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3

Fertility

A few resources control the production of living organisms. All living organisms are built mainly from six elements – CHNOPS (carbon, hydrogen, nitrogen, oxygen, phosphorus, sulfur). If any of these basic elements is in short supply, growth and reproduction will be slowed. Generally, it seems that the two most important elements are nitrogen and phosphorus – for both plants and animals. Hence, we can use the availability of nitrogen and phosphorus as one way to judge how suitable a habitat is for living creatures. The general word we use to describe this suitability is **fertility**. Let us start with plants.

3.1 Fertility and plants

Fertility controls primary productivity (biomass), with nitrogen and phosphorus supplies often limiting plant growth. Sites with low levels of these nutrients are termed infertile. While biomass is directly correlated with fertility, species richness is inversely correlated with fertility. The importance of particular nutrients can be determined through field experiments in which they are supplemented and the effects on plants documented.

3.1.1 Nitrogen and phosphorus often limit plant and animal growth

The availability of nitrogen and phosphorus determines how fast plants can grow. More fertile areas have, among other things, bigger plants, faster-growing plants, more biomass, and hence more production to support more animals. You can easily do the simple experiment of adding nutrients to plots in a marsh, and find, not surprisingly, that the plants get bigger. So what more, you might ask, do we need to know? Surprisingly, there are many unknowns, and many problems arise out of unexpected consequences of fertility. A most obvious example is the case of the Everglades, where millions of dollars are being spent trying to keep nutrients from entering the wetlands. There are often times when having more plant growth is not a good thing. So here are some questions that we need to answer.

- What levels of nitrogen and phosphorus produce fastest growth?
- Are some wetlands already saturated with nutrients?
- Which is more important, nitrogen or phosphorus?
- How does fertility affect species composition?
- Why do infertile habitats support so many species?
- Why does high fertility often cause rare species to disappear?

These questions indicate that not all wetlands respond to fertilization, and when they do, sometimes

the consequences are unexpected or undesirable. At the same time, the nutrient levels of many wetlands are being pushed higher by nutrient laden waters from farms and cities, and even by nutrients in precipitation.

3.1.2 Fertility increases biomass

Since wetlands are known to be areas with rapid plant growth, it seems reasonable to assume that nitrogen and phosphorus are often relatively available. This is likely because water runs downhill, steadily transporting nutrients out of upland areas and into wetlands.

As a simple experimental example of responses to fertility, we subjected plots of coastal Louisiana to three treatments that increased fertility: added sediment, added fertilizer, and added sediment and fertilizer. Biomass increased with all three experimental treatments (Figure 3.1). This result is not surprising, first because we know that fertilizer generally makes plants grow better. Moreover, the wetlands in this experiment were currently not

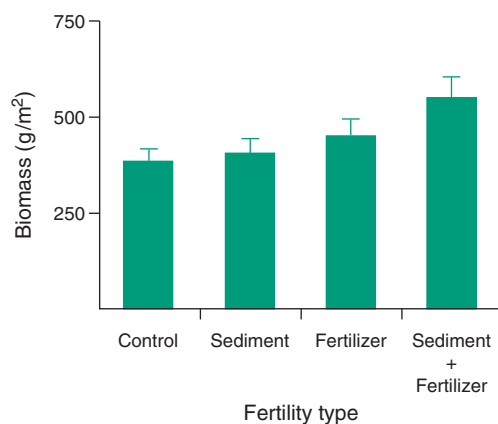


FIGURE 3.1 The short-term effects of increased fertility upon biomass of an oligohaline coastal marsh in Louisiana (mean \pm 1 SE, $n = 96$, $p < 0.001$). (From Keddy *et al.* 2007.)

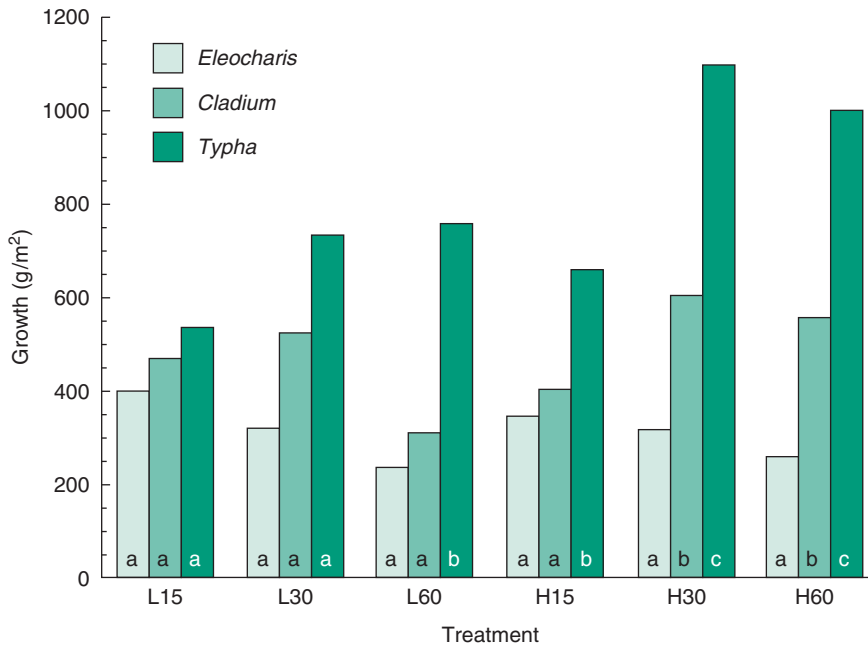


FIGURE 3.2 The effects of added phosphorus on the growth of three wetland plants, *Eleocharis interstincta*, *Cladium jamaicense*, and *Typha domingensis*. L = low nutrients ($P = 50 \mu\text{g/l}$, $\text{NO}_3 = 10 \mu\text{g/l}$), H = high nutrients ($P = 100 \mu\text{g/l}$, $\text{NO}_3 = 1000 \mu\text{g/l}$), each at water depths of 15, 30, and 60 cm. Histograms with the same letter indicate that the species are not significantly different from one another within the treatment. (From Newman *et al.* 1996.)

receiving annual spring flooding from the Mississippi River, and so were cut off from normal nutrient supplies.

Figure 3.1 showed that biomass increases with fertilization, but what of the individual species that make up the biomass? Let us switch examples to another study, one that will also be useful later in the book. Wetlands in the Everglades are naturally dominated by sedges including *Eleocharis interstincta* and *Cladium jamaicense*. These two species, and cattails (*Typha domingensis*), were experimentally subjected to two different nutrient levels. Take some time to explore Figure 3.2. First, note that all three species had similar growth – in shallow water at low nutrients. And, second, as you would expect, adding nutrients generally increased plant growth. But there were also differences among the species and treatments (Figure 3.2). First, consider the effects of fertilization. *Eleocharis* did not grow faster when fertilized. *Cladium* grew

only slightly faster. But *Typha* responded the most of all. Hence, on a relative basis, cattails were most affected by fertilization. *Typha* also grew better in the deeper water than the shallow water. Hence, more flooding and more nutrients leads to more cattails. This example typifies what has been found in many other studies – species that naturally occupy infertile areas show limited response to fertilization, it is invasive species that are best able to use the added nutrients to increase growth rates.

What about animals? Although the term fertility is normally associated with plants, there is good evidence that it may be usefully extended to other organisms such as animals and fungi, where rates of growth are also dependent upon the availability of resources. Most plant tissues have relatively low (<5%) nitrogen content, which greatly reduces their value to herbivores. We will see in Section 3.4, and in the later chapter on

herbivory (Chapter 6), just how few nutrients are available in plant tissues, and the extreme effort animals require to extract those nutrients. But we should introduce the concept here while we are still thinking generally about fertility. In order to gain precious nutrients, animals may feed selectively on newly growing shoots, or on seeds, or on the cambium of trees, in order to obtain slightly higher levels of key resources. They may have multiple chambered stomachs where microorganisms assist in breaking down plant tissues. They may even eat their own excrement to extract nutrients that the digestive system missed the first time through – a practice known as coprophagy. Coprophagy illustrates the extremes to which animals must go to obtain nutrition from plants. Beavers are a well-known example.

Hence, if fertilization increases the levels of N and P in plant tissues, we might expect it to increase the value of the plants to herbivores. Now return to Figure 3.1, and consider what happens in the presence of herbivores. In this experiment, half of the plots were surrounded by fence to keep out grazing animals, while half of the plots were open to grazing. To keep the figure simple, I have not shown the complexities of grazing effects. But they are simple to explain. Nutrients increase plant biomass – if there are no grazing animals present. In plots exposed to grazing, the newly growing plants were eaten so rapidly (mainly by nutria) that there was no change in biomass (Keddy *et al.* 2007, 2009a). Hence, in the absence of herbivores, fertilizing made more plant material; in the presence of herbivores, fertilizing apparently made more herbivores.

3.1.3 Sites lacking N and P can be called infertile or stressed

The opposite of a fertile site is an infertile site. Some wetlands, including bogs, wet pine savannas, pocosins, and parts of the Everglades, are extremely infertile. Such infertile sites can also be referred to as stressed sites. Any environmental factor that constrains plant productivity is generally termed a

stress (e.g. Grime 1977, 1979; Levitt 1980; Larcher 1995). Animal ecologists have used the word adversity to describe the same kind of constraints (Southwood 1977, 1988). Hence, we would say that plots on the left of Figure 3.1 were the most stressed of the four treatments.

Although nitrogen and phosphorus are the key elements to consider, they are of course, not the only elements that can limit plant and animal growth. For plants, other resources include potassium and magnesium, as well as carbon dioxide. In flooded sites, resources like soil oxygen can limit growth; in others (but rarely wetlands), scarcity of water has similar effects. Factors such as high salinity or low temperatures can also reduce growth rates, and therefore are also considered to affect fertility.

3.1.4 Nutrients often control primary production

The resources required by living organisms can be deduced from their chemical composition. Most, as noted, are composed of just the elements, C, H, N, O, P, and S. Table 3.1 shows the basic elemental composition of different species of wetland plants. Since plants have to accumulate the elements in this table, here is more good evidence that nitrogen and phosphorus are important. But which one is key? Here there are conflicting opinions.

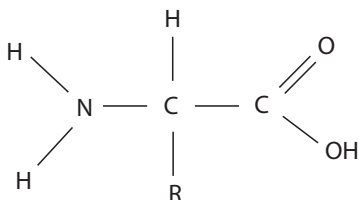
Table 3.1 Major nutrients in wetland plants

Element	Temperate species (%) ^a	Tropical species (%) ^b
N	2.26	1.99
P	0.25	0.19
S	0.41	—
Ca	1.34	0.88
Mg	0.29	0.29
K	2.61	3.10
Na	0.51	0.36

^a From Boyd (1978), *n* = 28–35.

^b From Junk (1983), *n* = 75.

The fundamental importance of nitrogen is illustrated by occurrence of an amino group ($-\text{NH}_2$) in every amino acid. Every protein requires that critical molecule of nitrogen.



The need for nitrogen is inescapable.

Some ecologists believe that nitrogen is the one key resource limiting terrestrial plant communities (Vitousek 1982; Tilman 1986; Berendse and Aerts 1987). However, such generalizations may be inappropriate for wetlands. Freshwater ecologists studying phytoplankton have concluded that phosphorus is the critical limiting nutrient (e.g. Vallentyne 1974; Schindler 1977; Smith 1982; Rigler and Peters 1995). This is why such an effort is made to remove phosphorus from sewage. So, if we seek the key nutrient controlling plant production in wetlands, would it be best to start with the terrestrial view and study nitrogen, or to start with the aquatic view and study phosphorus? There is no easy answer.

