Chapter 15
The Arid Savanna Biome

Key Concepts and Questions: This Chapter Will Explain

- *Why soil nutrient status, moisture relations and herbivory are the key drivers of arid savanna structure and function.*
- *How to define, recognise and understand the concept of 'arid/eutrophic' savannas.*
- *What the main types of arid savannas are, where they are to be found and what characterises them.*
- *Why a single tree species (*Colophospermum mopane—mutiati*) dominates such a large area of southern Africa, and what determines its distribution.*
- *How soil nutrients, drainage and chemico-physical reactions result in specialised plant/animal communities.*
- *Why a series of arid savanna ecoregions extend from the Cunene to the Congo—over the 1650 km of Angola's coastline.*

Context: The Arid/Eutrophic Savannas

Two features characterise arid/eutrophic savannas:

- Low and unpredictable rainfall which accounts for variable and usually low levels of primary production and thus low fuel loads for combustion by fire;
- Moderate to high soil nutrient status which supports nutritious grass and tree foliage that sustains high densities of mammalian herbivores.

Within the concept of arid/eutrophic savannas, a wide diversity of habitat physiognomies is found, including short grasslands, shrublands, open tree savannas, woodlands, thickets and dry forests. The general physiognomy of arid savannas (a variable mix of grasses, forbs, shrubs and trees) is not strikingly different to that of mesic savannas. However, the two savanna biomes differ significantly in the physical environments they occupy, and the evolved adaptations that account for their success. Arid/eutrophic savannas are typically found where mean annual precipitation ranges from ca. 250–650 mm, with more than eight dry months. Summers can be very hot; winters can have occasional to frequent frosts. Soils are mostly fine-textured,

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eutrophic, with an exchangeable base status of above 15 milli-equivalents per 100 g of clay. Mammalian herbivores are notable for their diversity, high biomass and their impacts on vegetation structure. Fires are infrequent, and usually follow seasons of exceptional rainfall and herbage growth. Other characteristics are summarised in Box 1.2.

Unlike the mesic savannas which typically occur on the old planation surfaces of the Central African Plateau, arid savannas occupy lower elevations, often on younger, eroded landscapes, or down-warped basins and rift valleys. Here the vegetation is mixed both structurally and floristically, especially at the interface between arid and mesic savannas. The baobab *Adansonia digitata* is found throughout the arid savannas of Angola and is emblematic of the country's hot dry lowlands.

In Angola, arid savannas include three ecoregions of the southwestern and coastal lowlands, from the lower slopes of the Angolan Escarpment to the sea. Maps of the distribution of these ecoregions are given in Figs. 3.30–3.32 to which reference should be made to orientate the following outlines.

- The Angolan Mopane Woodlands (Ecoregion 12, Fig. 3.30) of Cunene, Namibe and Benguela provinces merge gradually westwards into the
- Namib Savanna Woodlands (Ecoregion 13, Fig. 3.31) of Namibe and Benguela provinces, which in turn transition as rainfall drops below 150 mm per year to the
- Continuing northwards from the Namib Savanna Woodlands, from Sumbe, across Cuanza-Sul and Bengo provinces, as a narrow tongue to the coastal belt of Cabinda, is the Coastal Arid Savanna (Ecoregion 14, Fig. 3.32).

The Coastal Arid Savanna includes some of what Burgess et al. (2004) included in their definition of Angolan Scarp Savannas and Woodlands, here re-defined to separate the coastal lowlands from the escarpment. Some areas of the Baixa de Cassange might well fall into the category of arid/eutrophic savanna, but the lack of field information accounts for its inclusion in this study as part of the Western Congo Forest/Savanna mosaic (Ecoregion 2).

