Frequent inundation requires an ability to tolerate anoxia. (2) Frequent exposure to the atmosphere requires an ability to tolerate heavy

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FIGURE 1.21 Although the size and shape of the photosynthetic shoots vary, nearly all marsh plants emerge each year from deeply buried rhizomes.

herbivory or fire. During longer dry periods, dense canopies can develop, so these plants must also be able to tolerate shade. (3) Finally, there is mechanical disturbance. When water levels are at intermediate levels, waves can break over the plants. In northern climates, waves can also grind ice onto the shore. Ice can also freeze onto the shoreline, and when water levels rise, large pieces of vegetation can be torn away. In short, all these different constraints require a very special type of plant. Marshes are the result. Unlike in swamps, woody shoots are not suitable: they would be burned by fire, ripped out by ice, or torn away by floods. The above-ground parts are therefore herbaceous. Rather like prairie plants, the herbaceous shoots arise from deeply buried rhizomes (Figure 1.21), these being horizontal stems that provide anchorage for shoots during light disturbance, storage during periods of unsuitable conditions, and regeneration after heavier disturbance (Archibold 1995). Many years ago Raunkaier (1937) recognized the importance of protecting meristems from damage. Most marsh plants fall into his category of **cryptophytes**, plants that regenerate from buds, bulbs, or rhizomes that are completely buried in the substrate.

In cases of severe disturbance, even deeply buried rhizomes may be killed. This may occur when a site is deeply flooded for several years running. Managers have established that, in genera like *Typha*, the dead shoots can carry oxygen to rhizomes, but if the shoots have first been destroyed by fire or grazing, the rhizomes are far more sensitive to flooding (Kaminski *et al.* 1985). Intense grazing by mammals is well documented to destroy extensive stands of marsh plants (van der Valk and Davis 1978; Fritzell 1989). In addition to buried rhizomes, therefore, most of these species have long-lived seeds that persist buried in the soil (van der Valk and Davis 1978; Keddy and Reznicek 1986).

Since disturbance is intermittent, there are also periods when dense canopies may form and competition for light can become important. Deeply buried rhizome systems combined with dense arrays of shoots create strong interference with neighboring plants.

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Table 1.6 **The primary constraint of flooding creates a series of secondary constraints that determine the ecological attributes of wetland communities**

Wetland type	Nature of flooding: Mean level	Nature of flooding: Duration	Secondary constraints	Secondary characteristics	Key references to secondary constraints
Aquatic	High	High (continuous)	Low CO_2 Low light Waves	Stress tolerance	Sculthorpe (1967) Hutchinson (1975)
Peatland	Low	High (continuous)	Infertility	Evergreenness Mycorrhizae Carnivory	Grime (1979) Chapin (1980) Givnish (1988)
Marsh	Medium	Medium (50% growing season)	Mechanical disturbance Grazing Fire	Buried rhizomes Annual shoots Seed banks	White (1979)
Swamp	Low (with seasonal highs)	Low (30% growing season)	Disturbance Shade	Gap colonization Shade tolerance	Pickett and White (1985) Grime (1979)

Large clones of *Typha* and *Phragmites* are able to dominate wetland communities to the detriment of other species with smaller growth forms and shorter shoots (Gaudet and Keddy 1988; Gopal and Goel 1993; Keddy *et al.* 1998). Further, many common genera of marsh plants appear to have the ability to interfere with neighbors through the production of toxins (Gopal and Goel 1993).

Most of the species that form dense stands in marshes belong to one evolutionary lineage of plants – the Monocotyledonae. Their distinctive anatomy appears to be closely associated with these conditions of recurring flooding and disturbance.

In summary, the main wetland types arise because of the distinctive combination of secondary factors that result from flooding (Table 1.6). Wet meadows are the only one of the basic six wetland types that do not appear as a distinctive region in Figure 1.11. From this perspective, wet meadows are probably best imagined as a particular kind of marsh, but one where drought is a frequent occurrence. Wet meadows are similar to marshes, except that most plants are smaller, and rather than persisting with deeply buried rhizomes, they appear more dependent upon frequent regeneration from reserves of buried seeds. Wet meadows may therefore represent an extreme type of marsh where rates of disturbance are so high, and the habitat so short-lived, that even reeds and grasses cannot establish dominance.

1.6 Wetlands provide valuable functions and services

Human societies are entirely dependent, both for their survival and well-being, upon the biosphere, the 20-km thick layer that provides all the necessities of life. We can evaluate the benefits provided by the biosphere, and wetlands in particular, to humans by measuring the many services it provides.

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1.6.1 Ecological services: the de Groot approach

The overview by de Groot (1992) lists 37 services that natural environments perform for humans (Table 1.7). These range from the ozone layer's service of protecting humans from harmful cosmic influences to a landscape's service in artistic inspiration. Further, de Groot breaks these services down into four categories:

Table 1.7 **Services that may be performed by natural environments including wetlands**

Regulation services
1. Protection against harmful cosmic influences
2. Regulation of the local and global energy balance
3. Regulation of the chemical composition of the atmosphere
4. Regulation of the chemical composition of the oceans
5. Regulation of the local and global climate (incl. the hydrological cycle)
6. Regulation of runoff and flood prevention (watershed protection)
7. Water catchment and groundwater recharge
8. Prevention of soil erosion and sediment control
9. Formation of topsoil and maintenance of soil fertility
10. Fixation of solar energy and biomass production
11. Storage and recycling of organic matter
12. Storage and recycling of nutrients
13. Storage and recycling of human waste
14. Regulation of biological control mechanisms
15. Maintenance of migration and nursery habitats
16. Maintenance of biological (and genetic) diversity