Even in lakes, where phosphorus is the essential nutrient controlling algal biomass, it seems that nitrogen does play an important role by modifying the relationship between algal biomass and phosphorus (Smith 1982). Further, as the ratio of nitrogen to phosphorus increases, cyanophytes (blue-green algae) are replaced by other phytoplankton (Schindler 1977; Smith 1983). Thus N:P ratios can control both amounts and composition of phytoplankton.

You might ask if it matters. Here is one illustration that it does. The Everglades are receiving a steady input of both nitrogen and phosphorus from sugar cane plantations, and, as a consequence, the plants are changing, with apparently negative consequences for many other species including wading birds like the wood stork. If you were in charge of Everglades conservation,

would you put your money into controlling phosphorus or nitrogen (or both)? We will look at this situation more closely in Chapter 13, but meanwhile, the case of the Everglades illustrates just why we need to separate the effects of nitrogen and phosphorus in wetlands.

3.1.5 Is it N or P? Experimental assessments of nutrient limitation

One way to assess the relative importance of elements in controlling plant growth in wetlands is to supplement the nutrients in field experiments.

Let us start with an early study of fertilization in species-rich dune slacks (a type of wet meadow) where Willis (1963) added N, P, K, and NPK fertilizer to different plots. The dominant species were *Agrostis stolonifera*, *Anagallis tenella*, *Bellis perennis*, and three species of *Carex*. The plots receiving complete nutrients (NPK) produced three times as much biomass. The greatest deficiencies, concluded Willis, were for nitrogen and to a lesser degree, phosphorus. He then transplanted pieces of turf to the greenhouse and submitted them to different fertilization treatments. The results were similar to the field trials. He concluded “the sparse growth and open character of the vegetation of the Burrows are brought about mainly by the low levels of nitrogen and phosphorus in the sand ...” This work also showed how the changes in biomass were accompanied by changes in the species composition. The field plots that received complete nutrients had fewer plant species and were dominated by grasses. Willis also observed that sedges and rushes appeared to be particularly successful in areas of phosphorus deficiency. Hence, just as N:P ratios change the kind of phytoplankton in lakes, N:P ratios may control which particular plant group dominates a wetland.

Another fertilization study was carried out in three types of bogs in southern England (Hayati and Proctor 1991). A native species of sedge, *Carex echinata*, was planted in pots of peat from each site, and then different fertilizers were applied in factorial design.

Table 3.2 Limiting factors in seven habitat types, as determined by biomass response in fertilization experiments

Habitat	N	P	K	N + P	N + K	P + K
Wet grassland	3	0	2	0	4	0
Wet heath	0	3	0	0	0	0
Rich fen	7	5	0	0	0	0
Poor fen	2	1	0	0	0	0
Litter fen	1	2	0	1	0	0
Bog	1	3	1	0	0	0
Dune slack	5	2	0	2	0	0
Total (45 cases)	19	16	3	3	4	0

Note: Figures indicate number of cases in which the element was shown to be limiting.

Source: From Verhoeven *et al.* (1996).

There were three main effects: due to N, to P, and to between-site differences. Nitrogen was more limiting in the peat from wet heathlands, whereas P was more limiting in the peat from the blanket bog. There was a minor effect of K, suggesting that it was present in adequate supply everywhere except in the blanket bog.

While growing plants in pots provides simple experimental design, it is always open to the criticism that it does not necessarily show the importance of nutrients under more natural field conditions. But it is often convenient. Studies using sediment collected from different waterways and put into pots suggested that N rather than P usually limited plant growth (Barko and Smart 1978, 1979; Smart and Barko 1978). And the work illustrated in Figure 3.2 was also done in pots, albeit rather large ones.

The number of fertilization studies grows steadily. By 1996, Verhoeven *et al.* could review no fewer than 45 studies of fertilization in seven types of herbaceous wetlands. The result? There was an almost even split between nitrogen-limited sites and

phosphorus-limited sites (Table 3.2). Co-limitation, that is, a response only to combined fertilizations, was rare. Wet heathlands all had growth limited by phosphorus, whereas fens and dune slacks could be limited by either nitrogen or phosphorus. The wet grasslands were the most complicated, with cases of N, K, and N+K limitation. Regrettably, there was no category for floodplain.

The concentration of nutrients in plant tissues tells us something about the availability of nutrients and simultaneously tells us about the value of the plants to herbivores. The same set of 45 studies was explored for tissue nutrient concentrations (Verhoeven *et al.* 1996). The typical N:P ratio in control sites was 15 : 1. Their conclusion? “[T]he N:P ratio of above-ground biomass at the end of the growing season (August) provides a reliable indicator of the degree to which each of these elements has been limiting plant growth ...”. They conclude that N:P ratios greater than 16 indicate phosphorus limitation, while N:P ratios less than 14 indicate nitrogen limitation.

3.2 Infertile wetlands are constrained by low nutrient levels

Fertility levels in wetlands range between two extremes. At the high extreme, there are large floodplains and deltaic swamps, such as those of the

Mississippi, Rhine, or Amazon, where the eroded nutrients from an entire watershed are deposited. These areas have high nutrient levels and rapid plant

Table 3.3 Ionic composition (ppm) of rainwater and of runoff from rocks of different geological origin

Site/rock type	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	HCO ₃ ⁻	SO ₄ ²⁻	Cl ⁻
<i>Rainwater</i>							
Newfoundland	0.8	—	5.2	0.3	—	2.2	8.9
Wisconsin	1.2	—	0.5	0.2	—	2.9	0.2
Minnesota	1.0	—	0.2	0.2	—	1.4	0.1
Northern Sweden	1.2	0.2	0.4	0.3	—	2.5	0.7
Central Sweden	0.6	0.1	0.3	0.2	—	2.6	0.5
Guyana	0.8	0.3	1.5	0.2	—	1.3	2.9
<i>Runoff water</i>							
Nova Scotia							
Granite	1.0	0.5	5.2	0.4	^a	5.9	7.7
Quartzite and slate	2.1	0.4	3.0	0.6	1.8	5.2	4.9
Carboniferous strata	3.0	0.6	3.6	0.5	6.1	5.3	5.4
Bohemia							
Phyllite	5.7	2.4	5.4	2.1	35.1	3.1	4.9
Granite	7.7	2.3	6.9	3.7	40.3	9.2	4.2
Mica schist	9.3	3.8	8.0	3.1	48.3	9.5	5.4
Basalt	68.8	19.8	21.3	11.0	326.7	27.2	5.7
Cretaceous rocks	133.4	31.9	20.7	16.4	404.8	167.0	17.3

^a Not detected.

Source: From Gore (1983), after Gorham (1961).

growth and enormous production of wetland animals. Because of their economic importance, these fertile wetlands often receive much attention from ecologists.

Other areas are near the low extreme, and are inherently infertile, particularly those that occur on infertile substrates and are largely dependent upon rainfall for nutrients. Rainwater has very low nutrient levels relative to groundwater, although nutrient levels do increase as water flows downstream (Table 3.3). Examples of infertile areas include:

- Depressions in rocks such as granite or gneiss, which erode slowly, and consequently provide few minerals of use to plants (e.g. Guyana Highlands of South America).
- Sand plains left by retreating continental ice sheets after the ice age (e.g. sand plains of central Wisconsin).
- Old shorelines of lakes that no longer exist because of changes in climate (e.g. shorelines of glacial Lake Algonquin along Lake Huron).
- Peatlands, where accumulated peat stores nutrients, and prevents plant roots from reaching mineral soil (e.g. West Siberian Lowland).
- Old soils where recurring fire and heavy rain have depleted soil nutrients (e.g. Gulf Coastal Plain of the United States).
- Other areas where rain is the primary source of water (e.g. Everglades).
- Local features such as sand spits produced by coastal erosion and deposition (e.g. Long Point on Lake Erie).

These infertile areas are significant for several reasons. First, they develop distinctive types of wetlands such as peat bogs, wet meadows, or wet savannas. Second, they are very sensitive to any increase in nutrient availability. Third, they



FIGURE 3.3 Many wetlands have low fertility. Examples include peat bogs (*a*, Algonquin Provincial Park, Ontario), the Everglades (*b*), shorelines in sand plains (*c*, Axe Lake, Ontario; courtesy M. Sharp) and wet savannas with old soils (*d*, Buttercup Flats, De Soto National Forest, Mississippi). (See also color plate.)

have strong gradients in plant composition related to soil nutrient levels. Since human activity tends to increase nutrients flowing into wetlands – from human sewage, from erosion, and even from pollution falling in the rain – all these types of wetlands are at particular risk from added nutrients. We shall look at four examples here: peatlands, the Everglades, sand plains, and wet savannas.

3.2.1 Peatlands

We saw in Chapter 1 that infertility is a defining characteristic of peatlands (Figure 3.3*a*). Recall that is the result of low rates of decomposition – vital nutrients like nitrogen and phosphorus remain stored in organic molecules. Hence, small amounts of

groundwater can significantly affect nutrient availability, and the kinds of plant and animals that occur (Bridgham *et al.* 1996; Godwin *et al.* 2002). When the peat layer is thin, plants can obtain nutrients from groundwater and soil, but as peat depth grows, this source of nutrients is shut off. Eventually, only the nutrients in rainfall (and of course, from small amounts of decay) are available for plants. The result is that many plants have evergreen leaves to conserve nutrients. Others are carnivorous plants that obtain nitrogen and phosphorus from the bodies of insects and other small invertebrates. You saw three examples in Figure 1.17. Hence fertility gradients are very important in controlling the species composition of peatlands.

Among the dominant plants involved in building peatlands are mosses in the genus *Sphagnum* (Figure 1.18). There may be more carbon stored in *Sphagnum*, dead and alive, than in any other genus of plant (Clymo and Hayward 1982). When groundwater is available, more genera of mosses are found, particularly so when the groundwater is calcareous – examples include the genera *Scorpidium*, *Drepanocladus*, *Brachythecium*, and *Calliergonella* (Malmer 1986; Vitt 1990, 1994). It appears that calcium gradients are most important for controlling moss composition, with a clear shift away from *Sphagnum* mosses above a pH of 5. Nitrogen and phosphorus gradients are more important for vascular plant composition. It is probably best to treat these as two independent gradients – calcium controlling the pH, nitrogen and phosphorus controlling fertility (Bridgham *et al.* 1996; Wheeler and Proctor 2000). Hence, the composition of fens is strongly affected by the chemical composition of the bedrock.

3.2.2 The Everglades

The Everglades, too, were once a vast rain-fed wetland, with extremely low nutrient levels (Figure 3.3b). This region of North America is very flat, and a slow but steady flow of water flow from north to south produced a distinctive sedge-dominated vegetation type adapted to wet infertile conditions (Loveless 1959; Davis and Ogden 1994; Sklar *et al.* 2005). Phosphorus concentrations across most of the Everglades were likely as low as 4 to 10 pg/l and loading rates averaged less than 0.1 g P/m² per year.

The distinctive communities of the Everglades are a response to these infertile conditions. Saw grass (*Cladium jamaicense*) is particularly common. Pools of shallow water have carnivorous plants in the genus *Utricularia*. Cyanophytes, which, you recall, can fix atmospheric nitrogen, are prominent in the pools, and are the basis for a

food web which eventually supports wood storks and flamingoes.

3.2.3 Sand plains and shorelines

Some parts of the world have enormous sand plains (Figure 3.3c), most often the result of outwash from receding glaciers. Since sand contains few nutrients, and since it is easily leached, sand plains have distinctive vegetation. Small lakes often form on sand plains, with distinctive wet meadow communities. The figure shows a small lakeshore on the sand plain left by glacial Lake Algonquin. Another well-known example is the New Jersey Pine Barrens (Forman 1998; Zampella *et al.* 2006; Figure 14.17). Sand plains tend to have dry ridges alternating with wet valleys. Even in sand plains best known for dune systems, small wetlands may form in the swales between dunes.

