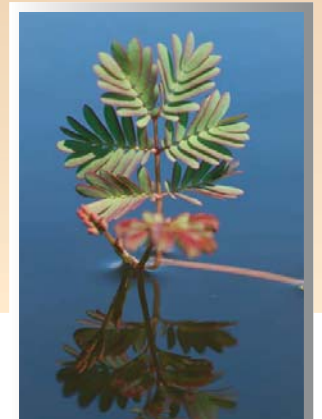


5

Plants: producers, filters and distributors

The variety of vegetation in the Delta gives it beauty, sustenance and diversity, and also controls many aspects of how this wetland works.



Water and nutrients are the primary resources that fashion the Delta. Both are inorganic, crucial to plant life and come directly or indirectly from areas outside the Delta, as described in the last chapter. Plants also require sunlight and carbon dioxide, which likewise come from remote sources. However, these two requirements are rather evenly available in any given area. The growth, abundance and structure of plants are therefore largely controlled by local variations in water and nutrient supplies. This is true throughout the world, and so it is for the Delta, as the following pages will show.

However, there is a difference! This is the important role plants perform in fashioning the living Delta, for example in causing channels to switch direction, sieving out mud and clay, and pumping water up into the atmosphere. These are local effects, which are as important as the external influences of floodwaters, nitrogen, phosphorous and other nutrients. Understanding and conserving the roles performed by plants is thus vital to the overall health and future of the Delta.

Much of this chapter focuses on higher, flowering or vascular plants which are dominated by grasses, sedges, forbs, shrubs and trees.² About 1,300 species have been identified so far, with the grasses (Poaceae) and sedges (Cyperaceae) being the largest groups, followed by the asters and daisies (Asteraceae) and leguminous bean and pea pulses (Fabaceae).³

Just over 75% of all species are herbaceous plants, while the remaining plants are woody trees, shrubs and dwarf shrubs. Eighteen species are parasites and 12 are carnivores (see page 74). In addition to the higher plants, there are also non-vascular plants such as mosses, algae and diatoms, blue-green algae (cyanobacteria) and dinoflagellates in this aquatic environment. Much less is known about them, and they are relatively sparse as a result of the nutrient-poor water. However, some information is available on diatoms (see page 82).

Do these 1,300 species constitute a particularly diverse assemblage of plants? In terms of Botswana, the answer is yes, because about ten times more species are found here than anywhere else in the country.⁴ Of six major freshwater wetlands in the world, the Delta has the second highest diversity of plants, surpassed only by the Brazilian Pantanal, but greater than the Florida Everglades, Indian Sundarban, Cambodian Tonle Sap and the Australian Kakadu wetlands.⁵

Patterns of diversity

Much of the high diversity in the Delta results from wetland and dryland species growing side by side. Perhaps surprisingly, about 60% of all the plants are dryland species that grow on islands and on tongues of dry Kalahari sand that

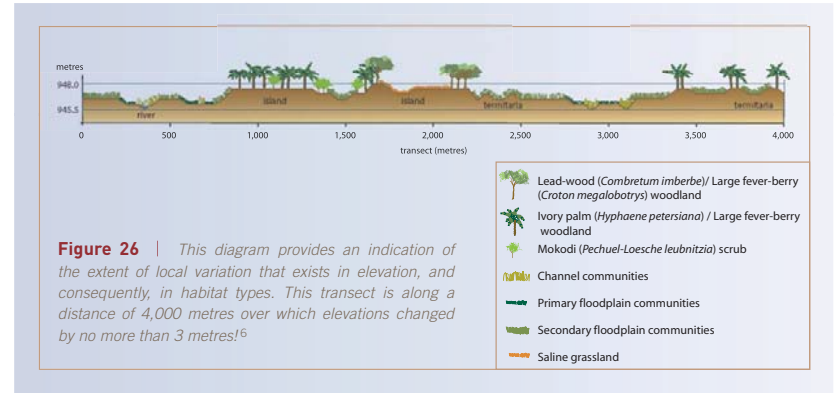


Figure 26 | This diagram provides an indication of the extent of local variation that exists in elevation, and consequently, in habitat types. This transect is along a distance of 4,000 metres over which elevations changed by no more than 3 metres!⁶

jut into the Delta (Figure 25). However, many of these dryland species are absent from the adjacent, more arid savannas because they require higher levels of soil and air moisture, or only grow in areas where groundwater is shallow. They are thus very much associated with the broader wetland conditions offered in and close to the Delta. Prominent examples of these are jackal-berry (*Diospyros mespiliformis*), knob-thorn (*Acacia nigrescens*) and lead-wood (*Combretum imberbe*).

Most plants thus grow in the habitats that are never or seldom flooded. By contrast, large areas of the Permanent Swamps are dominated by one or two species, particularly papyrus (*Cyperus papyrus*) and phragmites (*Phragmites australis* and *P. mauritanus*) reeds.