Carrier services: providing space and a suitable substrate for
1. Human habitation and (indigenous) settlements
2. Cultivation (crop growing, animal husbandry, aquaculture)
3. Energy conversion
4. Recreation and tourism
5. Nature protection

Production services
1. Oxygen
2. Water (for drinking, irrigation, industry, etc.)
3. Food and nutritious drinks
4. Genetic resources
5. Medicinal resources
6. Raw materials for clothing and household fabrics
7. Raw materials for building, construction, and industrial use
8. Biochemicals (other than fuel and medicines)
9. Fuel and energy
10. Fodder and fertilizer
11. Ornamental resources

Information services
1. Esthetic information
2. Spiritual and religious information
3. Historic information (heritage value)
4. Cultural and artistic inspiration
5. Scientific and educational information

Note: Services originally termed functions by de Groot.
Source: From de Groot (1992).

(i) *Regulation services* describe the capacity of ecosystems to regulate essential ecological processes and life support systems on Earth. Examples include regulation of the CO_2 and O_2 concentrations of the atmosphere.
(ii) *Carrier services* describe the space or suitable substrate needed for the conduct of human activities such as living, cultivation, and recreation. Examples include soil and rainfall for growing crops.
(iii) *Production services* describe the resources provided by nature, including food, raw materials for industrial use, and genetic raw material. Examples would include production of clean water for drinking and wood for building.
(iv) *Informational services* describe the role played by natural ecosystems in the maintenance of mental health by providing cognitive development, spiritual inspiration, and scientific appreciation of the world. Examples would include wilderness areas and historical landscapes.

1.6.2 Evaluating ecological services

Others have tried to work out dollar values for each service. Costanza *et al.* (1997a) tried to measure the

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value in dollars per hectare per year of 17 ecological services, including climate regulation, water supply and recreation, for 16 biomes. The total value of services performed by natural systems, $33 trillion, is roughly 1.8 times the global gross national product (GNP), itself an imperfect measure of human economic activity. Major services performed by wetlands included "disturbance regulation" at $4539 ha/yr, "water supply" at $3800 ha/yr, and "water treatment" at $4177 ha/yr. These numbers excluded estuaries, which themselves rated $21 100 ha/yr for "nutrient cycling."

The number of studies of economic value is steadily increasing. The World Wildlife Fund (also known as the World Wide Fund for Nature, WWF) undertook a review of 89 wetland evaluation studies (Schuyt and Brander 2004). To illustrate the types of services and their values, Table 1.8 shows the services provided by the Pantanal, one of the world's largest wetlands, and also with particularly high economic services (Seidl and Moraes 2000). You can see that flood control and water supply were the most important services in this wetland, followed by waste treatment, water regulation and cultural values. At the global scale, WWF concludes that the two most valuable services wetlands provide are (1) recreational opportunities and amenities (median value of $492 ha/yr) and (2) flood control and storm buffering (median value of $464 ha/yr). The most conservative estimate was that 63 million hectares of global wetlands provide services valued at $3.4 billion per year. This is conservative because the total area of wetlands, and the value per hectare, could both be larger. We will return to this study in Chapter 11.

The important point is that wetlands have enormous value, however you categorize the services that they perform. In Chapter 11 we will look at these services in more detail with particular emphasis upon production (including wildlife production), regulation of atmospheric carbon dioxide and methane levels, maintenance of the global nitrogen cycle, biodiversity, and recreation. When humans manipulate wetlands, whether by draining for agriculture, or flooding to increase certain species, many services are simultaneously changed, often with unknown consequences.

Table 1.8 **Economic value of the Pantanal wetland (millions of 1994 US dollars per year)**

Service	Value
Water supply	5322.58
Disturbance regulation	4703.61
Waste treatment	1359.64
Cultural	1144.49
Water regulation	1019.82
Nutrient recycling	498.21
Recreation	423.64
Habitat/refugia	285.04
Raw materials	202.03
Gas regulation	181.31
Erosion control	170.70
Food production	143.76
Climate regulation	120.50
Soil formation	60.22
Pollination	33.03
Biological control	30.39
Genetic resources	22.15
Total	15 721.12

Source: Adapted from Schuyt and Brander (2004) based on Seidl and Moreses (2000).

1.7 Causal factors in wetland ecology

As we have now seen, wetlands arise because there is water, but the particular kind of wetland, and the characteristics of its species or communities, will depend upon another set of environmental factors. The study of wetland ecology can therefore be approached as the study of these key environmental factors. If you know which factors predominate, you can predict the kind of wetland that will likely arise. Moreover, you will have a preliminary indication of which factors are important to the wild