3.2.4 Wet savannas

Those readers in the north temperate zone tend to take young landscapes for granted – most northern areas were buried in ice within the last 50 000 years. Other areas of the world, however, have not been glaciated, and may contain soils that have been exposed to weathering for millions of years. On the Gulf Coastal Plain of North America, soils tend to be very infertile. Recurring fire is an important cause: when plant tissues burn, the nitrogen is often returned to the atmosphere (a process termed volatilization), while phosphorus remains in the ash, often being leached by rainfall. Hence, these soils become increasingly deficient in key elements for plant growth. At the same time, however, their flat surfaces often restrict runoff, so large wet savannas (Figure 3.3d) can form (White *et al.* 1998; Christensen 1999). These savannas are dominated by grasses and sedges, but also include many species of orchids and carnivorous plants. Carnivorous plants are so abundant that these are sometimes known as pitcher plant savannas.

3.3 Other issues related to fertility

Having considered fertility and plants from the perspectives of primary productivity and low nutrient levels in wetlands we will now explore other adaptations of plants to differing degrees of fertility and the effects of gradients.

3.3.1 Infertile habitats have unique species

Plants in infertile wetlands have to be able to tolerate chronic shortages of nitrogen and phosphorus. Infertility is a major force affecting plant evolution, and plants found in infertile conditions share a set of traits such as slow growth, evergreen foliage, the uncoupling of growth from nutrient uptake, investment in anti-herbivore defenses, and the occurrence of mycorrhizae (Grime 1977, 1979).

Figure 1.17 introduced some plants from infertile wetlands. Let us explore this topic a little more. The evolution of carnivory is one of the most dramatic consequences of infertile conditions. Carnivorous plants obtain nitrogen and phosphorus from other sources than the soil (Givnish 1988). The Venus fly-trap is one of the best-known examples (Figure 3.4a). Many other plants are evergreen; these include herbaceous genera such as *Lobelia*, *Eriocaulon*, *Xyris*, and *Scirpus* as well as many trees and ericaceous shrubs (Richardson 1981; Richardson and Gibbons 1993). It is believed that evergreenness allows nutrient investment in leaves to be amortized over longer time periods.

Some evergreen species even use CAM photosynthesis, during which carbon is stored at night for later use during daylight (Boston 1986; Boston and Adams 1986). CAM is thought to be associated with deserts – hence, its presence in some wetland plants such as *Isoetes* is unexpected. A few plants have symbiotic sources of nutrients – the widespread *Myrica gale* of bogs and lakeshores has root nodules in which nitrogen fixation occurs (Bond 1963). Many wild orchids are mycorrhizal

(see Section 3.3.5) and occur in relatively infertile wetlands – the white spikes of eastern prairie fringed orchid (*Platanthera leucophaea*) are an increasingly rare sight, as the species is threatened or endangered throughout its range (Figure 3.4b).

In general, wetland managers will often find that infertile wetlands have rare species and relatively low rates of growth. Hence they are inordinately sensitive to factors like sedimentation from logging and disturbance from all-terrain vehicles or cattle.



FIGURE 3.4 Infertile wetlands often provide habitat for unusual plant species. (a) The Venus fly-trap (*Dionaea muscipula*; from Pietropaolo and Pietropaolo 1986), restricted to a few coastal bogs in the Carolinas. (b) The eastern prairie fringed orchid (*Platanthera leucophaea*; from Reddoch and Reddoch 1997), threatened or endangered throughout its range in North America.

3.3.2 Fertile habitats often have fast-growing species

In highly productive habitats, nutrients are, by definition, not limiting to growth. In such circumstances, light soon becomes limiting. Plants tend to be tall and fast-growing. Canopies are rapidly produced in the spring using reserves from buried rhizomes (Figure 3.5). Competition for light has been a factor in plant communities since the first terrestrial plants began to form erect shoots and shade one another. Thus, in herbaceous vegetation,

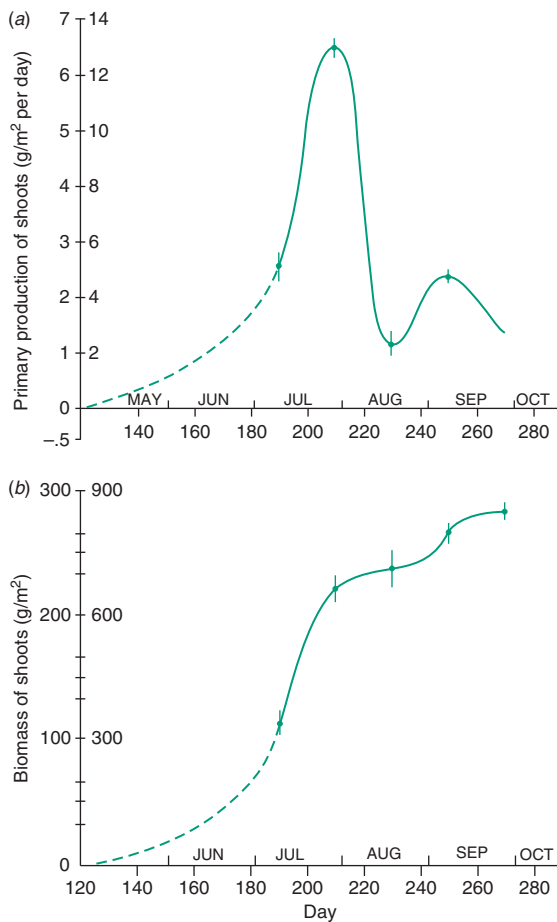


FIGURE 3.5 On fertile sites, there is rapid production of shoots in the spring, as shown by (a) primary production and (b) biomass as a function of time of year. (After Auclair *et al.* 1976b.)

tall shoots, broad canopies, and deeply rooted rhizomes for support all can be regarded as traits that arose out of intense competition for light (e.g. Grime 1979; Givnish 1982).

Dense stands of plants with tall shoots arising from deeply buried rhizomes occur around the world. Three examples are papyrus (*Cyperus papyrus*) along the Nile, reeds (*Phragmites australis*) along the Baltic Sea in Europe, and cattails (*Typha* spp.) in the Mississippi River delta. Most of these plants are in one evolutionary lineage, the Monocotyledonae, with the vast majority being in the Cyperaceae (e.g. *Carex*, *Scirpus*, *Eleocharis*, *Cyperus*, *Rhynchospora*, *Cladium*) or the Poaceae (*Calamagrostis*, *Glyceria*, *Oryza*, *Phragmites*, *Phalaris*, *Panicum*). Other families include the Typhaceae (*Typha* spp.), Sparganiaceae (*Sparganium* spp.), and Juncaceae (*Juncus* spp.).

While these areas may have high primary production, plant diversity is often low. 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; Moore *et al.* 1989). Since many species of waterfowl require open areas of water, and a mixture of different vegetation types for feeding, dense stands composed of a single species are often undesirable for wildlife as well. Wildlife managers strive for “hemi-marshes” that have a 50 : 50 mix of emergent vegetation and open water, as well as other sources of plant diversity such as shrub borders (Verry 1989). High fertility increases the rates at which the plants grow and refill gaps. Hence, managers often have to resort to artificially changing water levels, or burning, or even using heavy equipment, to retain the desired mixture of habitat types. We will return to this topic in Section 3.5.

3.3.3 Fertility gradients organize wetlands at different scales

Differences in fertility can explain many of the patterns one sees in wetlands. Within watersheds, for example, the headwaters may have small

sandy-bottomed streams, while the river mouth may have deep alluvial sediments. Within one lake, shores exposed to waves will have coarse infertile substrates, whereas shores in sheltered bays will have rich accumulations of silt, clay, and organic matter.

To illustrate the differences caused by soil fertility gradients, wetland plants can be grown in sediments collected from different habitats. For example, Smart and Barko (1978) grew four different marsh plants in different types of sediment. They found that the growth rates of these plants (*Spartina alterniflora*, *S. foliosa*, *S. patens*, and *Distichlis spicata*) were an order of magnitude higher on clay than on sand, with intermediate growth on silty clay. Similar kinds of experiments have shown that growth on fine substrates is much higher than growth on coarse ones for a wide range of wetland plants including submersed aquatics (Denny 1972), emergents (Barko and Smart 1978), and species on seasonally flooded shores (Sharp and Keddy 1985; Wilson and Keddy 1985).

One way to visualize the many effects of fertility is through multivariate analysis. One first collects information on a large number of plots, and then uses one of several multivariate methods to explore how measured nutrient levels are related to biological factors (Shimwell 1971; Digby and Kempton 1987). Figure 3.6 shows a typical result – the interrelationships of soil nutrients, biomass, and primary productivity in a riparian wetland. In this case, biomass and productivity are positively correlated with nitrogen ($r = 0.38, 0.39$) but negatively correlated with phosphorus ($r = -0.29, -0.23$).

It is difficult to know how far one can generalize from these sorts of studies. In a nearby *Carex*-dominated ecosystem, there were no significant correlations between production and either N or P (Auclair *et al.* 1976b). It appears that generalizations are difficult to achieve! Perhaps the relationships between fertility and biological factors such as biomass depend upon the scale at which you look. If you sample a small homogeneous area, patterns may not be detectable at all. If you sample a large heterogeneous area, patterns may be clear. To illustrate this scale effect, I have assembled a set of tables (Table 3.4)

showing correlations between nutrients and biological factors at five different scales, from the large scale down to the small scale. Let us begin at the large scale.

The upper panel (Table 3.4a) shows correlations among major nutrients in a series of wetland types representative of eastern North America, ranging from highly fertile sites (e.g. *Typha* marshes and floodplains) to highly infertile sand or gravel shorelines where insectivorous genera such as *Drosera* and *Utricularia* were common. At this scale, all major nutrients are positively correlated, so one can reasonably talk about fertility gradients without distinguishing among the major nutrients. Both organic matter and the silt and clay content are also positively correlated with these nutrient levels. This makes sense, since nutrients can attach to organic matter or clay particles.

At the intermediate scale, Table 3.4b shows correlations among major nutrients within a single lake. This gradient results from wave action and ice scour (Chapter 4). Again, major nutrients are positively correlated. Similar patterns occur within a single watershed (Table 3.4c).

Moving to smaller scales at the bottom of the table, at the most local scale, this pattern begins to disappear. Table 3.4e shows correlations among nutrients within one vegetation type – the *Carex* meadow mentioned above. Note that nitrogen is still positively correlated with soil organic matter, but phosphorus is negatively correlated with nitrogen. Similar results occur in the more heterogeneous *Scirpus*–*Equisetum* wetland (Table 3.4d). In neither of these latter habitats is N significantly correlated with P.

Hence, at landscape scales, natural fertility gradients appear to be a general feature of wetlands. At local scales, these patterns may be harder to detect.

3.3.4 Fertility gradients and the composition of peatlands

We have seen that peatlands are generally infertile, and that fens are strongly affected by the chemistry of the groundwater. Let us look at a few more examples.