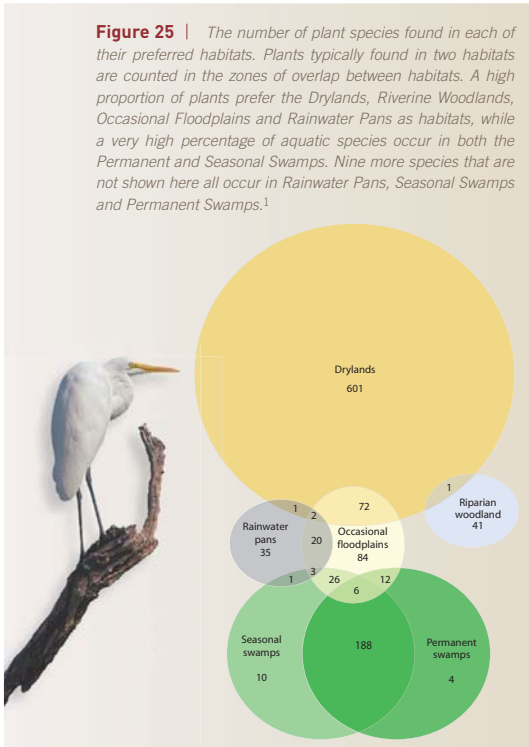
While the truly aquatic species are limited to areas of permanent or frequent flooding, many species grow in a wide variety of conditions of inundation. In fact, as many as 35% of all the Delta's plants grow in more than one habitat along a gradient ranging between swamp and dryland.⁷ Some of the plants adopt different growth forms depending on water levels. For instance, the floating heart water lily (*Nymphaoides indica*) has floating leaves when the water is high, but grows as a terrestrial plant when the floodplains dry. Its leaves then form compact rosettes. An important point is that the substantial – and frequent – variation in flooding has led to the evolution of physiological and morphological plasticity.

Islands support the highest density of species, especially along their margins where a concentrated mix of species hugs the interface between dryland and wetland. One study found between 20 and 83 species in different sample plots, each of which measured only 7 by 10 metres.⁸

The number of species found in any broad area reflects the diversity of habitats. Far from being a uniform wetland, the Delta is very much a patchwork of habitats, as many photographs in this book show. And so it is the mix of habitats that gives the Delta such biotic diversity. In addition, the variety of habitats contributes to the abundance of life because adaptable species can move from one habitat to another, growing and breeding as each habitat becomes productive when wetted, and then retreating elsewhere as the habitat dries. Much of the mix of habitats is due to tiny variations in elevation (Figure 26). Thus, a depression may be inundated for much of the year, while another area just 50 metres away may have standing water for only two months because it is 50 centimetres higher. And between these two, there might be a more elevated area that remains consistently dry.

Overall, the diversity and patchiness of habitats progressively increases from the Panhandle towards the Occasional Floodplains, reflecting both the increasing variation in flooding frequency and the greater number

Figure 25 | The number of plant species found in each of their preferred habitats. Plants typically found in two habitats are counted in the zones of overlap between habitats. A high proportion of plants prefer the Drylands, Riverine Woodlands, Occasional Floodplains and Rainwater Pans as habitats, while a very high percentage of aquatic species occur in both the Permanent and Seasonal Swamps. Nine more species that are not shown here all occur in Rainwater Pans, Seasonal Swamps and Permanent Swamps.¹



of islands in the more ephemeral areas (see page 57). These patterns of variety and the dynamic nature of habitats have several implications for the Delta's conservation. One is that looking after the Delta's biological wealth cannot be concentrated on small areas or particular habitats. Second, the variety of habitats stems from switching and seasonal pulses of water, and so anything that reduces the variation of flooding would lead to a loss of diversity. And third, plant communities may often be in a state of flux, called succession by botanists, as the supply of water waxes and wanes according to levels of inflow and distribution of water. Conservation measures should thus not aim to preserve a particular condition, other than to allow conditions to change naturally! Mechanisms that cause variability need to be preserved.

Reaching out across the water towards sedges and water lilies is this attractive legume *Aeschynomene fluitans*, probably one of many plants in the Delta that fixes nitrogen.



Processes of change that divide the Delta into its assorted habitats operate over a range of time scales, from decades upwards to tens of thousands of years (see page 25). Plant species in the Delta have thus had to track and adapt to frequent changes in habitat conditions. Consequently, we might expect many of the Delta's plants to be so specially evolved to local conditions that they are now endemic, and thus occur nowhere else. Adding weight to this expectation is the Delta's perceived isolation as a wetland, which should lead to its plants being genetically separated from those in other wetlands.

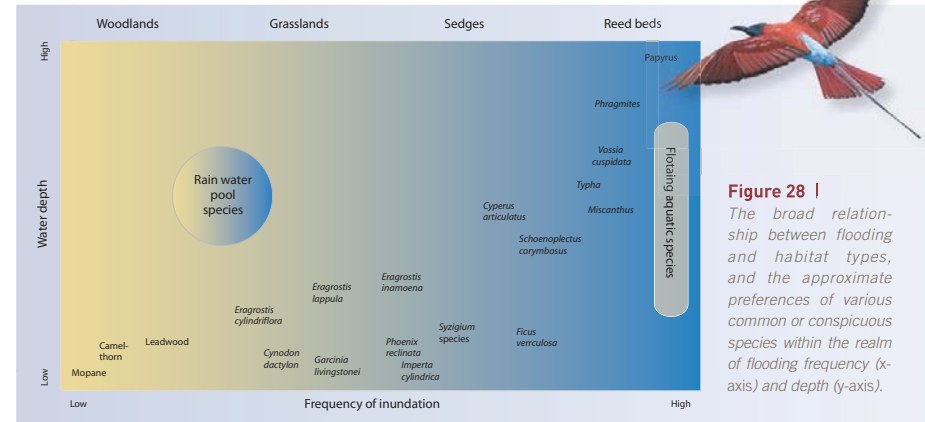
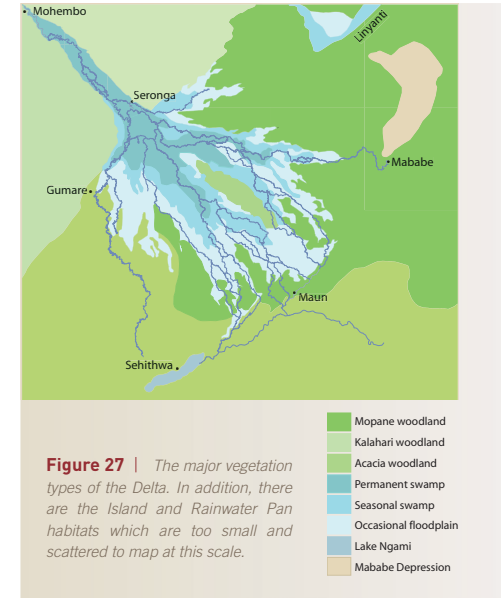
However, all the Delta's plants are found elsewhere in southern and central Africa, especially in wetlands to the north in Zambia.⁹ Similar distributional patterns are found for animals, most of which also occur in wetlands associated with the Zambezi River.¹⁰ These broader distributions reflect two features of the Delta and its biota. The first is that the Delta is not as isolated as we think. In the past it was part of much larger wetlands that were connected to those of the Zambezi (see page 24)¹¹, and the Selinda Spillway still provides intermittent connections between the Delta and the Linyanti Swamps. And from the Linyanti, there is continuous swamp all the way up the Kwando River (which is more an extremely long marsh than a river) to the wetlands from which both it and the Zambezi River drain.