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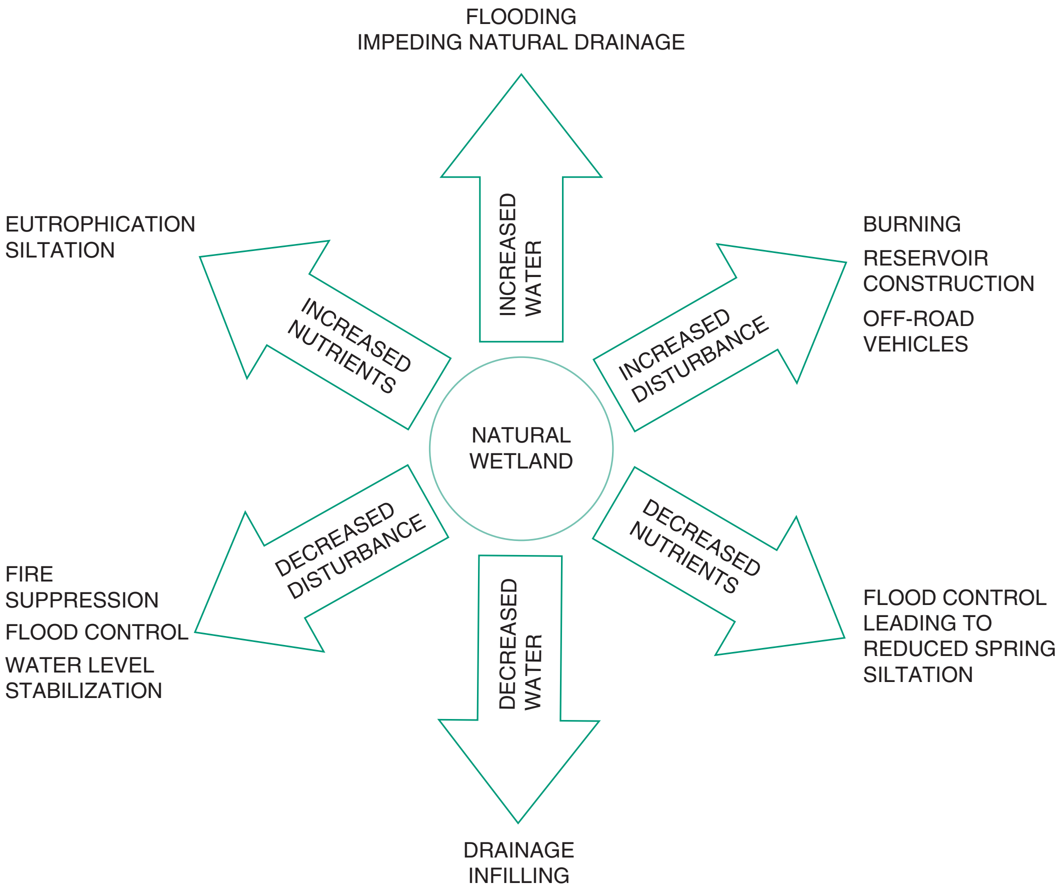

FIGURE 1.22 Three key factors (flooding, disturbance, and nutrients) control much of the variation in wetland communities. Hence, there is a chapter in this book for each of these key factors. If any one of these three factors is changed, the wetland will change in response.

creatures in that wetland. Take the Everglades as a well-known example. We shall look into the ecology of the Everglades in more detail later in the book. In terms of key factors, the Everglades are the result of extremely low nutrient levels, and seasonally varying water levels. Hence, the plants and animals that occur there must be able to tolerate these two key factors. And you can predict, with confidence, that if you increase nutrient levels, or change water levels, you will harm the species in that wetland. The key factor approach is therefore a very important way of thinking about wetlands. There are three principles that can guide our thinking about key factors.

1.7.1 Three principles

The first of the three principles, important in the study of key environmental factors that control wetland type and community composition, states that *a particular community or ecosystem is produced by multiple environmental factors acting simultaneously*. We can therefore picture any particular wetland (and that includes its species, communities, and services) as being a product of the pushing and pulling of opposing environmental factors (Figure 1.22). Any specific wetland you encounter has arisen as a temporary consequence of

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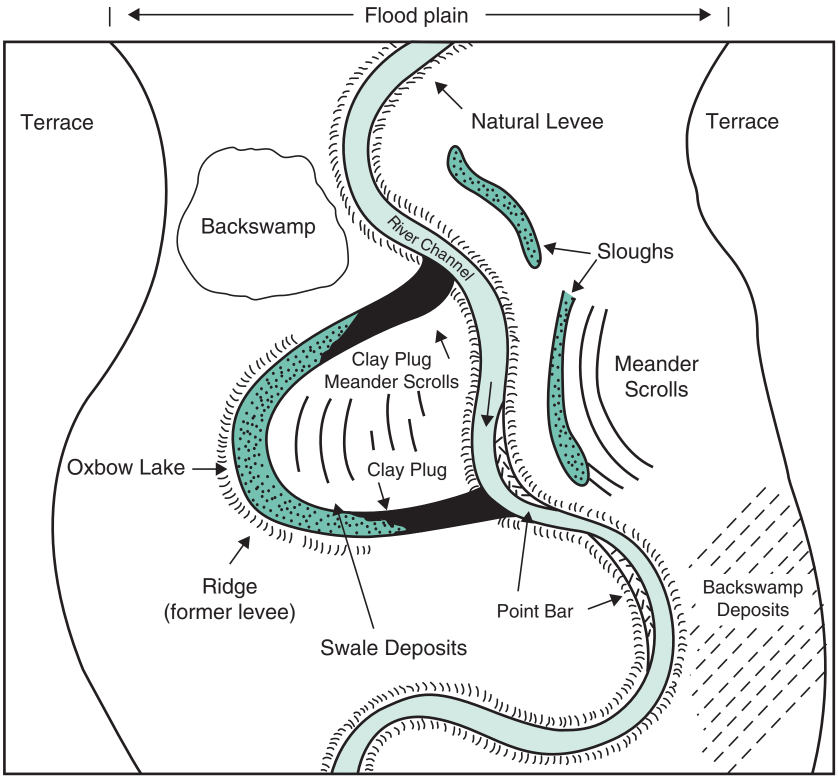