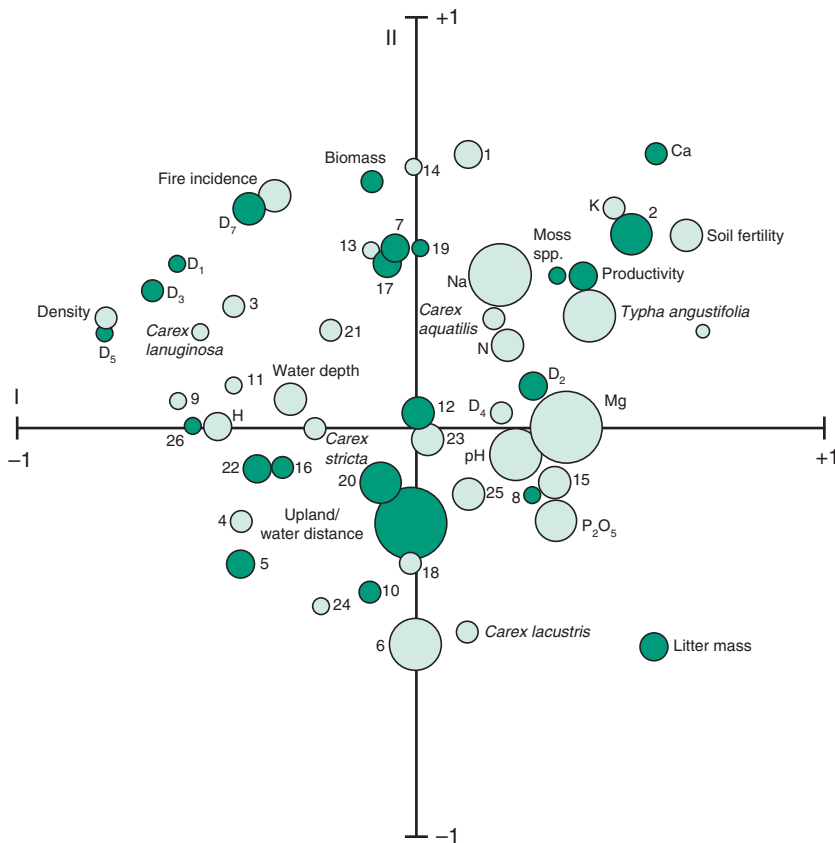


FIGURE 3.6 The interrelationships of fertility, productivity, and other biological features in a riparian wetland in eastern Canada. The multivariate method is factor analysis. The first and second components are shown on the horizontal and vertical axes, respectively. Factor loadings on the third component are represented by circle diameters (light = negative, dark = positive). D₁–D₇ are species diversity indices. Other variables include: 1, soil organic matter; 2, soil (Ca + Mg)/(K + Na); 3, days elapsed after 1 May; 4, tussock incidence; 5, distance to upland; 6, distance to water; 7, biomass; 8, average stem height; 9, *Equisetum fluviatile*; 10, *Onoclea sensibilis*; 11, *Thelypteris palustris*; 12, *Potentilla palustris*; 13, *Viola pallens*; 14, *Hypericum virginicum*; 15, *Galium palustre*; 16, *Lysimachia thyrsiflora*; 17, *Lythrum salicaria*; 18, *Cicuta bulbifera*; 19, *Utricularia vulgaris*; 20, *Impatiens capensis*; 21, *Lycopus uniflorus*; 22, *Campanula aparinoides*; 23, *Carex diandra*; 24, *Calamagrostis canadensis*; 25, *Sparganium eurycarpum*; 26, *Sagittaria latifolia*. (From Auclair *et al.* 1976a.)

In central North America, Glaser *et al.* (1990) studied a large peatland that included fens and a raised bog. This site had a strong chemical gradient. For example, the rich fens had a pH above 7 and Ca concentrations ranged from 20 to 45 mg/l. In contrast, the raised bog had a pH below 4 and a Ca concentration below 1.1 mg/l. The number of plant species tended to increase with rising pH and

Ca concentrations. In the foothills of the Rocky Mountains, Slack *et al.* (1980) described peatlands having pools of water alternating with raised ridges, a patterned peatland such as you saw in Figure 1.6a. The distribution of plant species was closely related to water level, with the wetter areas tending to be dominated by the moss *Scorpidium scorpioides* and the sedge *Carex limosa*.

Table 3.4 Fertility gradients in wetlands from large scale (top) to small scale (bottom). Note that patterns fade as the scale becomes smaller

(a) Marshes in northeastern North America

	% organic	P	N	K	Mg	pH
Standing crop	0.77	0.76	0.66	0.58	0.67	−0.28
% organic	1.00	0.77	0.57	0.50	0.51	−0.47
P		1.00	0.72	0.56	0.66	−0.13
N			1.00	0.53	0.63	−0.02
K				1.00	0.70	−0.28
Mg					1.00	−0.14

Source: From Gaudet (1993), Table 1.2.

(b) The shores of a temperate zone lake

	Mg	% organic	P	K	pH
Standing crop					
Mg	1.00	0.52	0.86	0.73	0.22
% organic		1.00	0.51	0.48	0.16
P			1.00	0.64	0.20
K				1.00	0.09
pH					1.00

Source: From Keddy (1984).

(c) One wetland complex in the Ottawa River watershed

	% organic	P	N	K	Mg	pH
Standing crop	0.74	0.80	0.69	0.76	0.69	−0.45
% organic	1.00	0.80	0.61	0.66	0.62	−0.61
P		1.00	0.62	0.82	0.59	−0.46
N			1.00	0.68	0.53	−0.18
K				1.00	0.64	−0.35
Mg					1.00	−0.72

Source: From Gaudet (1993), Table 1.4.

(d) One vegetation zone of the St. Lawrence River

	Standing crop	% organic	P	N	K	Mg	pH
Standing crop	1.00	0.34	−0.29	0.38	0.49	0.17	0.21
% organic		1.00	−0.27	0.37	0.75	0.59	0.18
P			1.00	−0.01	−0.48	0.33	−0.55
N				1.00	0.39	0.32	0.14
K					1.00	0.43	0.38
Mg						1.00	0.12
pH							1.00

Source: From Auclair *et al.* (1976a), Table 1.

Table 3.4 (cont.)

(e) *Carex* meadows, St. Lawrence River

	Standing crop	% organic	P	N	K	Mg	pH
Standing crop	1.00	0.13	−0.02	−0.02	−0.22	−0.23	−0.11
% organic		1.00	−0.39	0.30	0.52	0.17	−0.14
P			1.00	−0.26	0.18	−0.21	0.03
N				1.00	0.24	0.26	0.04
K					1.00	0.16	−0.01
Mg						1.00	0.52
pH							1.00

Source: From Auclair *et al.* (1976b), Table 1.

In European peatlands, similar patterns and gradients are evident, although distance from the sea often becomes an added factor, particularly in controlling Na, Mg, and Cl concentrations (Malmer 1986; Wheeler and Proctor 2000). One large wetland occurs in the floodplain of the Biebrza River in northeast Poland (Wassen *et al.* 1990). The larger part consisted of fens with species such as *Carex lasiocarpa* and *C. chordorrhiza* but floodplain marshes occurred further downstream and along river margins dominated by *Glyceria* (Palczynski 1984). Shrubs such as *Betula humilis* occurred on drier sites. Parts of the valley are mowed and grazed by either cattle or elk. Flood frequency and soil nutrients were apparently the primary factors controlling species composition. The number of plant species was greatest (33 species/10 m²) in those fens receiving only groundwater and having low productivity (ca. 1 kg/m²); the typical sedge was *Carex limosa*. The number of plant species was lowest in the fertile *Glyceria maxima* floodplains (13 species/10 m²) where productivity was highest (ca. 6 kg/m²).

A survey of 45 fens in New York State documented the importance of groundwater characteristics in controlling species composition (Godwin *et al.* 2002). In particular, this study documented the importance of setting in the

landscape: geology, connection to watercourses, and wetland area were all important factors affecting composition. The pore water of isolated fens was significantly more enriched than the pore water of fens connected to surface water. Hence, it would appear that fens are particularly sensitive to changes occurring in the surrounding landscape.

Peatlands also occur in the southern hemisphere. The Magellanic moorland comprises some 44 000 km² distributed along the southwestern edge of South America, from Tierra del Fuego north to about 45° S (Arroyo *et al.* 2005). These peatlands tend to be embedded within a matrix of southern temperate forest. There is a strong gradient in rainfall and wind speed, declining inland from west to east. In the drier east, ombrotrophic blanket bogs are most common, and *Sphagnum* is dominant. In the wet and exposed western regions, cushion-forming plants are more common than *Sphagnum*. This region has a flora with an evolutionary history rooted in the old continent of Gondwana; hence the species and families are often unfamiliar to those with experience in the northern temperate zone – typical wetland dominants include *Astelia* (Bromeliaceae), *Donatia* (Donatiaceae), and *Gaimardia* (Centrolepidaceae). In spite of the fact that the names and evolutionary origins are different, gradients of moisture supply, nutrients, and location remain important factors controlling peat depth and species composition.

3.3.5 Mycorrhizae can supplement nutrient availability

Fungi associated with plant roots are called mycorrhizae. They assist in taking up nutrients, particularly phosphorus, from infertile soils (e.g. Read *et al.* 1976; Smith and Douglas 1987; Marschner 1995). The orchids are one group that are well known for having mycorrhizae (recall Figure 3.4b). In general, we can say that mycorrhizae are widespread across the plant kingdom. For example, in coniferous forest, more than 90% of the species are infected. We also know that mycorrhizae are particularly important for phosphorus uptake. Yet, in spite of their general importance, mycorrhizae are not so prevalent in wetlands (e.g. Anderson *et al.* 1984; Peat and Fitter 1993; Cornwell *et al.* 2001). This may be another consequence of hypoxic soils – most fungi require oxygen to grow. We may speculate, therefore, that soil nutrient gradients – particularly phosphorus gradients – are even more important in wetlands than in terrestrial habitats.

In one survey across many species and moisture levels, mycorrhizal infection declined with flooding from 27% infection in dry areas to less than 1% in wet areas (Rickerl *et al.* 1994). *Carex atherodes* and *Juncus tenuis* had no mycorrhizae. *Scirpus fluvialis* had no mycorrhizae in wet sites, but was slightly colonized in dry areas.

Or consider the enormous sedge genus, Cyperaceae, which often occupies infertile habitats – an example is the vast areas of saw grass (*Cladium jamaicense*) in the Everglades. Sedges are apparently not commonly

mycorrhizal (Peat and Fitter 1993). In the sedge genus *Carex* there seem to be three groups, one group that is not mycorrhizal, one group that is consistently mycorrhizal, and one group where status is closely dependent upon local conditions (Miller *et al.* 2001). In fens, all the dominant monocots appear to be non-mycorrhizal, although the subdominant dicots are mycorrhizal (Cornwell *et al.* 2001).

There are other exceptions – the aquatic plant *Lobelia dortmanna* is mycorrhizal. This may be related to the release of oxygen by *Lobelia* roots, which can create local aerobic pockets (Pedersen *et al.* 1995).

Bogs also appear to be exceptions. Overall, there are three main types of mycorrhizal association (endomycorrhizae, ectomycorrhizae, and ericoid mycorrhizae), each associated with different soil types (Read *et al.* 1985; Lewis 1987). In bogs, the ericoid association is predominant. In this mycorrhizal association, ascomycete fungi are affiliated with ericaceous plants. The fine individual hyphae, ramifying near the soil surface, appear to capture nitrogen (Read *et al.* 1985; Lewis 1987). Ericoid mycorrhizae apparently provide lower rates of nitrogen uptake than other mycorrhizae, thereby supporting correspondingly low plant growth rates (Woodward and Kelly 1997).

In general, then, it appears that the anoxic conditions in wetlands reduce the presence and abundance of most mycorrhizae. This limits nutrient uptake, particularly phosphorus uptake. But there are also conspicuous exceptions.