Secondly, aquatic species in the tropics and subtropics have evolved to be highly mobile because freshwater wetlands are often ephemeral. This is true at time scales of seasons, decades or centuries, depending on the reliability of water sources that fill the wetlands. Species that depend on wetlands thus need to develop ways of moving to patches of water as they become available, and leaving when they dry up. Plants use a number of strategies to spread themselves, for example, by having seeds that float, seeds carried by animals in their guts or as attached burrs, seeds that germinate after varying periods of desiccation, and seeds and bulbs that survive long dry periods. In addition, some plants have rhizomes and stolons that creep along under the ground, while aquatic species have flowers above water to enable pollination between plants over wide areas.

Habitats

The distribution of major habitats in and around the Delta is shown in Figure 27. This map presents a neat demarcation of labelled categories, and it is broadly valid in reflecting where different habitats predominate. However, demarcations on the ground are far from simple because there are also many sub-groups characterised by more subtle assemblages of species. Moreover, quite different habitats are often found cheek by jowl because of the local variation in topography and inundation (Figure 26). And habitats change when water flows shift from one area of the Delta to another. For example, the swamplands that predominated in the western Delta turned into dry grasslands when the Thaoge River dried up over a hundred years ago (see page 50).

Studies by several plant ecologists have all shown that hydrology is the key factor that determines how vegetation is structured into habitats (Figure 28).¹² Three aspects of hydrology stand out: the frequency of flooding, its duration and the depth of water. These are of course often correlated, so that places that are frequently flooded also have the deepest water for the longest periods. Nutrient availability is also important, but less is known about the role of nutrient conditions because these are harder to measure and evaluate. Other significant impacts are from soil salinity (see page 78), fire (page 84) and foraging by herbivores (page 87).



1. Permanent Swamps

While water levels may drop temporarily to ground level in the Permanent Swamps, they do not drop below its surface. This is a key factor for plants in this habitat, since all are true aquatic species. Four plants are especially abundant and domineering along the margins of the channels and in their immediate back-swamps: papyrus, the two phragmites reeds (*Phragmites australis* and *P. mauritanicus*) and the swamp grass (*Miscanthus junceus*). Their growth and abundance is largely determined by water depth, flow rates and their ability to capture nutrients from the passing water. Thus, tall papyrus and phragmites reeds dominate the deeper waters of the Panhandle and upper alluvial fan, while swamp grass is abundant in the shallower lower reaches in the alluvial fan. The plants cannot encroach into channels as long as water flows remain strong, and growth is also limited by their ability to take up soluble nutrients from the water.

Few plants grow in the lagoons or lakes because of their depth, but their perimeters have communities similar to those of the shallow back-swamps. Once dislodged from the bottoms of the lakes by decomposition and methane production, blocks of peat may rise to the surface as floating sudd mats which are then colonised by plants such as *Pycnopus nitidus*, *Websteria confervoides*, *Cyperus pectinatus* and *Oxycaryum cubensis*.

The four species lose their dominance away from the main channels and back-swamps where the water is shallower and nutrients from inflows of the Okavango River are less available. These more open waters are occupied by a greater variety of plants, most of which grow as emergent, floating and submerged species. Examples are the bulrush (*Typha capensis*); the sedges *Pycnopus nitidus*, *Cyperus pectinatus* and *C. articulatus*; blue water lily or tswii (*Nymphaea nouchali*); the floating heart lily (*Nymphoides indica*); *Brasenia schreberi*; *Ottelia* species; and *Potamogeton* species.

Although some plants are rooted in sandy substrates, others grow on layers of peat that are widespread in the Permanent Swamps. The peat consists largely of decomposing organic plant matter but may also contain considerable proportions of clay. This is particularly true in the Panhandle where much of the suspended clay load is filtered out of the inflowing Okavango River water. Indeed, inorganic sediments may comprise 60-85% of the peat in the Panhandle, compared to less than 15% in peat further downstream in the alluvial fan. The densest layers of peat form beneath phragmites reeds.

No other species characterises the Permanent Swamps as much as papyrus, especially where it is so dominating that it may comprise up to 90% of all plant biomass. This is perhaps the main ecosystem engineer of the Delta because papyrus forms large areas of peat, helps filter out much of the incoming clay, uses much of the inflowing nutrient resource, and is largely responsible for causing major changes in the distribution of water and habitats (see page 51).

The Permanent Swamps are the most stable areas of the Delta. Although rates of plant biomass production are higher than elsewhere (Figure 29), almost all the production is through the few dominant perennial papyrus and reed species which take up and retain most nutrients. Few nutrients are thus available in the Permanent Swamps to other organisms which are also constrained by a lack of oxygen in the peat and water. However, the swamps are important refuges for fish before the annual floods. They then leave the swamps for the temporary



The swamp grass (*Miscanthus junceus*), here surrounding the chick and nest of a saddle-billed stork, usually occurs where seasonal changes of water levels are less than 30 centimetres. It thus replaces papyrus and phragmites in the shallower areas of the Permanent Swamps.