FIGURE 1.23 The wetlands in floodplains are the result of three principal processes: flooding, erosion, and deposition. These create a physical template that controls the composition and processes in wetlands along most rivers and in many deltas. (From Mitsch and Gosselink 1986.)

these multiple factors. It may be useful to consider this set of physical factors as a kind of *habitat template,* which both guides and constrains the biological communities and ecological processes that occur. Along most watercourses – the Mississippi River, the Danube River, the Amazon River, or the Yangtze River, for example – the movement of water, and particularly the movement of floodwaters, creates gravel bars, eroding banks, sand bars, oxbows, and deltas (Figure 1.23). Along such watercourses, the three most important factors in the habitat template may be (i) flooding, (ii) erosion, and (iii) deposition. These are not entirely independent, of course, but for the purposes of this book I have tried to tease them apart somewhat. There are therefore separate chapters for flooding, disturbance, and burial. Similarly, in small European peatlands, the most important factors in the habitat template may be (i) water availability, (ii) fertility, (iii) frequency of disturbances such as fire, and (iv) intensity of grazing. Again, these are not independent of one another, but there are separate chapters on flooding, fertility, disturbance, and herbivory.

Each of these environmental factors has its own set of effects on a wetland. The second principle therefore states that *to understand and manage wetlands, scientists must determine the quantitative relationships between environmental factors and the properties of wetlands*. The study of each factor in the habitat template provides an opportunity to study such quantitative relationships. Examples might include (i) the production of fish as determined by floodplain area, (ii) the diversity of plants as controlled by fertility, or (iii) the composition of invertebrates produced by different rates of burial by sediment. These relationships summarize the state of human knowledge about the factors that create and control wetlands. The challenge for the scientist is to unravel these factors, discover their consequences

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for wetlands, and determine their relative importance. Throughout this book, I will try to share figures that show you key factors that control the properties of wetlands. The challenge for managers and conservationists is to first document these relationships, and then, if necessary, manipulate or regulate one or more of them to maintain or produce the desired characteristics of a wetland.

These challenges are made difficult by the many kinds of wetlands, and the many factors at work in them. The difficulty is compounded by a third principle: *the multiple factors that produce a community or ecosystem will change through time.* Wetlands are no different from other ecosystems, where disturbance from fire, storms, landslides, and floods controls the communities and species at a site. If humans change the factors acting on the wetland in Figure 1.22, say by decreasing spring flooding or increasing fertility, the balance of forces will shift and the wetland composition or function will begin to shift as well. The habitat template along watercourses in Figure 1.23 is constantly changing as moving water reshapes the environment. It is far too easy, and therefore far too common, for humans to study small fragments of this habitat complex (say one species or one vegetation type in one oxbow lake), losing track of the fact that the particular species and community types are but transitory occurrences at any location. To understand wetlands, and to manage them wisely, it is essential to appreciate their *multi*factoral and dynamic nature right from the start of our inquiry. Thus the introduction of these principles is early in the book.

All of the chapters that follow can be treated as elaborations on these principles, expanding the description of known relationships, and then discussing how these influence the study, conservation, and management of wetlands.

1.7.2 Six causal factors

By now you will appreciate how important it is for us to understand which environmental factors are dominant in each wetland we encounter. Yes, flooding is necessary, but so are other factors such as fertility and disturbance. The factors allocated separate chapters in this book are **hydrology**, **fertility**, **disturbance**, **competition**, **herbivory**, and **burial**, arranged (roughly) in declining order of importance. We can think of these as a kind of shopping list of factors that will operate to some degree in almost any wetland you encounter. (Note that ecologists may use slightly different words for referring to key factors – they are also called environmental filters, habitat templates, or causal factors, depending upon the situation.)

Other factors might be added. Four in particular should be mentioned at the start: salinity, positive interactions, time, and roads.

Salinity I have deliberately not added salinity in as a separate factor because this would immediately create a ghetto of sorts for saline wetlands, leading readers to overlook the many ways that saline wetlands are similar to freshwater wetlands. Often, however, you will see freshwater and saltwater wetlands (or interior wetlands and coastal wetlands) treated as if they were entirely different systems. If salinity had its own chapter, then peatlands might next have their own category, and would be a further loss of unity in the book. This sort of division of research by wetland type is something I actively sought to avoid. I do discuss salinity and its effects explicitly in Section 8.1. Further, there are also many excellent treatises on saline wetlands (e.g. Chapman 1974, 1977; Pomeroy and Wiegert 1981; Tomlinson 1986; Adam 1990; Silliman *et al.* 2009) which a single chapter could not duplicate.

Positive interactions Positive interactions could include floodplain trees providing food for fish, beavers creating ponds for frogs, and *Sphagnum* moss creating peat for orchids. While these may be locally important, I have not given them chapter status. This may appear to contradict my own work, since I have written about how textbooks ignore positive interactions (Keddy 1990a). There are fine

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reviews on mutualism (Boucher 1985; Smith and Douglas 1987). There is increasing evidence for positive interactions in wetlands (Bertness and Hacker 1994; Bertness and Yeh 1994; Bertness and Leonard 1997). But rather than combine such positive interactions in one chapter, I have sorted them by their main effects: fish and plants are discussed under flooding, alligator effects are discussed under disturbance, and peat accumulation under succession and burial.

Time Time is a critical factor that could have been included: entire lakes have come and gone over the 20 000 or so years since the last ice age, peat has accumulated for thousands of years as continental glaciers receded, beaver ponds come and go over centuries, and riparian wetlands are flooded each year. I have not included time as a separate factor, since time is often a surrogate for other causal factors that vary with time. Hence, time is rolled into each chapter: changes in hydrology during glaciation are introduced in hydrology, changes in fertility with peat accumulation are discussed under fertility, fire cycles are discussed under disturbance, succession is discussed under zonation and burial, and so on.