3.4 Animals and fertility

The very concept of fertility is usually seen to be an issue only for plant ecologists. It is not. Although many studies focus on plants as a source of energy for animals, it is possible that plants are equally important as a nitrogen source (White 1993). Animals must get their nitrogen from plants in the form of ready-made amino acids. Because nitrogen is in such short supply, plants are very economical in their use

of nitrogen. Table 3.1 suggested an average nitrogen content of around 2%, less than half that of animal tissues. Even when plants are grown under fertile conditions, nitrogen content is rather similar and very low – between 0.5% and 2% (Figure 3.7). At very best, by concentrating on seeds, pollen, or cambium, animals may be able to harvest a food source that is about 5% nitrogen dry weight (White 1993). This has

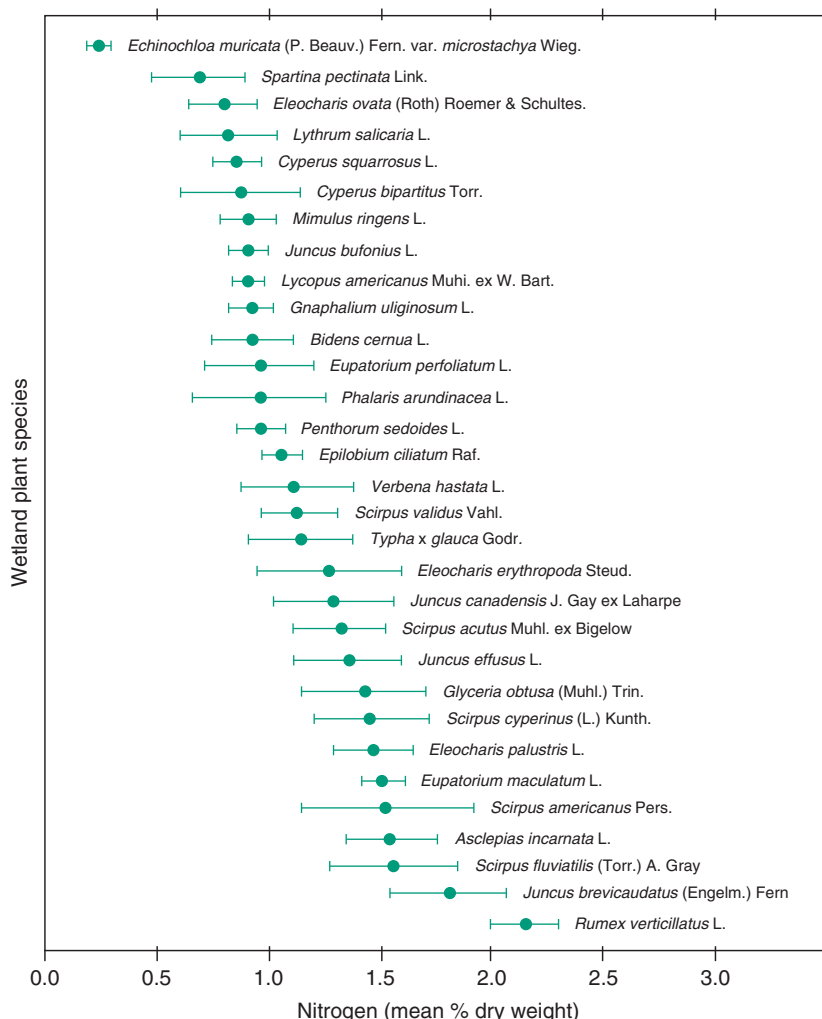


FIGURE 3.7 Nitrogen concentration of emergent wetland plants grown under similar conditions with sustained fertilization. Such concentrations provide an impoverished diet for animals ($n = 4$ or 5 , error bars denote SD). (From McJannet *et al.* 1995.)

led some to suggest that nitrogen, not energy, is the limiting resource for animal communities. White provides extensive documentation of nitrogen limitation in the animal kingdom. Animals may therefore be more sensitive to soil fertility gradients than we might at first assume.

We already know that plants, although bathed in atmospheric nitrogen, are often desperately short of nitrogen. It now appears that the situation may be even worse for animals. White therefore suggests that animals have been strongly selected to counter these environmental shortages. He identifies six basic strategies:

- (i) synchronizing life cycles with availability of food with higher nitrogen content;
- (ii) selecting those tissues with higher N content;
- (iii) eating quickly and digesting more efficiently;
- (iv) supplementing plant food with animal protein;
- (v) territoriality and social behavior;
- (vi) enlisting the help of microorganisms.

Many examples of (i) to (v) can be seen throughout the animal kingdom. We could reinterpret a majority of dietary studies around the theme of extracting nitrogen from an impoverished environment. White's book is replete

with examples. This is useful to consider before beginning the chapter on herbivores – wetlands may look green, but much of the green tissue may be of little value to herbivores.

Point (vi) may be worth a brief digression. Over the past decades, plant ecologists have increasingly studied the role of mycorrhizae in plant nutrient budgets. Now White reminds us that animals too have associations with microorganisms to cope with

chronic nutrient limitations. For example, microorganisms provide a large part of the nitrogenous food of ruminants (Janis 1996). Instead of excreting urea in urine, ruminants will often transport urea back to the rumen. Some nitrogen-fixing microorganisms live in animal guts. Perhaps the use of microorganisms to escape nitrogen limitation is an important evolutionary parallel in plants and animals.

3.5 Eutrophication: too much of a good thing

We have already discussed the effects of nutrient levels on fertility. What happens when eutrophication occurs and why?

3.5.1 Human activity often increases nutrient levels in wetlands

A major consequence of industrialized civilization has been the erosion of soils and heavy fertilization of agricultural ecosystems. As a consequence, nitrates and phosphates have increased in rainwater and runoff (Figure 3.8). Moreover, much of the nitrogen used in agriculture has not been obtained from natural sources, but extracted from the atmosphere industrially using the Haber process. This process was only developed in the early 1900s, but it has radically altered the global nitrogen cycle by vastly increasing the amount of biologically available nitrogen in the biosphere (Pimental *et al.* 1973; Freedman 1995). To put the Haber process in context, the amount of industrially fixed nitrogen applied to crops during the period 1980 to 1990 more than equaled all industrial fertilizer applied previously in human history (Vitousek *et al.* 1997).

Wetlands are places where such nutrients tend to accumulate. Overall, there seem to be four general consequences. First, in marshes and wet meadows, fertilization alleviates nutrient limitation, and causes an increase in biomass, thereby reducing the number of species present. Small plants, carnivorous plants, and evergreen plants are particularly likely to

disappear. Second, those plants receiving the nutrients may become more palatable to herbivores, increasing herbivore populations. Third, in shallow water, increased populations of floating algae can kill aquatic macrophytes. Fourth, when the algae and macrophytes decay, oxygen is consumed, leading to hypoxic conditions that kill fish.

The study of nutrients in lakes helps us understand impacts on wetlands, which often fringe lakes. Eutrophication has had major negative effects upon fish production in the Great Lakes (Christie 1974; Vallentyne 1974). Decreasing N:P ratios can also cause nitrogen-fixing cyanobacteria to replace other

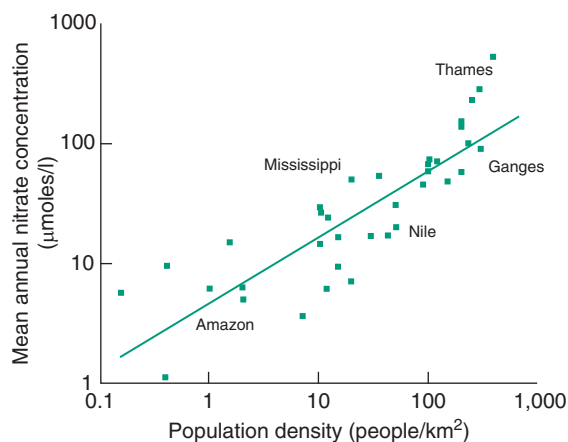


FIGURE 3.8 Nitrate concentration of water in 42 major rivers plotted against population density in the surrounding region. (From World Resources Institute 1992.)

species of planktonic algae (Schindler 1977; Smith 1983). So let us look more closely at the process of eutrophication in lakes.

3.5.2 Runoff carries nutrients into lakes, rivers, and wetlands

So far we have treated fertility as an independent variable, and we have asked about its effects on wetlands. Now let us move back one step in causation, and treat fertility as the dependent variable. Let us ask what factors determine the levels of nutrients arriving in a wetland. There is a large scientific literature on this topic because the negative effects of eutrophication upon water quality have been a matter of great concern for decades (e.g. Vallentyne 1974; Rigler and Peters 1995), and because the effects of eutrophication on wetlands like the Everglades are increasingly obvious (Newman *et al.* 1998; Sklar *et al.* 2005).

Since the Great Lakes, North America, are among the largest bodies of fresh water in the world and have been well studied, let us use them as the main example (International Joint Commission 1980). Phosphorus is the major nutrient of interest, owing to the fact that these studies were carried out with an emphasis upon phytoplankton and fish production. Table 3.5 shows that the major sources of phosphorus in the Great Lakes arise from sources including urban areas, land use (mostly rural), and atmospheric deposition. Let us consider urban and

rural runoff first, leaving atmospheric deposition for Section 3.5.3.

Urban areas can be considered to be point sources, unlike rural areas which are diffuse sources of nutrients. Point sources have high inputs per hectare from small areas, whereas diffuse sources have low inputs per hectare but from much larger areas. To help us think clearly, we can use forested areas as a natural reference point. They have the lowest levels of P loading, less than a kilogram per hectare per year, often much less (0.02 to 0.67 kg/ha per year). Urban areas may contribute much more phosphorus, from 0.1 to 4.1 kg/ha per year. Areas under construction have an even higher load as a consequence of soil erosion (see also Guy 1973 and Chapter 7). Apart from erosion during construction, sewage is an obvious factor in urban areas. Runoff into storm sewers is also important: the latter contains high concentrations of nutrients from lawns and pet feces. Such urban nutrient sources are rather straightforward – one needs proper sewage treatment, and effective treatment of runoff from storm sewers. These can be dealt with technologically (wastewater treatment) or culturally (by encouraging citizens to reduce lawn area, use less fertilizer, or reduce the numbers of outdoor pets).

Rural land use is very variable. Runoff contributes from 0.1 to 9.1 kg P/ha per year. The amount of phosphorus in stream water has been related to a variety of predictors that describe land use. The lowest levels, as you might expect, are for areas

Table 3.5 Major sources of phosphorus (metric tonnes) in the Great Lakes

Source	Lake Superior	Lake Michigan	Lake Huron	Lake Erie	Lake Ontario
Municipal sewage	268	2298	515	6828	2815
Industrial	135	279	122	347	102
Land use	2238	1891	2442	8445	3581
Atmospheric	1566	1682	1129	774	488
Upstream lakes	—	—	657	1070	4769
Total	4207	6150	4857	17 464	11 755

Source: After International Joint Commission (1980).