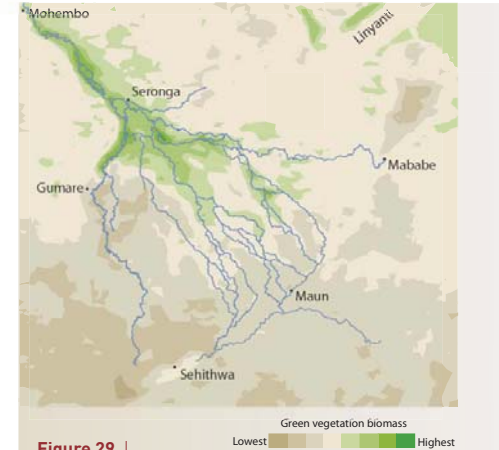


Figure 29 | A measure of average plant production over 16 years, which shows that most biomass is produced in the extensive papyrus and reed beds of the Permanent Swamps.¹³



In addition to their upright stalks, phragmites reeds have stems called stolons that grow below the ground where they are protected from burning. The stolons sprout after fire, enabling this vigorous species to recolonise burnt areas rapidly. These elephants have uprooted the reeds in their quest for the soft, nutritious stolons and newly grown stems.



Utricularia gibba, one of 12 carnivorous plants in the Delta. These carnivores overcome shortages of nutrients by obtaining them from animals which are trapped and then digested in the small bladders shown immediately above. Species of the genus *Utricularia* have attractive flowers and are most abundant. But the Delta is also home to *Aldrovanda vesiculosa*, which is rare throughout the world.



Papyrus (above) is not rooted in the sandy substrate of the Delta, but instead grows and reproduces on layers of peat. This is why it floats so easily on gradually rising water levels. The wide spacing between its stems allows water to percolate through to the back-swamps. The slowing of water flow in blocked channels enhances the growth of papyrus, which then soon invades and further clogs the waterways. But strong flows of water can also break off chunks of papyrus which float off as sudd. If the sudd becomes lodged elsewhere, new communities of papyrus form downstream. Such propagation is very important, since papyrus only reproduces vegetatively. Papyrus also sprouts new growth after fire, as long as their rhizome roots have remained permanently submerged.



The Permanent Swamps typically consist of rather uniform expanses of reeds and papyrus broken only by meandering channels and lakes or lagoons of various sizes. The channels and lakes are often connected by tunnels maintained by hippos [see page 42].

floodplain grasslands during the floods to capitalise on the terrestrial nutrients that are mobilised there. And when the flood waters recede, the fish swim back upstream to the Permanent Swamps. Sandbanks along channels in the permanent Panhandle are the most important nesting grounds for crocodiles and African skimmers (see page 96).

2. Seasonal Swamps

Whereas the majority of plants stand tall in the deep waters of the Permanent Swamps, most of those in the shallower Seasonal Swamps are shorter. And unlike the evergreens in the Permanent Swamps, many die back when the water dries, to sprout new stems and leaves only when they are next inundated. The key characteristic of this habitat is that flooding is sufficiently regular and deep to support the growth of all life forms of aquatics, especially submerged species. But it is really the sedges that characterise the Seasonal Swamps, setting them apart from the reeds of the Permanent Swamps, the grasses of the Occasional Floodplains, and the woody trees and shrubs of the Drylands (Figure 28).

The arrival of seasonal floodwaters sets in motion a burst of production, which starts when the first microbes are rehydrated. They begin decomposing

organic debris, while germinating plants and the regrowth of those that died back in the dry season soon follow. A surprising contest for nutrients that have lain dormant in the terrestrial sediments also begins. As the first bacteria and fungi are revitalized by the water, they start to decompose wetted detritus, rapidly depleting the oxygen in the water to do so. Anaerobic conditions develop, forcing the microbes to use different molecules to metabolise energy, in a chemical process known as reduction.¹⁴ Life is hard without oxygen, and the tough community of different microbes function slowly because using molecules other than oxygen for respiration is a protracted, inefficient process.

The molecules reduced by the microbes for their respiration are also those that plants require as nutrients. Moreover, some molecules become volatile as a result of reduction and then evaporate into the atmosphere. To counter the shortage of nutrients, plants pump oxygen down to their roots, creating micro-atmospheres of oxygenated rhizospheres around their root hairs. The oxygen is for the use of other microbes which congregate around the rhizospheres and use it to oxidise molecular nutrients into forms that the plants can indeed use.



The Seasonal Swamps support a diverse assemblage of short-lived sedges, grasses and aquatics. The mix of species in one any one place depends strongly on the frequency, depth and duration of flooding, so that grasses predominate in areas that seldom receive water, while taller sedges, swamp grass and aquatics are more abundant in the wettest areas.

While the flooding lasts, the competition for nutrients is fierce and rates of production are rapid, since all plants and animals need to maximise their production within the limited and unpredictable period of inundation. The gist of the competition is for nutrients which can only be obtained from inert detritus when the seasonal floodwaters arrive. While decomposition of the detritus leads to a loss of oxygen, the mass of resulting bacteria and fungi feeds swarms of zooplankton, fish and other animals (see page 100). When the waters recede, much of the plant biomass produced during the flooding returns as desiccated detritus to the soil, where it will lie until the Angolan water next arrives in the Seasonal Swamps.