Roads Roads do not fit neatly into any category, yet roads in particular, and paving in general, are causing major changes in wetlands. I have therefore added in this edition a new chapter called "other factors" that includes effects of roads (Section 8.2), coarse woody debris (Section 8.3), and some other factors that are important but that do not fall obviously into the main chapters.

I do not want you to think this is the only way to sort the many topics covered in this book. A book with separate chapters on salinity, positive interactions, and time could be written, and would undoubtedly have its merits. Those of you who wish to see time and positive interactions as separate chapters can consult my book *Plants and Vegetation* (Keddy 2007) to see wetlands viewed from this perspective.

1.8 More on definitions and classification of wetlands

Now, having a better understanding of the main types of wetlands, environmental conditions they have in common, and factors important in wetland creation and maintenance, let's return to our discussion of wetland definition and classification.

1.8.1 More on defining wetlands

We started with a single definition for a wetland in Section 1.1.1. Many other definitions, particularly longer ones, are possible. Some definitions are predominantly written by and for scientists, others by and for lawyers. We do not want to get tangled up in definitions – as Shakespeare observed, "How every fool can play upon the word." Yet many court cases that deal with wetlands can hinge upon definitions. So before we look at more definitions, we should understand whether they are scientific or legal in their audience.

A scientific definition is a tool for the analysis of nature. The first definition described the domain of inquiry of wetland ecology. It also directed our attention to some processes in wetlands. But a tool should be retained only if it is useful. As our knowledge of a discipline grows, we may expect our definitions to slowly change too. There is an evolutionary process at work here: definitions help us investigate nature, and our investigation of nature helps definitions. Is a marine rocky intertidal zone a wetland? Are the contents of the leaf of a pitcher plant a wetland? How dry does a site have to become before it is no longer a wetland? These sorts of questions arise, and can confuse us. The definition above is quite satisfactory for beginning this book.

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A legal definition is another matter. Although legal definitions can also evolve, the process is often much slower. Moreover, a clever lawyer can exploit any weakness in a definition, with the risk of serious social, economic, and environmental consequences. One can even have Supreme Court justices with no training in wetland ecology presuming to write definitions. Often these create more confusion than clarity.

The Ramsar Convention is an international treaty for wetland conservation. Adopted in 1971 in the city of Ramsar, in Iran, the "Convention on Wetlands of International Importance especially as Waterfowl Habitat" had 158 contracting parties by the end of 2008. Altogether, 1828 sites totaling some 168 million hectares have been designated. Participants accept the obligation to promote "as far as is possible the wise use of wetlands in their territory." Wise use is interpreted to mean the maintenance of the ecological character of wetlands (Navid 1988). The Convention uses a particularly broad definition of wetlands in Article 1:

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

Moreover, the area of coverage is broadened by Article 2, which provides that wetlands

> . . . may incorporate riparian and coastal zones adjacent to the wetlands and islands or bodies of marine water deeper than six meters at low tide lying within the wetlands.

As a consequence, the Ramsar Convention includes rivers, coastal areas, and even coral reefs (Navid 1988). Although I have adopted a relatively broad coverage of wetland types in this book, coral reefs and rocky marine shorelines are excluded.

The Ramsar definition is short and all-inclusive. Not all are. The Committee on Characterization of Wetlands (1995) has prepared an entire book on this topic for the United States! One ventures into terrain with "national delineation manuals," "interagency manuals," and "revised manuals" that arise as different agencies and government bodies struggle to legally define wetlands. Flawed definitions can easily allow a wetland to be destroyed by developers. The Committee on Characterization of Wetlands therefore developed a "reference definition" to stand outside of any single agency, policy or regulation. Their reference definition is:

> A wetland is an ecosystem that depends on constant or recurrent, shallow inundation or saturation at or near the surface of the substrate. The minimum essential characteristics of a wetland are recurrent, sustained inundation or saturation at or near the surface and the presence of physical, chemical, and biological features reflective of recurrent, sustained inundation or saturation. Common diagnostic features of wetlands are hydric soils and hydrophytic vegetation. These features will be present except where specific physiochemical, biotic, or anthropogenic factors have removed them or prevented their development.

This longer definition still contains the essential elements of my shorter one: water, modified substrate, and distinct biota. We shall let Mitsch and Gosselink (1986, pp. 16–17) have the last word on this topic.

> Because wetland characteristics grade continuously from aquatic to terrestrial, any definition is to some extent arbitrary. As a result, there is no single, universally recognized definition of what a wetland is. This lack has caused confusion and inconsistencies in the management, classification, and inventorying of wetland systems, but considering the diversity of types, sizes, location, and conditions of wetlands . . . the inconsistency should be no surprise.

Enough on definitions. Applying a simple definition in a commonsense way allows us to begin. The Earth has about 5.6 million square kilometers of wetlands (Dugan 1993), an area equivalent to roughly ten times the size of France or nearly four times the size of Alaska. This book will emphasize what wetlands

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have in common. All the time, of course, we know that they will differ in detail – no two wetlands will ever be identical. Until the similarities are described, it is difficult to decide which differences are the important ones. This book therefore deliberately takes a top–down approach. We will begin with commonalities among wetlands at the global scale. Then, gradually, patterns can be dissected to uncover differences.