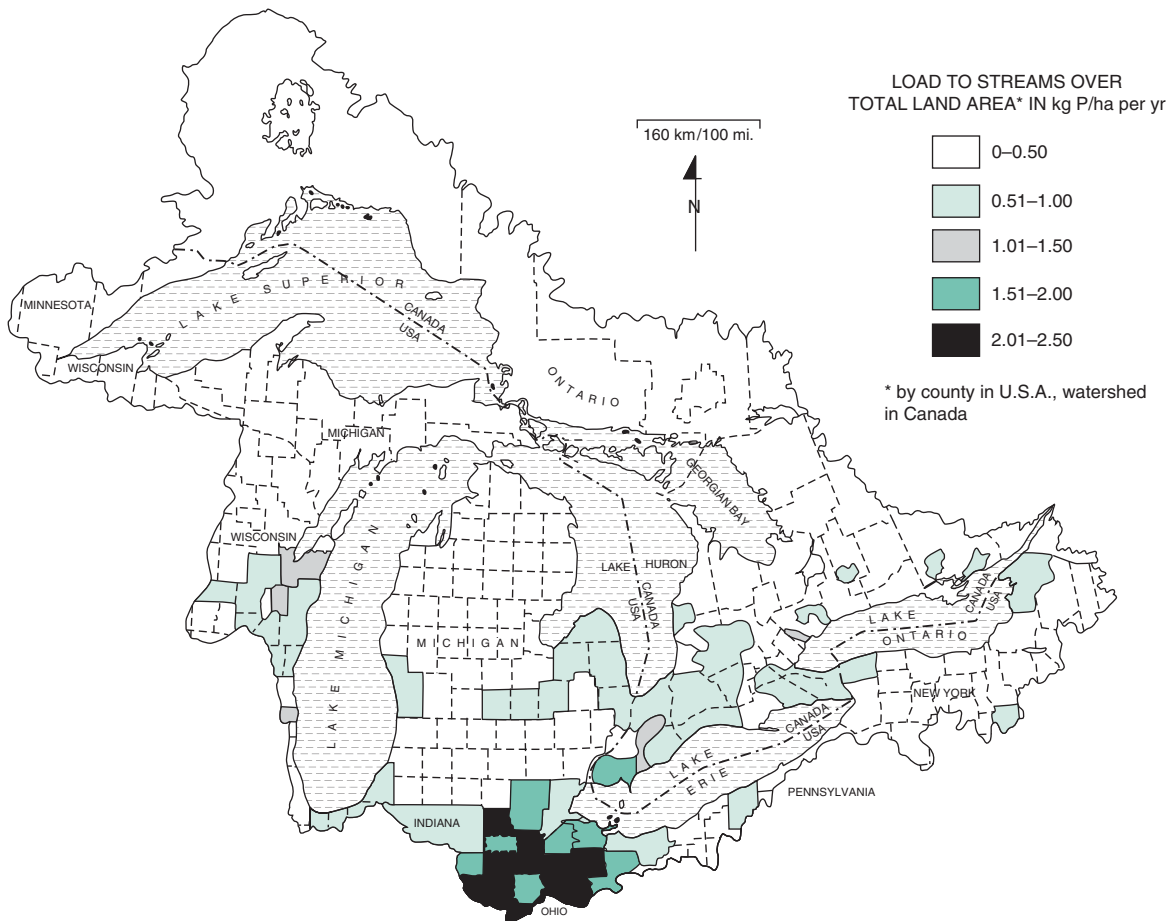


FIGURE 3.9 Agricultural contributions to nutrient levels in streams entering the Great Lakes. (After International Joint Commission 1980.)

under forest. The best predictor for high phosphorus is the amount of the watershed in row crops (International Joint Commission 1980). In lakes with agricultural watersheds (Lake Michigan, Lake Huron, Lake Erie) two-thirds of the diffuse load of nutrients was attributable to runoff from cropland (Figure 3.9). In watersheds without agriculture, forestry becomes a more important source of nutrient loading to lakes. In an artificially deforested watershed, dissolved nitrogen jumped from ca. 1.0 to >40 kg/ha of nitrate, and from ca. 33 to >300 kg/ha of particulates (Bormann and Likens 1981). Sediment yield is also affected by the nature of forestry practices, with

a commercial clearcut yielding turbidity values between 10 and 10^2 times larger than a cut conducted to protect water values (Lee 1980). Road construction is one of the greatest impacts of forestry upon water quality (Forman and Alexander 1998). Agriculture and forestry can therefore be modified to greatly reduce diffuse nutrient loading.

The Great Lakes can be considered the classic example for the study of nutrient inputs from watersheds. Now let us consider a few more examples. Much further south, in Tampa Bay, the largest open-water estuary in Florida, over 2 million people live in the adjoining watershed, contributing

nitrogen, phosphorus, and suspended solids (Greening 1995). Shading by algae has damaged seagrass (*Thalassia testudinum*) beds. Nitrogen was emphasized in this study, with over half of the nitrogen loading attributable to diffuse sources including residential runoff (13%), rangelands (14%), and intensive agriculture (6%). A further one-fourth came from atmospheric deposition. Thus, a full three-fourths of the nitrogen load came from non-point sources. Although this study represented a different geographical region, and a different major nutrient, the importance of rural land use was again emphasized.

In the nearby watershed of Lake Okeechobee, dairy farms are the major source of phosphorus loading, followed by cattle ranching (Rosen *et al.* 1995). Land management activities have been undertaken to reduce phosphorus loading; these included fencing cows away from streams, maintaining vegetation strips adjacent to streams, constructing cattle crossings over streams, and recycling dairy barn wash water. In some cases, there have been cash payments to buy out dairies, with restrictive deeds on the property to prevent future use as a dairy. Changing the use of land is quite a different technical problem from constructing urban sewage treatment plants, but as the above studies show, it is equally important for the reduction of eutrophication of wetlands.

We should briefly mention two other examples of downstream effects from nutrients produced by intensive agriculture, the Everglades and the Gulf of Mexico. Upstream land use is a major cause of eutrophication in the Everglades. When changes in land management upstream were unable to reduce nutrient levels sufficiently, managers built enormous treatment ponds, where, it is hoped, agricultural runoff can be treated much like point sources of pollution (Newman *et al.* 1998; Sklar *et al.* 2005). It is, however, not yet proven that plants in treatment ponds can sufficiently reduce nutrient levels, and the costs involved may require managers to consider purchase and decommissioning the sugar cane fields. The Gulf of Mexico is surprisingly similar. Here

nutrients generated far upstream, as far north as the cropland south of Lake Erie in Figure 3.9, are transported south by the Mississippi River, where they generate large populations of phytoplankton along the coast. When the phytoplankton die, they sink in the water and decay, producing a large hypoxic zone (known popularly as “the dead zone”) which damages marine fisheries (Mitsch *et al.* 2001; Turner and Rabelais 2003). Such examples invite you to consider how nutrients link humans to wetlands – the sugar you consume in your diet is responsible for gradual destruction of the Everglades, while the corn that is used to produce beef is damaging fish production in the Gulf of Mexico.

You will often hear that wetlands are nutrient sinks which trap nitrogen and phosphorus, reducing the eutrophication of downstream aquatic ecosystems (Richardson 1985). Is this true, and what might its effects be upon the wetlands? Comparative studies of phosphorus retention capacity among 20 sites showed, however, that it was extremely variable, with a phosphorus absorption index ranging from 163 in swamp forests to a mere 8 in pocosin peats (Richardson 1985). Richardson then compared four different sites that had received high loadings of phosphorus-laden wastewater. The abandoned old field continued to remove 96% of the added phosphorus in spite of a loading three times as high as the three wetlands (Figure 3.10). “Collectively, these data indicate that high initial rates of phosphorus removal will be followed by large exports of phosphorus within a few years” (p. 1426).

The design of artificially constructed wetlands for removing nutrients from wastewater (Hammer 1989, Kadlec and Knight 2004) is a topic we will consider further in Section 11.3.5. If there is an emerging consensus, however, it is the view that it is better to manage landscapes carefully to reduce the nutrients that are released, rather than to try to remove the nutrients once they have entered surface water. The fact that nutrients are increasingly falling in rain and snow only serves to emphasize the need to address the problem at its source.

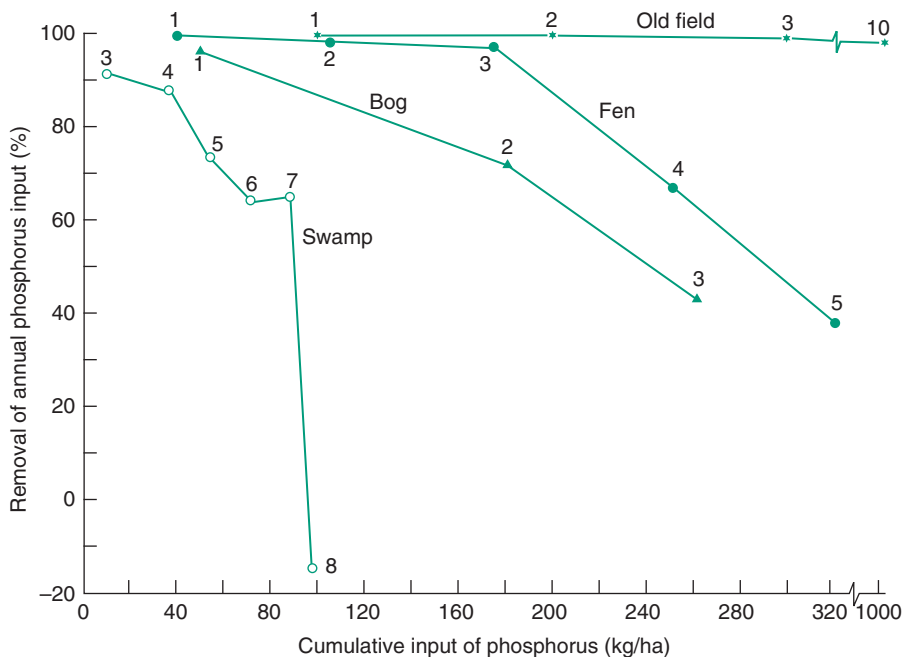


FIGURE 3.10 The change in phosphorus removal efficiency of four habitats – a fen, a white cedar swamp forest, a blanket bog, and an abandoned old field – as a function of cumulative phosphorus inputs. The numbers along each line indicate the number of years of phosphorus addition. (From Richardson 1985.)

3.5.3 Precipitation also is a source of nutrients

Although sewage and runoff are the major sources of nutrient inputs to some wetlands, nutrients carried by precipitation also fertilize landscapes (see line 4 in Table 3.5). Much of this comes from human sources, but even before humans began generating pollution, dust storms in deserts contributed nutrients to the atmosphere. The dust was transported long distances and fell in rain (Jickells *et al.* 1998). The large areas of the Earth that are covered with loess or wind-deposited soil testify to the enormous amounts of dust that move through the atmosphere. In addition to these sources, the burning of fossil fuel, and to a lesser extent, biomass, now adds both nitrogen and sulfur to rainfall (Vitousek *et al.* 1997). Over the last century, the concentration of nitrogen-containing compounds in rainwater has steadily increased. Germany now

receives in the order of 25 kg N/ha each year in rainfall (Ellenberg 1989). This is enough to produce significant changes in vegetation. More recently, pollution control measures may be having some positive effect. In the United States, over the period of 1980–92, SO_4^{2-} concentrations fell at 42 of 58 monitoring sites in the country (Lynch *et al.* 1995). Less than a fifth of these sites showed significant declines in NO_3^- , however.

There are good reasons for expecting atmospheric pollution levels to continue increasing, given the growth of the world's population and the burning of coal and oil. To put the problem in context, long pollution records can be obtained from ice cores taken from glaciers (Figure 3.11). These data suggests that any short-term reductions of nutrients in precipitation still leave us well above pre-industrial deposition rates. The scattered peaks of sulfate deposition can be traced back to volcanic eruptions such as Lab (1783) and Tambora (1815).

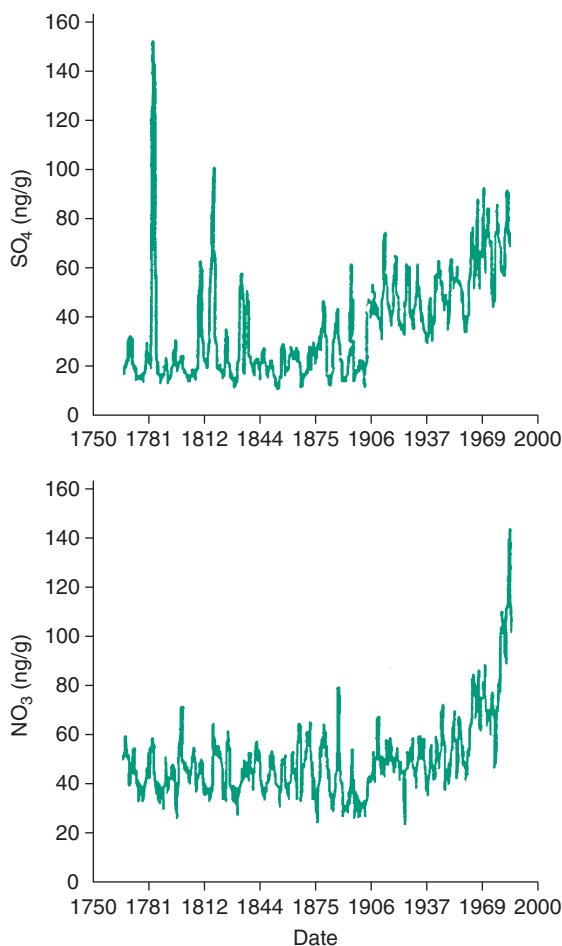


FIGURE 3.11 Sulfate (top) and nitrate (bottom) concentrations in glacier ice taken from Greenland. (From Mayewski *et al.* 1990.)