The Seasonal Swamps provide such rich grazing that the high abundance of herbivores in the Delta is probably attributed more to this habitat than to any other. What is especially important is the availability of this grazing during the long, dry winter months when forage in the surrounding Drylands is depleted. Succulent

shoots produced by growing grass and from the rhizomes of sedges attract buffalo and zebra within weeks of the floodwaters arriving. They forage in shallow water, while impala graze the fringes of green grass along the shores, and red lechwe feed in the deepest areas. As the waters recede at the end of the flood season, tubers and rhizomes provide food for many baboons and warthogs, and termites proliferate, actively harvesting dead reeds and grass. Attracted by the nutritious termites, dozens of predators arrive to feast their fill.

3. Occasional floodplains

It is often hard to distinguish the Occasional Floodplains from the Seasonal Swamps, and many ecologists prefer not to draw a firm line between the two habitats. Indeed, the boundaries between them (Figure 27) are somewhat arbitrary, and also shift in response to longer term changes in flooding frequency. And although the Occasional Floodplains are dry for much of the time, their soils were nevertheless largely formed by alluvial sedimentation.



Grasses with scattered bushes and copses of trees dominate the vegetation of the Occasional Floodplains which are flooded so infrequently that many people would not regard them as floodplains. The most characteristic and common grasses are *Aristida stipoides*, *Chloris virgata*, *Sporobolus ioclados*, *Wilkommia sarmentosa*, *Cynodon dactylon*, *Bothriochloa bladhii*, *B. insculpta* and *Schizachyrium jeffreysii*.



About 220 species of grasses and 120 sedges occur around the Delta. Many of them have small, but intricate flowers, clockwise from top left: *Schmidtia pappophoroides*, *Enneapogon cenchroides*, *Cyperus zollingeri*, *Melinis kallimorpha*, *Kyllingiella microcephala*, *Pennisetum macrourum* and *Dactyloctenium giganteum*.

However, the Occasional Floodplains have a high proportion of plants that occur in no other habitats (Figure 25). Here, regular, annual production depends on rains that fall locally. These features set the Occasional Floodplains apart from the Seasonal Swamps which receive regular pulses of floodwater and share many species with the Permanent Swamps. The Seasonal Swamps also have many more sedges than the grassy Occasional Floodplains.

Since rainfall is usually limited, rates of growth and production in the Occasional Floodplains are generally mediocre (Figure 29). However, during years of flooding, large reserves of nutrients that have accumulated here

over many years are mobilised by the water, and production then booms. Large flocks of birds, swarms of insects, herds of mammals and schools of fish are attracted to these productive events. Not only do the animals thrive on this bonanza, but these uncommon episodes of surplus and bounty enable many organisms to reproduce rapidly and prolifically. It is very likely that much of the Delta's biological wealth is indeed produced on the Occasional Floodplains.

4. Islands

The role of island plants in helping to maintain the Delta as a freshwater system by pumping water into the atmosphere was described in Chapter 4 (see page 55). The islands also contribute a great deal to the Delta's overall biological diversity, since the estimated 150,000 islands support the most diverse assemblage of species. This is a product of the close combination of terrestrial and fringing aquatic communities and the considerable changes in soil chemistry between the margins and centres of islands. As a result, quite different plants occupy different soil zones.

The biological diversity of island vegetation is valuable in a broad sense, but island plants also provide a suite of resources that support many of the animals in the Delta. For example, grazing and browse is available for herbivores and fruit for frugivores, while many birds use the islands for nesting and roosting. And of course, islands form oases for the myriad of insects, spiders, reptiles and other animals that simply prefer to stay dry.



Changes in soil chemistry across islands are the result of water transpiration by plants, particularly the riparian trees. By drawing up and transpiring water from beneath the ground, a gradient is formed of increasingly concentrated groundwater from the edges to the centres of islands. Calcium and magnesium precipitate out as carbonates on the fringes where the deposits build the slight ridges to be seen around the edges of islands. These precipitates and the gradual accumulation of organic debris cause the islands to grow in size. Sodium, by contrast, precipitates in the middle of the islands where it often forms a salt crust. This crust of sodium carbonate is poisonous to most plants, so the island centres are mostly barren except for a few salt-tolerant species, such as the grass *Sporobolus spicatus* and the ivory palm (*Hyphaene petersiana*).

The fringes of freshwater-loving riparian woodland vary in width from one island to the next. Some are only a few trees and shrubs wide while others extend up to 200 metres in breadth. The commonest and biggest trees in



The variety of species found on an island is broadly related to its size. Thus, the smallest islands are covered by a handful of trees and shrubs, while on the larger, older islands concentric rings of different riparian communities surround zones of grassland growing on saline soils.

riparian woodlands are knob-thorns, lead-woods, jackal-berries, sycamore figs (*Ficus sycomorus*), water-berries (*Syzygium cordatum*), wild date palms (*Phoenix reclinata*), large fever-berries (*Croton megalobotrys*), mangosteens (*Garcinia livingstonei*), rain trees (*Philenoptera violacea*), sausage trees (*Kigelia africana*) and marulas (*Sclerocarya birrea*). Beneath and around the trees are diverse communities of grasses and many broad-leafed shade herbs.

5. Rainwater Pans

Although they cover a tiny area of the Delta, Rainwater Pans are disproportionately important because they contain rich accumulations of nutrients and are often centres of biological production. And since they are usually filled by summer rain before the later spread of Delta floodwaters, the Pans provide water to herbivores that have moved into the Drylands to graze fresh



The number and size of Rainwater Pans depend on rainfall, as does the length of time that they offer water to wildlife. Their special value lies in the fact that the Pans often supply water in places that are far from sources of Delta water.

pastures that sprout after summer showers. The waters and bottoms of the Pans are also much more clayey than other areas of the Delta. Their most characteristic species are *Echinochloa crus-galli*, *Lemna aquinoctialis*, *Portulaca oleracea*, *Tragus berteronianus* and *Chloris gayana*.¹⁵ About one-third of the plants found in the Pans also occur in the Occasional Floodplains (Figure 25), which is indicative of the ephemeral nature of both habitats where so many species lie dormant until they are activated by water.