1.8.2 More on classification systems

We started with some simple classification concepts – six types of wetlands, controlled by their location, and hydrology. As soon as you try to apply a simple system, it becomes clear how complicated nature is. This is particularly so in tropical landscapes where there are large numbers of species, or at larger scales where climate, soil, and biota change, or in areas where topography produces many kinds of unusual circumstances. Hence, wetland classification systems can become rather larger and more complicated. Here are three examples.

Tropical Caribbean system

The challenge of any classification system is to simplify a complicated world. The Caribbean illustrates just how complicated it can be. In Cuba alone it is possible to define 27 classes, 53 orders, 80 alliances, and 186 plant associations, of which nearly one-quarter are wetlands. Cuba also has the largest wetland complex in the Caribbean; on the south coast near the Peninsula de Zapata there are some half-million hectares of mangroves and freshwater marshes. The diversity of wetlands across the Caribbean probably results from a combination of factors including the excess of rainfall over evapotranspiration, the varied topography, and the complex geology. The island of Puerto Rico, for example, has volcanic, plutonic, limestone, serpentine, sedimentary, and sandstone formations, and mountains exceeding 1000 m in the Cordillera Central, producing 164 soil types. Given the rich flora of the Caribbean, and the large number of endemic species, a classification system using plant species names becomes too complex. Lugo *et al.* (1988) therefore recognize three main kinds of wetlands based upon geology and hydrology: riverine, basin, and fringe wetlands. Modifiers such as salinity, dominant life form, and nutrient status can then be superimposed. Adding three salinity levels (freshwater, oligohaline, and saline), three plant forms (herbaceous, scrub, and forest) and three nutrient levels (oligotrophic, eutrophic, and dystrophic) yields ($3 \times 3 \times 3 \times 3$) 81 basic wetland types, a system that is broad enough to include everything from mangal to montane seeps, yet simple enough to require only four main criteria for classification. The diversity of wetland types in Cuba, for example, is then reduced to 24.

African wetlands

Thompson and Hamilton (1983) use an even simpler system of our basic categories for describing the wide array of African wetlands. They recognize four main wetland types: (i) mangrove swamps and coastal peatlands, (ii) swamp forests, (iii) grass, sedge, and reed swamps, and, in uplands, (iv) flushes, cushion-bogs, and tussock sedge mires. Further subdivision can be based upon location (e.g. valley bogs) or dominant species (*Typha* marsh, *Papyrus* marsh). Compared with Lugo *et al.* (1988), formal rules and criteria may seem to be lacking, but this system none the less appears sufficient for a preliminary description of wetland types. (Note, however, that they use the word swamp more broadly than we do in this book; I recommend that we reserve the term swamp for only wooded wetlands: see Sections 1.2.1 and 1.5.3)

European phytosociology

Those reading the European literature will find that classification continues to finer and finer scales where each community type is ultimately given a separate name. For example, a *Phragmites communis* marsh in Poland would be placed in the Class Phragmitetea (R. Tx. et Prsg. 1942), Order Phragmitetalia eurosibirica (R. Tx. et Prsg. 1942),

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Alliance Phragmition (Koch 1926), and Association Scirpo-Phragmitetum (Koch 1926) (vegetation type authors, not references, in parentheses). Palczynski (1984), for example, recognizes 7 classes, 10 orders, 14 alliances, and 37 associations in the Biebrza valley in Poland. Beeftink (1977) uses the same approach to classify salt marshes in northwestern Europe. I have not used such terminology in this book, but you can read more about it in sources such as Shimwell (1971) or Westhoff and van der Maarel (1973). At times, it seems that this creates confusion by distorting plant names and making work in wetlands obscure to all but a narrow group of experts. Perhaps local users, however, find it valuable, particularly in small reserves in human-dominated landscapes. In this book, I have tried to keep to simpler terminology. Thus the Scirpo–Phragmitetum Association would simply be called a *Scirpus–Phragmites* floodplain or *Scirpus–Phragmites* marsh, depending upon the circumstances.

1.8.3 Some confusions in terminology

Speaking of geographical and political regions, problems can easily arise. The word **swamp** causes much confusion between North Americans and Europeans. Inconsistent use of the word “swamp” causes problems even within England (Burnett 1964). The term “swamp” in British usage generally applies to wetlands in which the normal water level is above the soil surface, usually dominated by reeds (*Phragmites*), tall grasses, sedges, or rushes; the commonest kind being a “reed swamp.” Similarly, in Africa, we saw that Thompson and Hamilton (1983) used the term swamp for grass-, sedge-, and reed-dominated herbaceous wetlands as well as for forested areas. In the definition used in this book (p. 7) herbaceous wetlands lacking peat are simply a kind of marsh; they may be further qualified with modifiers such as an “emergent marsh,” “*Phragmites* marsh,” “*Papyrus* marsh,” or “lacustrine marsh” as the need arises.

Owing to the long history of interest in **peatlands**, there is a particularly diverse terminology here (Gore 1983; Wheeler and Proctor 2000). In this book I use the world peatland inclusively, and avoid the word mire entirely. One might hope that the Russians would have sorted it out for us, having lived with peatlands for centuries, and having the world’s largest, the West Siberian Lowland. Yet Zhulidov *et al.* (1997) tell us that until recently, there was not even a word for the general concept of “wetland.” More than 30 local names (from *alasy* to *zaymischa*) existed and could be understood differently in different parts of the country. There is the further problem of translation from Russian to English.