The ratio of nutrients in rainfall has also been changing. Pre-industrial concentrations of nitrate were roughly twice those of sulfate; in contrast, at the turn of the nineteenth century, they were nearly equivalent. Recent surges in nitrate emission have again caused nitrate levels to exceed sulfate (Mayewski *et al.* 1990). Hence, the changes associated with eutrophication seem likely to continue as both runoff and rainfall are contaminated by high levels of elements including nitrogen and phosphorus.

3.5.4 Eutrophication reduces diversity in wet meadows and marshes

In general, higher nutrient levels lead to higher amounts of biomass. Higher amounts of nutrients, combined with higher biomass, almost without exception cause the composition of wetlands to change, and plant diversity to decrease. It is important to understand the pattern: that increased nutrient levels reduce plant diversity, particularly affecting uncommon types of species. Since managers are faced with these sorts of nearly irreversible changes, it is also important to understand the mechanism that causes these changes. Many arise out of the effects of fertility upon competition, which we shall explore in more detail in Chapter 5. But let us have a quick introduction here.

Experimental fertilization provides one tool for studying effects of eutrophication. Figure 3.12 shows the results from a study where 12 experimentally created wetland habitats were generated under both low and high fertility. High fertility levels led to much higher levels of biomass (left, dark histograms), irrespective of the habitat types. Simultaneously, high fertility levels led to reduced numbers of plant species (right, dark histograms). The general explanation is that fertilization increases competition, particularly for light, as we shall see in Chapter 5.

We shall see field data from wetlands in eastern North America show similar patterns (Section 9.4). We will see more about this problem in the Everglades in (Section 13.2.2). Fertilization in salt marshes also results in dramatic changes in zonation (Section 10.3.7).

3.5.5 Eutrophication can lead to die-offs of aquatic plants

The effects of eutrophication on aquatic wetland communities are studied rather less than effects on phytoplankton and fish. It often appears that eutrophication is associated with declines in the abundance of macrophytes. This at first

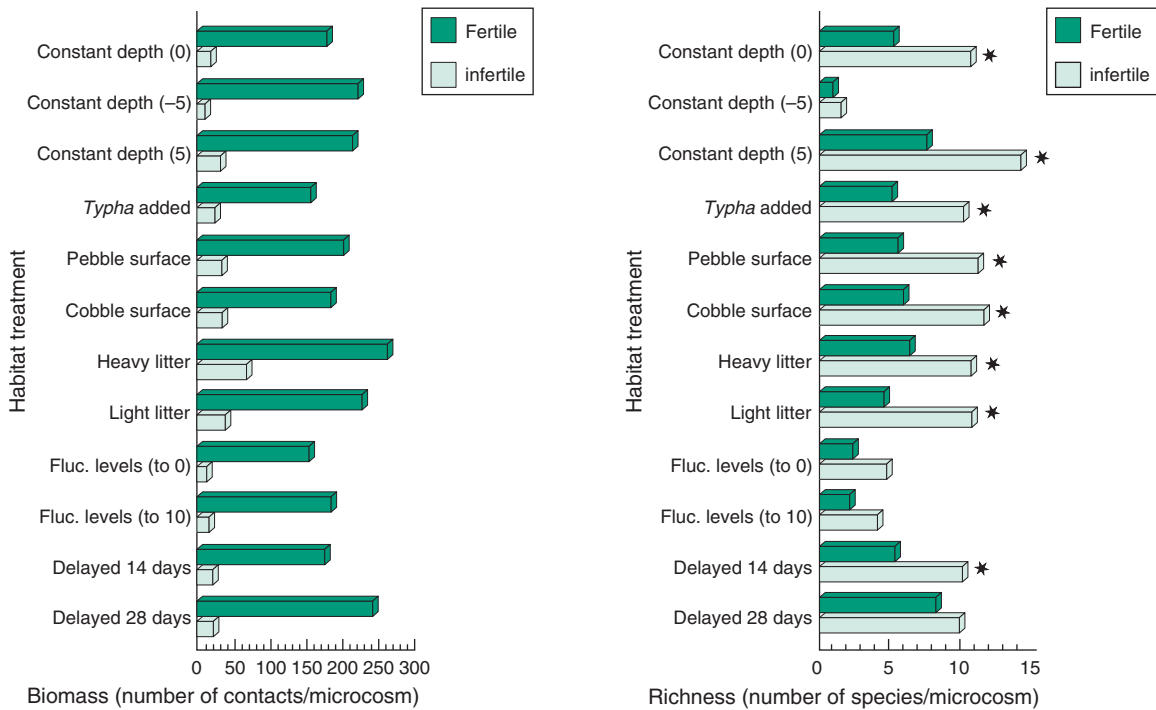


FIGURE 3.12 The effects of eutrophication on biomass (left, all differences significant) and number of species (right, * indicates significant differences) in 12 artificially created wetland habitats. (From Wisheu *et al.* 1990.)

appears counterintuitive. It certainly is the opposite of what we see in marshes and wet meadows. The presumed explanation is that increased fertility leads to increased phytoplankton biomass. The plankton then absorb light and shade out macrophytes (Phillips *et al.* 1978; Moss 1983; Pieczynska 1986; Osborne and Polunin 1986). Figure 3.13 presents a hypothesis that relates the decline in macrophytes to eutrophication. In estuaries, eutrophication appears instead to stimulate macroalgae, which, through shading or anoxia induced by decomposition, eliminate macrophytes such as *Zostera marilla* (Valida *et al.* 1992).

In order to understand the effects of eutrophication, it is necessary to know whether aquatic plants are able to use nutrients in the water column as opposed to the substrate.

Carignan and Kalff (1980) used radioactive phosphorus to compare sediment vs. the water column as sources of phosphorus in nine common aquatic plants, and found that the majority of nutrients are removed from the sediments (Table 3.6). Even under hypertrophic conditions, the sediment contributed nearly three-fourths of the phosphorus taken up during growth. This has two important implications. First, from the point of view of this chapter, aquatic plants are not that different from other wetland plants. We can talk about fertility gradients in the substrate even among aquatic plants. Second, macrophytes may be visualized as pumps that remove nutrients from sediments and return them to open water (Barko and Smart 1980). This may affect attempts to manage wetlands for reduced nutrient levels.

Table 3.6 Uptake of phosphorus from sediments by nine macrophyte species

Species	Percentage uptake from sediments
<i>Myriophyllum alterniflorum</i>	104.4
<i>Potamogeton zosteriformis</i>	107.4
<i>Potamogeton foliosus</i>	98.6
<i>Callitriche hermaphroditica</i>	94.2
<i>Elodea canadensis</i>	99.0
<i>Najas flexilis</i>	100.8
<i>Myriophyllum spicatum</i>	99.4
<i>Heteranthera dubia</i>	95.2
<i>Vallisneria americana</i>	103.1

Source: After Carignan and Kalff (1980).

3.5.6 Eutrophication is reducing diversity in European vegetation

Western Europe, with its high human population density and long history of human use, may be a useful general model. As noted above, nitrogen levels in rainfall have become very high. Ellenberg (1985, 1988) predicts that species normally found at low fertility will gradually disappear from the European landscape. Ellenberg has ranked species according to the nitrogen levels at which they normally occur, thereby identifying the subset of plants that require infertile habitats. These are species at risk. Because eutrophication is occurring across the entire landscape, a significant proportion of the European flora is at risk (Figure 3.14).

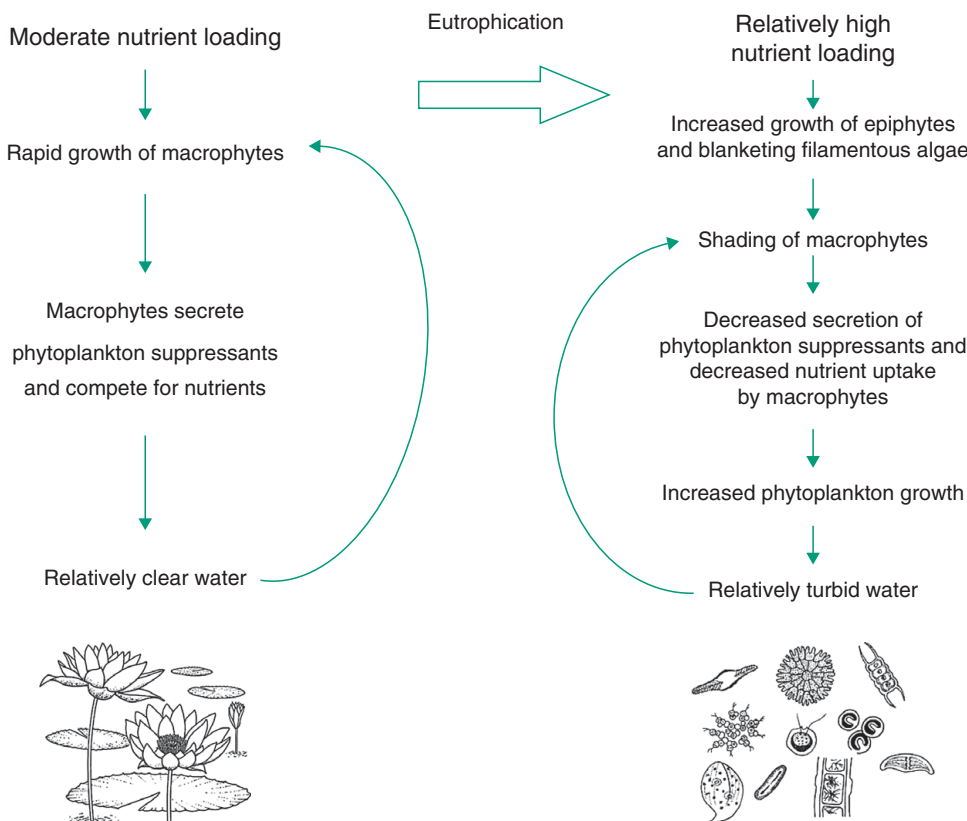


FIGURE 3.13 Eutrophication may increase phytoplankton populations and thereby reduce the abundance of aquatic macrophytes. (After Phillips *et al.* 1978.)

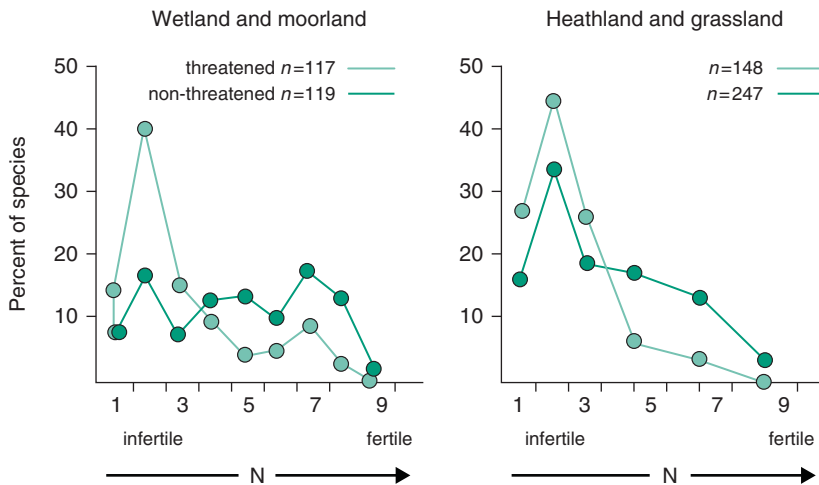


FIGURE 3.14 The threatened flora of Europe (light line) is concentrated in nutrient-poor conditions. Note that the nitrogen level of the sites increases from left (infertile) to right (fertile). (From Wisheu and Keddy 1992 after Ellenberg 1985.)