6. Dryland woodlands

The three types of woodlands surrounding the Delta are associated with different soils (Figure 27). Thus, the broad-leafed deciduous Kalahari Woodlands to the north are on aeolian sands, the Acacia Woodlands to the west and south grow on deep alluvial sands, while Mopane Woodlands to the east are rooted in alluvial sediments that are more clayey and shallow.¹⁶ The alluvial soils of the Mopane and Acacia Woodlands were formed during much wetter periods when the floodplains of the Delta were several times their present size and the Makgadikgadi mega-lakes extended over huge areas of Botswana (see page 25).

The composition and structure of the woodlands is rather homogenous in many areas where just a handful of tree species dominate the landscape. However, there is also much local variety, particularly where soils have been changed by water flows and sedimentation. For example, the Kalahari Woodlands (characterised by red syringa (*Burkea africana*), Zambezi teak (*Baikiaea plurijuga*), and Angolan teak (*Pterocarpus angolensis*) are interspersed with inter-dune valleys where acacias predominate on soils that are more clayey. Similar mixes are to be found in Mopane Woodland where uniform stands of mopane occupy higher ground while mixed communities of camel-thorns, jackal-berries, lead-woods and rain trees grow along old, low-lying drainage lines. Large patches of shrubland savanna dominated by shrubs (mainly species of *Grewia*, *Rhus*, *Maytenus*, *Ximemia*, *Croton* and sickle-bush [*Dichrostachys cinerea*]) mixed with occasional trees (*Acacia*, *Combretum*, and Shepherd's Bush [*Boscia albitrunca*]) occur where soils are sandier than most of those in the Acacia woodlands.



The Acacia Woodlands are characterised by camel-thorns, which have deep roots to tap the groundwater, while mopane have extensive shallow root systems to take advantage of even the smallest local rainfall event. The clayey soils preferred by mopane also hold more water than the sandier soils in which camel-thorns grow.



Mopane Woodlands are relatively tall and dense close to wetlands, while on drier areas they are more open with most trees of uniform height. There are also large areas of shrubland known locally as *gumane* where the mopane shrubs appear stunted, perhaps by fire, frost, browsing by elephants or some feature of the soil.

The woodlands provide valuable pastures and browse, especially highly nutritious seed pods, for herbivores associated with the Delta. Without the woodlands there would be few impala and kudu, for example, and it is probably the large areas of mopane wood- and shrubland that allow the huge elephant populations to exist (see page 106). Pastures in the Acacia and Mopane Woodlands are substantially more productive because the nutrient content of their alluvial sands and clays is higher than that of the wind-blown sands of the broad-leafed Kalahari Woodlands.

7. Lake Ngami and the Mababe Depression

Sediments very rich in nutrients have accumulated in these low-lying extensions or overflows of the Delta as a result of their repeated flooding and drying over hundreds of thousands of years (see page 25). Both have been dry for most of the time in recent decades, and neither has filled anything



Thousands of hectares of Lake Ngami were covered by very dense stands of *Datura ferox* early in 2009 (left). An extensive community of umbrella-thorn trees had grown up in a zone around Lake Ngami that was last flooded in the late 1970s. Flowers dropped by the trees produced carpets of yellow when the exceptional flood waters arrived in the second half of 2009 (right).

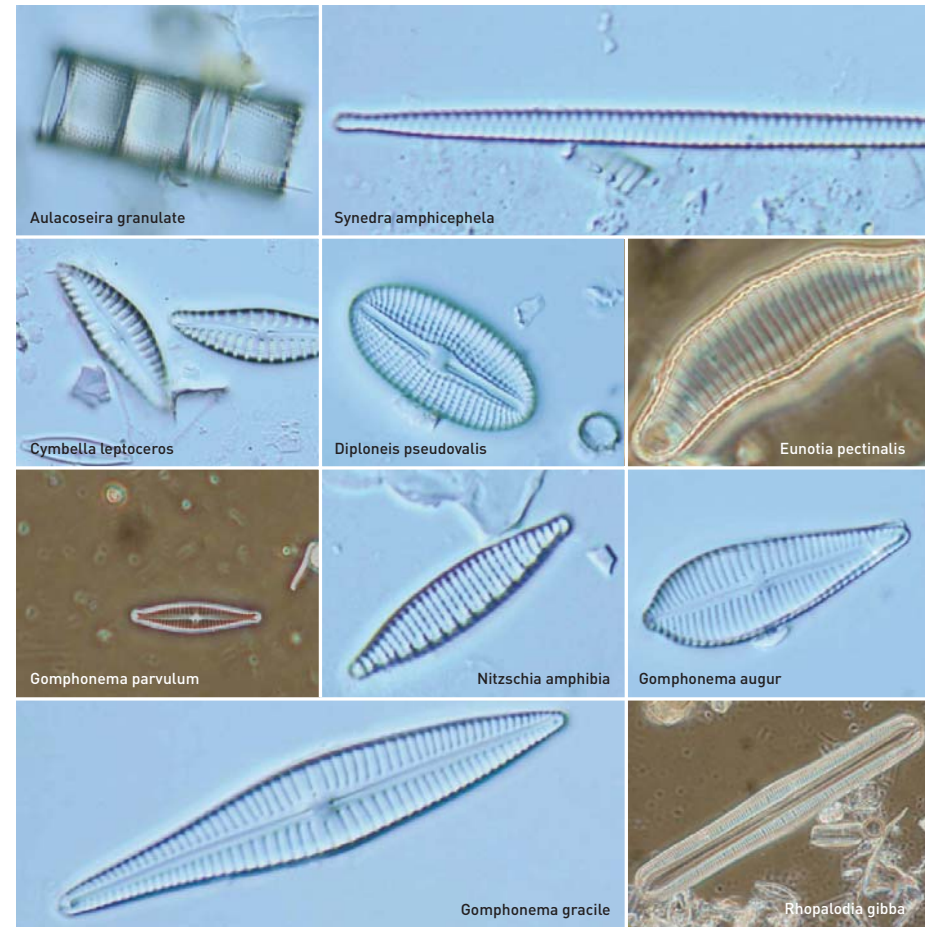
like as much as in the past.¹⁷ As elsewhere, the structure and composition of plant communities in Lake Ngami and the Mababe Depression are strongly influenced by inundation. Those in the lowest, frequently flooded areas consist of grasslands when dry, and a variety of sedges, reeds and floating plants when wet. Algae are particularly abundant because of the rich supply of nutrients in the sediments. However, other than the hardy couch grass (*Cynodon dactylon*), little grass cover remains in the bed of Lake Ngami because of very high grazing pressures by cattle. The removal of native species has enabled substantial stands of invasive pioneer plants, such as *Datura ferox* and *D. stramonium*, the burweed (*Xanthium strumarium*) and *Sesbania* species to take hold. Cattle are absent from Mababe so that the grasslands, dominated by nutritious buffalo grass (*Cenchrus ciliaris*) and couch grass remain in good condition here.