Angola's Arid/Eutrophic Savannas (Ecoregions 12–14)

15.1 Angolan Mopane Woodlands (Ecoregion 12)

Distribution and Climate

This ecoregion (WWF 34, Barbosa 20, 21) is unique in Angola, and indeed in Africa, for being dominated and characterised by a single tree species—*Colophospermum mopane*. Known as *mutiati* in Angola or *mopane* over most of its range, it is a leguminous tree or multi-stemmed shrub of the Fabaceae family. Mopane-dominated ecosystems occupy 607,000 km^2 of southern Africa (Burgess et al., 2004), lying between 9 and 25 degrees of latitude, across Angola, Botswana, Malawi, Mozambique, South Africa, Zambia and Zimbabwe (Fig. 15.1). It is not found on the Central

African Plateau, being confined to the hot dry valley bottoms and adjacent plains of the Cunene, Zambezi, Luangwa, Save, Shire and Limpopo rivers. Throughout its range, mopane is found on rich alluvial and basaltic plains, on calcisols over calcrete pavements and on well-drained slopes of rocky hills. *Colophospermum mopane* is usually found on fine-textured (clayey) soils, but will penetrate sandy soils where they overlie clay or calcrete. At its boundaries with other ecoregions, the transition of soils and vegetation type often happens abruptly—over a few metres - for example, where clay soils meet the sands of the Kalahari, and where *Colophospermum* woodland is replaced by *Baikiaea* woodland.

In Angola, *Colophospermum mopane* occurs in the far southwest, from Mupa National Park, down the Cunene, across the foothills of the Chela Escarpment to within 40 km of the sea near the mouth of the Coporolo river (Fig. 3.30). Ranging in altitude from ca. 1000 m on the slopes of the Serra da Chela, to 100 m near the coast, it occupies arid regions with less than 650 mm annual rainfall, hot summers and dry mild winters during which frost is infrequent. However, in the lower Cunene valley, occasional heavy frosts do occur. (Figs. 3.33, 15.2 and 15.3). Mopane is an extremely resilient species, and extends deep into the Namib Woodlands and the

Fig. 15.1 The distribution of *Colophospermum mopane* in Africa. From Stevens (2021) *Ecology and Evolution,* https://doi.org/10.1002/ece3.7377

Angolan Namib ecoregions as scattered trees and shrubs, within rainfall zones of less than 150 mm per annum (Table 15.1).

Floristic Composition and Physiognomy

Over much of its range, *Colophospermum* is the dominant tree species, varying in density from short, stunted and dense shrublands of 1–4 m in height, through open tree savannas of 5–10 m in height with several companion species, to tall mono-specific woodlands of 10–20 m in height on deep alluvial soils. Soil depth and water relations appear to be responsible for the great diversity of *Colophospermum* growth form. Shallow calcisols derived from calcrete, with limited root access to permanent water

Fig. 15.2 Mixed mopane woodlands and thicket below granite domes and inselbergs below the Angolan Escarpment, between Lubango and Caraculo

Fig. 15.3 Mixed mopane woodlands and thicket below granite domes and inselbergs below the Angolan Escarpment, between Lubango and Caraculo. Morro Maluco (*Dente do Dragão*) in background

Table 15.1 Climatic data for stations in Angolan Mopane Woodlands

	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month(°C)
Chitado	Cunene	1000	405	24.0	27.4	19.2
Bruco	Namibe	699	466	23.8	25.7	19.5

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

supplies, result in dense shrub communities. Where breaks in the calcrete substrate allow deep penetration of roots to more reliable water supplies, tall trees establish, often forming single- or multi-stemmed groves of trees to 20 m height. In Angola, most of the tall woodlands that used to occupy the richer, deeper soils at the base of the Chela escarpment have been felled for charcoal production. Mature stands of tall mopane woodland survive in parts of Mupa National Park and the western Cuvelai.