Continuing with peatlands, the gradations between **bog** and **fen** also generate a great deal of terminology. The key factors appear to be the acidity of water, and the nutrient status of the water (Bridgham *et al.* 1996; Wheeler and Proctor 2000). These in turn control other characteristics such as rate of peat accumulation and plant species composition. Another set of terms emphasize the source of water, with bogs often being dependent upon rainfall (hence, **ombrotrophic**), while fens are connected to flowing groundwater (hence, **minerotrophic**). There are many more specialized terms. Where the groundwater has calcium as the dominant cation, fens with large numbers of plant species often arise, hence the utility of recognizing **calcareous fens** (Godwin *et al.* 2002). In cold climates, the flowing water though peatlands creates alternating ridges and pools at right angles to the direction of water flow (Figure 1.6*a*), producing **patterned fens** or string bogs (Foster *et al.* 1983; Mark *et al.* 1995). Around raised bogs, where water flowing off the bog meets mineral soils, a trough called a **lagg** is often found (Damman and Dowhan 1981; Godwin 1981). Overall, the proliferation of terms can be confusing to even the experts, in which case the simple distinctions between bog and fen, along with the categories shown in Figure 1.19, should suffice for most cases.

What to you call a wetland after people have built a wall around it? In the United States, these walls are often called levees, but levees also refer to natural features that arise along rivers. Hence, the term levee

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is misleading, unless you refer to "natural levee" and "artificial levee." The terms embankment or dyke might be better, with embankment implying an earthen structure and dyke implying a more elaborate one. An area surrounded by an embankment and drained does not seem to have a name in the United States, but is called a **polder** in Europe. Such terms must create nightmares for translators. Hence, as one example, one reads of polders (usually associated with the Netherlands) in Chinese landscapes. Although a Dutch word for a structure in China at first seems surprising, it actually is a step forward to consistency. I will use the term polder throughout this book.

These issues of terminology make it difficult for students and professionals alike. They make it difficult to communicate with other cultures. When it took a month to sail across the Atlantic, cultural differences in classification were perhaps inescapable. But in an era of international flights, e-mail, and global telephone linkages, not to mention books, scientific dialects are no longer acceptable. Let us hope that teachers will try to bequeath to their students one standard terminology. If we make the effort, perhaps we can all speak one language when in comes to wetlands. Hence, in this book, the narrow use of the word **swamp**, the broad use of the word **peatland**, and the consistent use of the term **polder**.

CONCLUSION

Let us conclude this chapter by reviewing the topics we have discussed so far, applied to one of the world's largest wetlands, the Pantanal. This wetland is an enormous savanna floodplain – 140 000 km^2, roughly the size of England – in central South America (Alho *et al.* 1988; Junk 1993; Alho 2005). Pantanal National Park protects part of the area.

The source of flooding is the Paraguay River, which flows southward through central South America, and eventually enters the ocean at Buenos Aires. The annual flood regime provided by the river is a critical factor. Much of the floodplain is seasonally flooded grassland where water levels can rise and fall many meters each year. The timing of the annual flood depends upon the rainfall upstream, which falls October through April, along with the lag until it reaches the Pantanal. Wildlife life cycles are closely tied to flood regimes. For example, consider fish. During the flood season fish move out of the river into the floodplains, while during dryer periods, the fish concentrate in pools where they become prey for birds. The birds use the fish to feed their young.

Depending on the depth and duration of flooding, different types of wetlands arise. These have local names in Portuguese (depressions are known as *corixos* and shallow water paths as *vazantes*. The rivers are lined with gallery forests and more elevated areas have semi-deciduous forests (Figure 1.24). As a consequence, aquatic and terrestrial vegetation (including cacti) are interspersed (Prance and Schaller 1982; Alho *et al.* 1988; Junk 1993). Much of the Pantanal, however, is marsh. One classification recognizes seven types of wetland vegetation, depending upon flooding regimes (Neiff 1986). Cattail swamps (Neiff's terminology), for example, are inundated only by occasional floods (5–10 years). The wetland can also be divided in to 11 geographical