The higher zones around both depressions are wooded, with umbrella-thorn (*Acacia tortilis*), camel-thorn (*Acacia erioloba*), buffalo thorn (*Zizyphus mucronata*) and lead-wood being conspicuous and abundant.

DIATOMS

Early studies focused on documenting what species occur in the Delta, and over 180 species of diatoms have been identified so far.¹⁸ More recent research has sought to understand the preferred ecological conditions of different species and to evaluate the potential for using diatoms as indicators of water quality and the overall health of the Delta. These latest studies found that the Delta's diatoms are characteristic of species that prefer water with low alkalinity, that most species also occur elsewhere in the world and Africa, and that different communities of diatoms inhabit different areas of the Delta. Factors that appeared to influence the distribution and abundance of diatoms included water chemistry – such as levels of calcium, silica and alkalinity – and the duration of flooding. A few rare species of diatoms were found, but more work needs to be done to determine if they are endemic to the Delta or not.¹⁹

None of the species shown on the facing page have English or other common names, and they are very small, ranging from less than 0.01 to 0.3 of a millimetre. The plants in these images have thus been enlarged about 1,000 times.

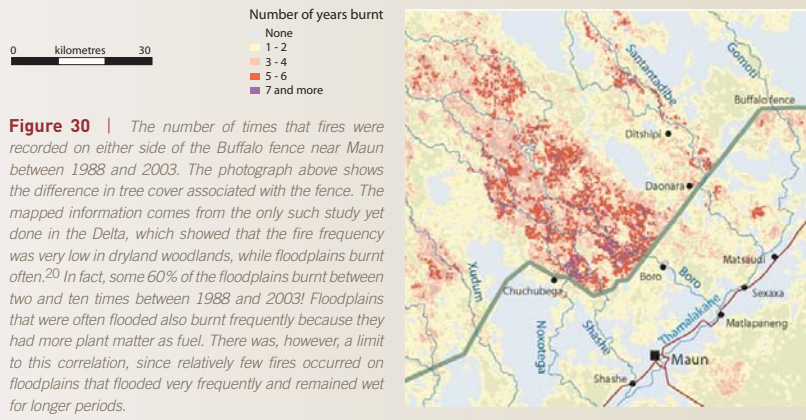


Diatoms are tiny algae found in most aquatic environments. Each plant consists of a single cell, the walls of which are composed of silica sculpted in intricate structures that are unique to each species. As photosynthetic algae, diatoms are primary producers and add oxygen to the Delta's waters. They also play important roles in cycling chemicals, particularly silica, and in contributing to the diversity and ecological resilience of the Delta. An average litre of water in the Delta may contain from tens to thousands of individual diatoms, most of which would be attached to underwater stems.

Fire, herbivores and people

The Buffalo Fence separates areas of the Delta used for wildlife management from those where cattle and other livestock are held (see page 78). It is a small, simple wire fence but its position is easily visible from space because of differences in vegetation on either side of the barrier (see, for example, the book cover and the image on page 44). More specifically, the differences are in the

density of trees and shrubs, so the darker areas on the images have more woody plants whereas grasses are more abundant in the paler areas. Most people agree that these differences are a consequence of different grazing pressures by livestock and/or wildlife. But just how this results in more or less grass, or greater or lesser woody plant cover, is debateable. The debate revolves around several possible consequences of grazing.



The great majority of Delta fires are started by people, mainly during May before the annual floods and in September before the summer rains and first associated lightning.²¹ Some are accidental while other fires set on purpose often run away out of control. A host of reasons have been offered for the setting of fires: to attract wildlife to fresh pastures for hunting and to offer tourists greater chances of seeing wildlife, to improve the quality of grazing for livestock and wildlife, to gain access to fishing grounds, to improve the quality of thatching grass, reeds and papyrus, and to clear land for cultivation.



A variety of plants are used by residents of the Delta. For example, the rhizomes of blue water lilies (locally called *tswii*) are eaten, while the leaves of *Neptunia oleracea*, *Hibiscus cannabinus* and *Alternanthera sessilis* are cooked as spinach. The last species is also used to make soap and can be used to treat digestive problems. Marula berries are a popular food. The fruit of water-berries are edible, can be used to treat diabetes and make alcoholic beverages. Sap from the ivory or real fan palm (*mokolwane*) is fermented into wine. The bark of large fever-berries is used to poison fish. *Indigofera tinctoria* and bird plum (*Berchemia discolor*) are used to dye baskets. Phragmites is widely used for thatching roofs and making palisade walls. Mokoro canoes are hollowed out of the trunks of rain trees and jackal-berries.