The Angolan Mopane Woodlands ecoregion has a very low diversity of plant species, both within communities (alpha diversity), between communities (beta diversity) and across landscapes (gamma diversity). This characteristic has not been explained, and is remarkable given the wide geographic range of mopane and the diversity of landscapes, soils and regional climates that it occupies. *Colophospermum mopane* has a number of companion species across its extensive range, including *Acacia nigrescens, A. nilotica, A. tortilis, Adansonia digitata, Albizia harveyi, Balanites angolensis, Boscia foetida, B. albitrunca, Combretum apiculatum, Commiphora spp., Dalbergia melanoxylon, Kirkia acuminata, Sclerocarya birrea, Spirostachys africanus, Terminalia prunioides* and *Zizyphus mucronata*. Grasses of the genera *Anthephora, Aristida, Cenchrus, Eragrostis, Enneapogon, Schmidtia, Stipagrostis* and *Themeda* dominate the short, herbaceous layer.

Grass cover can vary from very sparse during dry periods to dense after rains. Mopane herbaceous communities are climate-driven, being dependent on infrequent but occasionally high intensity rainfall, differing fundamentally from the herbaceous strata of mesic miombo systems, which are fire-driven. Drought conditions are frequent, broken by rare but powerful floods. Fires are infrequent, especially if herbivore biomass is high relative to the available forage. While the woody component is resilient to rainfall variations from year to year, the herbaceous layer is very sensitive. In droughts, perennial grasses and herbs might be completely removed by the grazing and trampling of herbivores, with rapid replacement by annual grasses and herbs following the first rains. Perennial grasses usually have a good seed store in the otherwise barren soil, and within one or two good rainy seasons these grasses can recover to pre-drought cover and biomass.

Soils play an important role in the species composition of *Colophospermum mopane* communities. Where clays transition to sands, *Terminalia sericea* replaces *T. prunioides*. On the vertic swelling/shrinking clays of basalts, such as those along the Caculovar, *Acacia kirkii* is abundant together with stunted *Colophospermum*, replacing *A. tortilis* and *A. nigrescens* as companion species. On the rocky, shallow soils of well-drained hills, *Combretum apiculatum* is in mixed communities with *Colophospermum mopane, Boscia foetida, Terminalia prunioides, Commiphora angolensis* and the shrubs *Catophractes alexandri, Grewia flava, Rhigozum brevispinosum* and *Sesamothamnus lugardii*. The range occupied by *Colophospermum* extends deep into the Namib, where it is found together with *Welwitschia mirabilis* in deep coarse sands of dry river beds.

Determinants of Distribution and Population Dynamics

Perhaps because of the singular physical characteristics of mopane and its sharply delimited geographic range, the factors that determine its distribution have attracted much interest from ecologists. Recently, researchers have provided mechanistic models of key constraints to *Colophospermum mopane* distribution and growth form, at local scales in terms of physiological performance (February et al., 2020), and at regional scales in terms of environmental determinants (Makhado et al., 2014) and demographic dynamics (Stevens, 2021).

Early studies suggested that the southern limit of mopane occurs where the average July minimum temperatures fall below 5 °C, and where frequent frosts and cold snaps in valleys caused by cold-air drainage result in tree mortalities. The northern limit was explained by higher rainfall, with higher fuel loads and higher fire impacts on seedling and sapling recruitment. Rainfall timing and amount was also considered to influence competition from faster growing grasses for resources such as moisture, nutrients and sunlight. Day length, and hence latitude, too, were considered, as were excessive herbivory and damage by elephants. Locally, soil conditions, through physiological drought in clay soils, or waterlogging on sites with impeded drainage, were also proposed as constraints to the distribution of mopane. These explanations of the sharp limits to mopane distribution have recently been addressed systematically by Stevens (2013, 2021).