Let us look more specifically at heathlands, a kind of peatland. In western Europe, species diversity has declined, and evergreen *Erica tetralix* heaths have been replaced by the grass *Molinia caerulea* (Aerts and Berendse 1988; Sansen and Koedam 1996). A nitrogen deposition rate above 10–15 kg N/ha per year is sufficient to accelerate this change – present rates in Flanders exceed 40 kg N/ha per year! Sod cutting may help reverse this process, and retain species rich peatlands, with more deeply cut and regularly flooded sites allowing the growth and persistence of pioneer species such as *Drosera intermedia* and *Rhynchospora fusca*. Eventually, however, *M. caerulea* achieves dominance, and at current nitrogen deposition rates, Sansen and Koedam (1996) believe that sod cutting frequencies will have to be increased from 50-year to 10-year intervals. Verhoeven *et al.* (1996) point out that if mowing removes nitrogen faster than it is deposited, it may be possible to retain a species composition more typical of pristine areas.

The experimental application of nitrogen fertilizer for agricultural purposes also illustrates

the potential changes in vegetation with atmospheric deposition. In the moors of Somerset, UK, which are wet grasslands on lowland peat, experimental applications of nitrogen fertilizer at levels greater than, or equal to 25 kg/ha produced striking changes in the vegetation (Mountford *et al.* 1993). After only 4 years, sedges such as *Carex nigra* and rushes were replaced by widespread agricultural grasses such as *Holcus lanatus* and *Lolium perenne*. While there was an upward trend in species richness in control plots, richness declined in high nitrogen treatments.

To take a global perspective, nitrogen deposition maps for Earth (Townsend *et al.* 1996) show that high rates of deposition already occur in western Europe and eastern North America, and that there are early signs of a third area in eastern Asia. The examples in this chapter show that dealing with eutrophication and the problems posed by species requiring infertile habitats will be a long-term problem facing both scientists and managers.

3.6 Calcium interacts with fertility in peatlands

Thus far in this chapter we have concentrated on nitrogen and phosphorus. This is justified because of

their abundance in plants and animals. They are not, of course, the only elements that affect wetlands.

Others important elements include magnesium, potassium, iron, and calcium. Calcium stands out since it is closely related to the acidity of groundwater (Bridgham *et al.* 1996; Wheeler and Proctor 2000).

The difference between acidic sites and calcareous sites has long been known to affect plant growth and plant distributions, with those species restricted to calcium-rich soils being known as **calciphilous** (Weaver and Clements 1938). The principal factor controlling calcium concentrations is the parent material. Peatlands on limestone or marble, for example, have higher concentrations of calcium in the groundwater. Calcium concentrations reduce acidity of the groundwater. This is not the sole affect. Under alkaline conditions, Ca^{2+} will bind with P to form calcium phosphates, lowering the amount of P available to plants (Bridgham *et al.* 1996). This process may explain the phosphorus deficiency of some European peatlands.

Plants can further modify the water chemistry of a site. *Sphagnum* mosses are thought to acidify water (Bridgham *et al.* 1996; Verhoeven and Liefveld 1997). The litter of most plants is deficient in calcium, which can further acidify the substrate (Fitter and Hay 2002). Oxidation by roots and aerenchyma also affect the soil chemistry (Section 1.3).

Overall, calcium concentrations, in association with pH, have a large effect on the type of wetland

that arises. These two factors are particularly important for the distinction between bogs and fens (Figure 3.15). Fertility, principally nitrogen and phosphorus availability, is then another independent factor. If we treat pH and calcium as one acidity gradient (since they are correlated), acidity co-varies with fertility to produce the major vegetation types of peatlands (Figure 3.16).

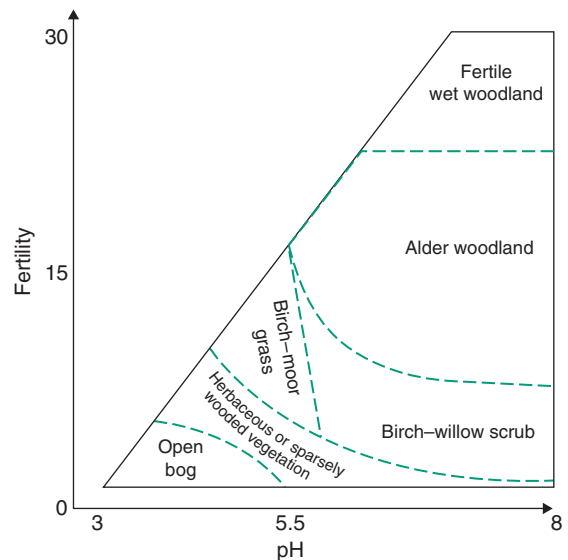


FIGURE 3.16 Fertility and pH control the vegetation types in British peatlands. (From Wheeler and Proctor 2000.)

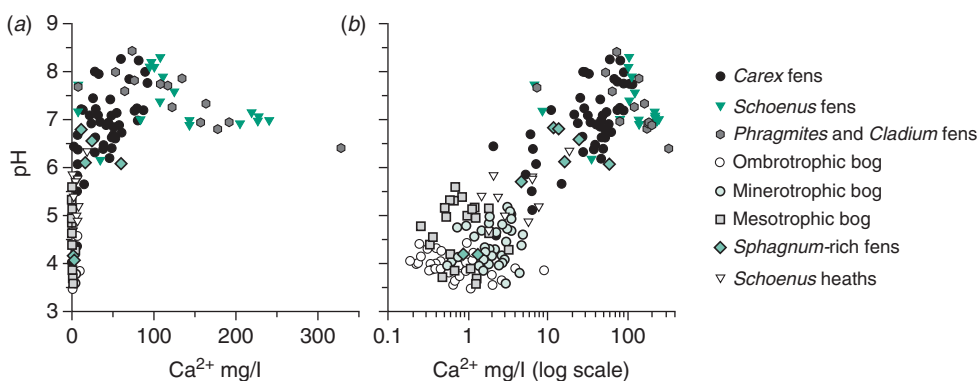


FIGURE 3.15 The relationships between pH, calcium concentration, and vegetation type for 193 water samples from peatlands in Britain and Ireland plotted using (a) arithmetic and (b) logarithmic scales for calcium. (From Wheeler and Proctor 2000.)

3.7 Fertility and hydrology explain a great deal about wetlands

The wetland classifications introduced in Chapter 1 assumed that hydrology and fertility were the two controlling factors in wetlands. Now that you know more about fertility, let us look at one final scheme, Figure 3.17, that combines fertility on the horizontal axis (from infertile to fertile) with hydrology on the vertical axis (duration of waterlogging superimposed upon water level changes). Four wetland types are then produced from left to right: bogs, fens, marshes, and swamps. The figure further discriminates between infertile fens and fertile fens. The addition of salinity as a factor produces both salt flats at the upper left and salt marshes at the lower right. Superimposed upon these is the zone of peat formation, showing the interaction between fertility and waterlogging. Finally, the region which woody plants can occupy is stippled. Many of the factors discussed so far are therefore neatly combined into one figure. Note too that there is a region between the peat formation and tree formation zone, showing that

in some hydrological regimes, open meadows may be formed where the soils have limited amounts of peat, but are still too wet for trees to occur. Other factors such as peat production and the phase transition between woody and herbaceous species are also illustrated.

The diagram in Figure 3.17 raises other challenging questions to consider. Where, for example would carnivorous plants occur? Is there a region where particular kinds of disturbance are most severe? Where might gap colonization predominate? Where would the most methane be produced? Where might above-ground competition give way to below-ground competition? Where would grazing be the most intense? Which areas would have the most wading birds? And how will wetlands change if eutrophication continues? Some answers appear obvious; others are not. A diagram such as this one challenges ecologists to put the pieces together into meaningful patterns.

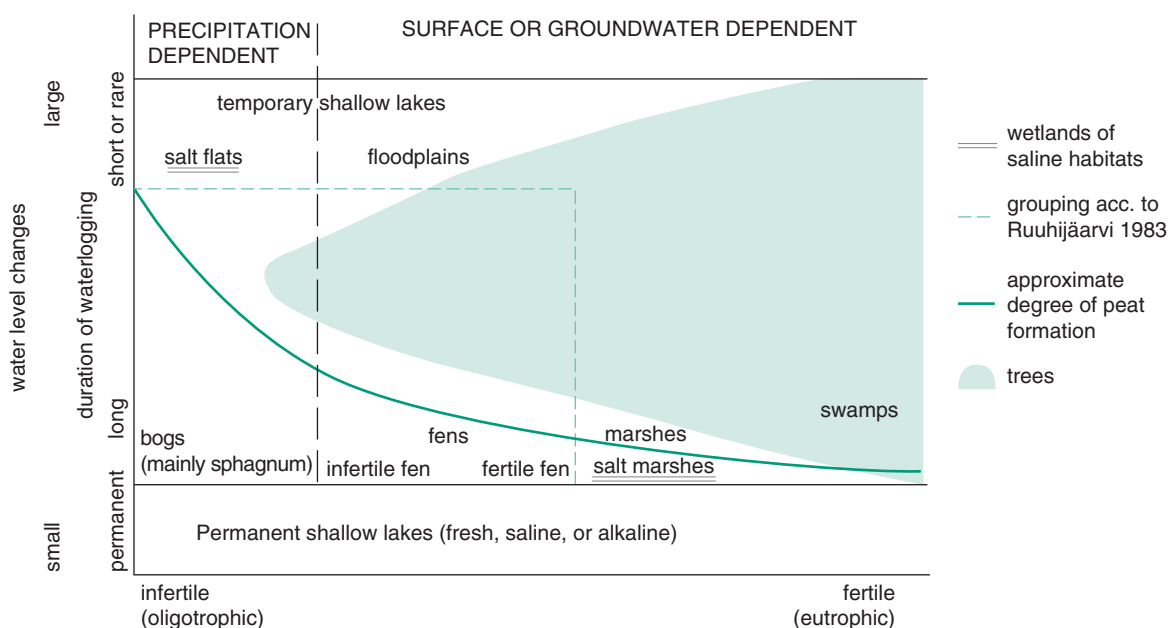


FIGURE 3.17 The major world wetland types can be related to two causal factors: water level changes and fertility. (From Gopal *et al.* 1990.)

CONCLUSION

Plants and animals are CHNOPS organisms, being composed primarily of these elements. Among them, nitrogen and phosphorus are particularly important since supplies often limit the growth and reproduction of both plants and animals. The importance of particular nutrients can be determined through field experiments in which they are supplemented and the effects on plants documented. While biomass is directly correlated with fertility, species richness is inversely correlated with fertility. Infertile sites such as sand plains, depressions in weather-resistant bedrock, and peatlands, where nutrients are in short supply, are typically rich in plant species and may harbor species adapted to such conditions. Variation in fertility can account for wetland patterns at multiple scales. In peatlands, fertility co-varies with a calcium–acidity gradient to produce the vegetation array observed. In some wetlands mycorrhizae increase nutrient availability. Eutrophication of wetlands as a result of excess nitrogen from human activities reduces wetland species diversity and can result in aquatic plant die-off. Infertile wetlands are particularly at risk. Together, fertility and hydrology explain a great deal about wetland composition, function, and distribution.