Most people appreciate elephants very much, but their rapidly growing numbers (see page 106) are cause for concern because woodlands in and around the Delta are increasingly being decimated. Mopane Woodlands suffer the greatest damage since elephants relish their leaves and bark. Trees that have been killed or pushed over provide fuel that intensifies fires.

First, high stocking rates and over-grazing may *limit* the abundance of woody species when herbivores physically damage young woody plants by trampling or browsing them. In addition, grazing may stimulate perennial grasses to grow so vigorously that this, too, constrains the growth of young shrubs and trees. Densely stocked areas then have less shrub and tree cover. Second, the removal of grass by grazers can *encourage* the growth of woody shrubs and trees because more water and nutrients are available to them. High stocking rates then leads to the opposite effect: greater bush density.

A third consequence of high grazing pressures is that they reduce the availability of dry grass fuel for fires which curtails the intensity and spread of burning. Woody shrubs and young trees are therefore not killed or burnt back, while those in ungrazed areas are burnt down each time a hot fire passes over them.

This third effect is perhaps apparent on either side of the Buffalo Fence close to Maun (Figure 30). To the south and east of the fence where cattle are abundant, fires are infrequent (and probably less intense) and there is a dense, bush-encroached cover of young mopane. The same trees are virtually absent a few metres across the fence where hot fires are frequent and grazing pressures are low. Another explanation, which does not invoke burning, is that the woodiness south of the fence is due to a combination of livestock grazing intensity (the second idea described above) and a lack of browsing by elephants.

The association between an absence of fire and bush encroachment is troublesome because grass production decreases as bush densities increase. Pastures for both cattle and wildlife are thus lost. The problem is also hard to reverse, since the chances of having fires hot enough to remove woody plants diminish as bush densities



The waters of the Delta are adorned with attractive flowers, clockwise from top left: *Nymphaoides indica*, *Cycnium tubulosum*, *Nymphaea lotus*, *Nymphaea nouchali*, *Utricularia foliosa*, *Ottelia ulvifolia* and *Lagarosiphon iticifolius*.

increase and fewer grasses establish themselves. Fire is also a problem in the Kalahari Woodlands (see page 80) where frequent, intense fires gradually convert the tall savannas into shrubland. Mature trees are killed by the fires as a result of the progressive burning of their stems and bark. The trees are seldom replaced because there are too few fire-free years for young trees to grow tall enough to escape the effects of hot fires. In essence, there are just too many hot fires which rage through the Kalahari woodlands almost every year.

Fires are a problem too, when resources such as thatching grass, reeds, timber and even homes are lost.²² Burnt landscapes also have no aesthetic appeal for tourists. Furthermore, urgent concerns are often raised about the impact of frequent, hot fires in changing the composition of plant communities, and causing losses of wildlife, water birds and fish production. Good evidence for the nature and severity of these impacts is lacking, however.²³

One study compared plant and animal production between two adjacent Seasonal Swamp areas, one of which had just had a very intense fire.²⁴ All the organic debris and peat was removed by the fire. No grasses and sedges grew in the first season when floodwaters returned to the burned floodplain, but its production of algae was substantial. By contrast, production on the unburned floodplain was dominated by bacteria that decomposed plant litter. Populations of zooplankton (see page 100) were similar on the two floodplains, but the number of fish fry on the burned area was 15 times lower than on the unburned floodplain.

The reason for this dramatic difference was not clear, and the results need to be confirmed. But it is clear that by removing the grass-sedge-litter matrix, hot fires change the habitat structure and decomposition of organic debris. Their impacts on the functioning of floodplains may therefore be considerable, and this needs more investigation. Research is also needed to study what is widely agreed to be two major benefits of fire in the Delta. The first is the role of fire in releasing nutrients that have accumulated in peat and other organic debris (see page 59). Without fires, much of the biological value of nutrients that have built up in the Delta would probably not be available. Secondly, fires appear to play a major role in causing changes to the distribution of water (see page 51), thereby adding to the Delta's diversity and allowing some areas to be wetted and others to dry (and therefore, paradoxically, to be burnt).

While fires are perhaps more frequent than before (because most are set by people), it is also obvious that burning is a natural process. Communities of plants, animals and people have endured the costs and enjoyed the benefits of fires in the Delta for time immemorial. There are also costs if fires are too infrequent, for example when the hot, killing infernos consume large masses of plant material that have accumulated over years. The challenge now is to learn more about the effects of frequent, hot fires and to understand how the devastation of burns (as particular events) measures in relation to burning (as a process).

KEY POINTS

1. Plants are important 'engineers' in causing channels to switch direction, sieving out mud and clay, and pumping water into the atmosphere which helps maintain the freshwater of the Delta.
2. About 1,300 species of flowering plants have been identified in the Delta. Most are grasses, sedges, asters and daisies, and bean and pea pulses.
3. Most plant species occur in habitats that are never or seldom flooded, whereas areas that are permanently flooded are dominated by a handful of species, particularly papyrus and phragmites reeds.
4. The number of species found in any broad area reflects the diversity of habitats, of which there are many in the Delta. It is thus the mix of habitats that gives the Delta such biotic diversity.
5. Most of the Delta's plants are found elsewhere in southern and central Africa, especially in wetlands to the north in the upper Zambezi River Basin.
6. The frequent fires have a variety of effects. On the one hand, plant resources, wildlife, fish production, and nutrients may be lost. But fires also release nutrients held in peat and other organic debris, and cause changes to the distribution of water which add to the Delta's diversity.
7. Conservation should not aim to protect particular habitats or conditions, but rather preserve processes that allow for change and plant diversity.