Stevens has reviewed available literature and has undertaken field and laboratory studies on the demographic factors that influence mopane seed production and germination, and seedling, sapling and adult growth and survival to reproduction. She concluded that a series of demographic processes and environmental pressures interact to shape the species' current range. Individual plants have to pass through several **growth thresholds**, most importantly, to escape top-kill. **Top-kill** is the process whereby fire or herbivory suppresses saplings from developing into mature trees. Once saplings reach over 2 m height, they can escape such damage. Stevens found that these pressures often maintain mopane at a coppicing multi-stemmed shrub form, which is functionally sterile (Fig. 15.4). The growth thressholds include:

- First, specific rainfall events and adequate seed resources must be sufficient to drive a pulsed episodic recruitment of seedlings;
- Second, seedling root growth must be sufficiently rapid to reach moisture below the evaporation layer of the topsoil;
- Third, sapling growth must be sufficiently fast to reach over 2 m height in order to escape top-kill from fires and herbivory; and,

Fig. 15.4 Shrub growth form of *Colophospermum mopane* in central Kruger National Park, with isolated tall trees where access to water or protection from fire resulted in rapid growth above the fire and herbivore 'top-kill'. *Photo* Izak Smit

- Fourth, adults must pass a height threshold of 4 m at which flowering, wind and insect pollination, and the production of seeds is more successful.

Once established, mopane communities of either shrub or tree forms are resilient to drought, heat, frost, fire and herbivory. While top-kill can result in coppicing, mortality resulting from this process is seldom recorded, except in local patches during extended droughts, or recurrent fires, or where elephants exert high levels of damage, transforming tall woodlands into isolated trees within a coppicing shrubland. Once the structure of a tall woodland has been reduced by damage into a shrubland, return to a woodland is prevented by a strong coppicing habit in response to disturbance. Stevens (2021) noted that mopane trees do not self-prune, and that the coppicing shoots do not thin out to develop a single leading shoot that becomes a tree. Instead, the multi-stemmed shrub form persists. In the absence of tall trees, the seed source for seedling recruitment is severely reduced.

In the Luangwa National Park of Zambia, Caughley (1976) reported that large areas of mopane woodland had been transformed by elephant damage into a functionally sterile shrubland. During the drought of 2015/2017, a similar impact from elephant damage was experienced in Kruger National Park.

In summary, Stevens (2021) proposed that the range limits of *Colophospermum mopane* and the development of short mopane shrublands are determined by the interactions of disturbance events (fire, frost and herbivory). These factors lead to a high proportion of effectively sterile shrubs, and the lack of recruitment of mature, fertile trees sufficient to maintain a viable population. Stevens planted mopane experimentally at sites outside its natural range—at higher, cooler elevations and higher latitudes (more than 500 km south of its southern limit). She found that the seedlings survived and grew especially in the absence of grass competition, so that climate and soil did not directly limit distribution. She therefore argued that climate-based range predictions for mopane do not reflect the demographically-driven constraints on the species' distribution, determined by top-kill, by fire or by herbivory, and therefore not by climate. This hypothesis merits testing in Angola, especially in the lower Cunene Basin, where frost can be a limiting factor.

Box 15.1 Sodic Soils and Salt Licks in Mopane Woodlands

A common feature of mopane woodlands and other arid savannas are **sodic soils**, often found at the base of catenas in the granite hills of undulating landscapes. In these sites, *Colophospermum mopane* forms a pattern of wooded patches scattered within a matrix of bare, salt-rich soils. The shrub *Euclea divinorum* and succulents such as *Sanseviera pearsonii* and *Aloe zebrina*, and even the epiphytic orchid *Ansellia gigantea* on large mopane trees, are typical of such communities along the Cunene River near Humbe.

Such bare patches of pale-coloured clay soils are often considered to be due to local overgrazing by herbivores, but they are a world-wide phenomenon in arid savannas. They are typically formed by natural, evapotranspiration-driven hydrologic processes in sodium-rich granitic landscapes (Khomo & Rogers, 2005). The colluvial runoff of salts down the catena accumulates at the base of slopes. Salts are further concentrated by the high evapotranspiration rates of the hot dry climate. On filtering into the soil, the sodium causes clays in the A-horizon to **deflocculate** (disperse) and form an impermeable B-horizon, cutting off the movement of water that would normally move upwards by hydrological processes. This sodic water seal causes the death of plants not adapted to such conditions. Bare patches are typically associated with such sodic soils (Fig. 15.5).