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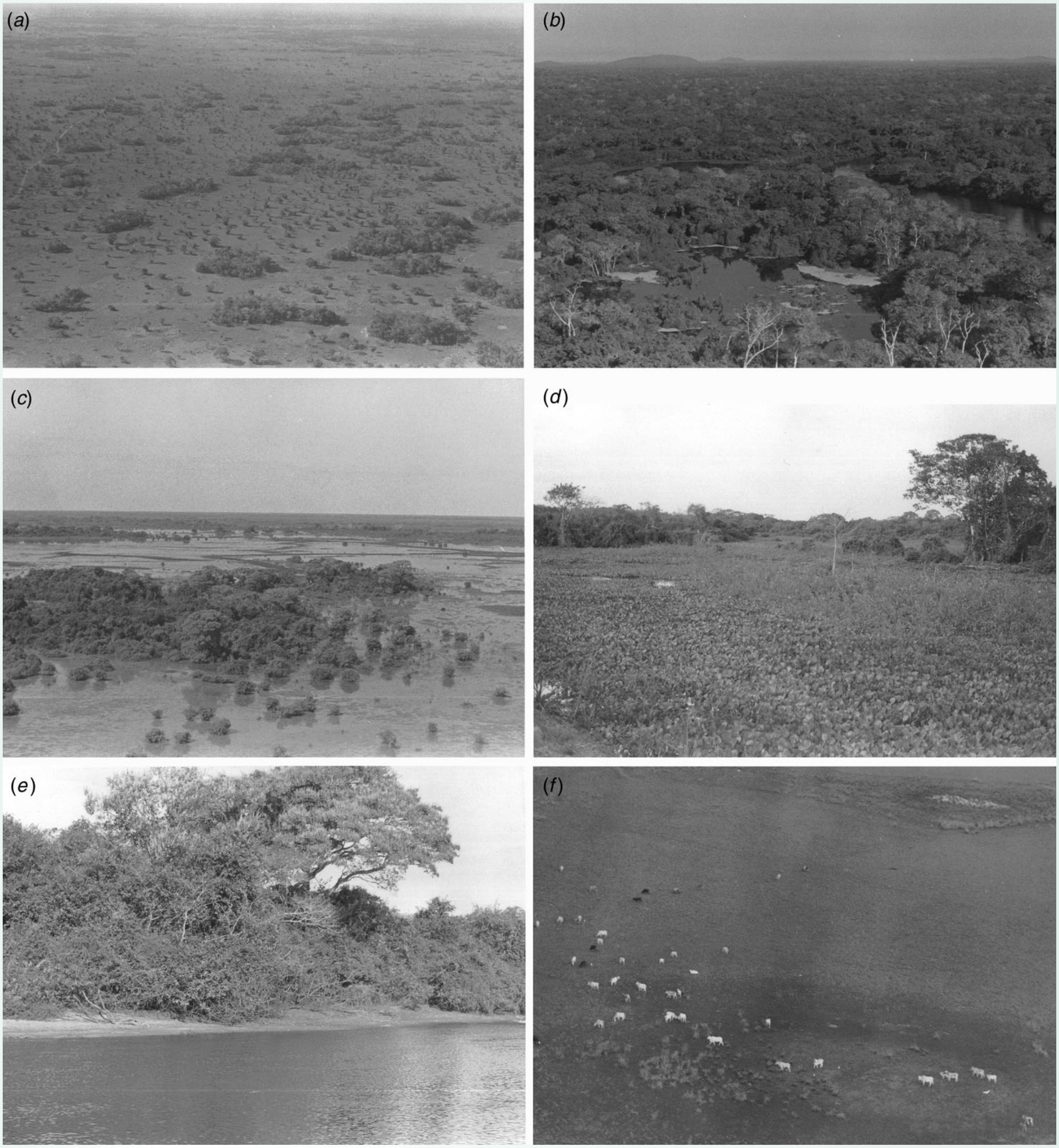

FIGURE 1.24 Some scenes from the Pantanal. (*a*) vast area of seasonally inundated cerrado with forest islands, (*b*) gallery forest in foreground and semi-deciduous forest in background, (*c*) flooded savanna and gallery forest, (*d*) pond filled with *Eichhornia* and *Pontederia*, (*e*) sandy margin of Rio Negro showing *Vochysia divergens*, a tree characteristic of seasonally flooded areas, and (*f*) cattle grazing in a seasonally flooded savanna. (Courtesy G. Prance and J. Schaller.)

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subregions – the Cáceres region, as one example, floods for up to 6 months out of the year, while others flood for lesser periods.

To put this in a regional context, a number of terrestrial vegetation types meet here: the cerrado biome of Central Brazil on the East, the semi-deciduous Amazonian forest to the northwest, and the chaco-like forest of Bolivia to the southwest. The wildlife is correspondingly rich, including jaguar, ocelot, giant anteater, giant otter, giant armadillo, crab-eating fox, pampas deer, and swamp deer, all threatened or endangered (Alho *et al.* 1988). There are 13 species of herons and egrets, 5 species of kingfishers, and 19 species of parrots. More than 540 species of fish have been recorded for the river systems as a whole.

The Pantanal provides many important services to the surrounding region (recall Table 1.8). Overall, the threats posed to this wetland, and the management problems that arise, typify the perils facing many of the world's wetlands.

Ranching Native populations of grazing animals have been slowly replaced by ranches. The subdivision of these ranches and intensification of grazing is even more detrimental to native plant communities.

Poaching The trade in animal hides continues. Just one 2500-kg shipment of hides contained 70 000 individual skins including jaguars, maned wolves, caimans, and snakes; the smugglers admitted that this shipment represented only 13% of all the skins (more than a half a million animals) that had been sent to Germany in the preceding 6 months (Alho *et al.* 1988). The added effects of removing large predators from this ecosystem are unknown.

Large-scale agriculture The native vegetation is being replaced with cropland, and the river thereby contaminated with herbicides, pesticides, and sediment. Alcohol distilleries for biomass fuels add to the contaminant load.

Deforestation This ongoing problem is being accelerated by illegal sawmills and fires set by ranchers.

Canalization The greatest threat may be the proposed Hidrovia Project (Bucher *et al.* 1993), a scheme that will use dredging and canals to create a 3440-km long waterway starting at Puerto Caceres in Brazil and ending at Nueva Palmira in Uruguay. The 1670 km of this project going straight through the heart of the Pantanal would be bound to cause major changes in hydrology and cause major changes throughout the flood zone.

A list like this can be depressing. This is why we need to understand key factors and causes and effects in wetlands. Without a general understanding, we end up only with a depressing list of threats, and no obvious course of action. This book

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provides an approach to addressing such problems. We begin with the simple question: where do wetlands occur and what types of wetland are present? We then ask which environmental factors produce each type of wetland. The most obvious causal factor is, of course, flooding, but secondary factors also produce the many different kinds of wetlands seen in a landscape. Once we understand the factors that produce the array of wetlands, and the different kinds of species in them, we are better able to predict the possible consequences of human actions. We can then make more intelligent assessments of which problems need to be solved first, and we can come up with a list of possible actions. In the final chapter we will explore the approaches that have been used to protect important wetlands.

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