Fig. 15.5 An example of a sodic patch in Kruger National Park. These open sites in wooded landscapes are often at the foot of granite hills, or next to rivers. Their whitish appearance is due partly to their high sodium content. They play a critical role in the life of herbivores in arid savannas. *Photo* Izak Smit

While sodium is not an essential plant nutrient, it is essential for mammals. The bare patches are thus attractive to herbivores, not only because of the salt content of the soil, but also because these soils are favoured by nutritious grasses, which have higher levels of sodium in their leaves than even the same species growing on adjacent low sodium soils. The herbivores concentrate on these bare patches, reducing plant cover, increasing soil nutrition via their faeces, compacting the surface through trampling, and gradually reinforcing the denudation of the habitat. Pools formed during rainy periods are rich in clays and are used as mud baths by warthogs. Sodic patches provide fascinating venues to study soil/plant/animal interactions within the broader matrix of arid savannas.

15.2 Namib Savanna Woodlands (Ecoregion 13)

Distribution

The Namib Savanna Woodlands Ecoregion (WWF 104; Barbosa 27) is a narrow belt of arid shrublands, savannas and woodlands extending northwards from the Cunene

River to Sumbe in Cuanza-Sul (Fig. 3.31). It lies between the Angolan Namib Desert and the Angolan Mopane Woodlands ecoregions. In the south, it occurs on the hilly and mountainous hinterland of Iona National Park and up the rugged Cunene valley to Chitado. Barbosa (1970) used the term 'steppe' for this vegetation formation, but this term is inappropriate for use in Africa. The vegetation comprises short trees, shrubs and grasses—a typical tropical arid savanna. Rainfall increases from south to north, and from west to east, and ranges from 150 to 400 mm per annum. The high peaks of the Cafema and Tchamalinde mountains in Iona National Park possibly receive somewhat more rain than the plains, but the vegetation throughout is arid to sub-desertic.

The topography varies from broad, almost flat coastal peneplains, often with extensive calcrete pavements, to scattered hilly outcrops of limestone, sandstone, gneiss, granite and schist. Soils are shallow and comprise calcisols, lixisols, leptosols and arenosols. Ephemeral rivers and streams cut across the landscape. The valleys are usually shallow, but in some cases, rivers such as the Curoca, Bero, Giraul and Bentiaba, have cut deep ravines, with sandy bottoms, subject to rare but intense flooding events. The perennial Cunene follows a deep gorge between the Tchamalinde Mountains of Angola and the Baynes Mountains of Namibia, both of which reach over 2000 m.

Serra da Neve, an isolated inselberg of igneous alkaline carbonatite (Fig. 15.6), which rises above the plains covered in Namib Savanna Woodlands, is of particular biogeographic interest. Reaching 2489 m above sea level, it carries a succession of vegetation types similar to those on the Leba Pass described in Chap. 5.7, but awaits detailed exploration. The high peaks of Serra da Neve, Cafema and the Tchamalinde possibly also benefit from orographic cloud brought in off the Benguela Current, but this has yet to be documented (Fig. 15.7 and Table 15.2).

Floristic Composition and Physiognomy

This ecoregion, perhaps more than any other in Angola, has fine-scale vegetation patterns where topography, geology, soil depth and texture offer different moisture and nutrient conditions. Between Sumbe and Iona, over a distance of 550 km, plant communities display a rapid turnover in floristic and structural composition. Although species diversity is low, the floristic composition and height, density and architecture of both woody and herbaceous components, is ever changing.

The general pattern is a mix of a limited set of woody and herbaceous species, forming short open savannas and woodlands on hills and open grassland on the deeper sands of intermontane plains. Communities of *Acacia mellifera* can cover large areas, to be followed by savannas of *Acacia nilotica, A. tortilis* or *A. reficiens*, or mixed communities including *Acacia tortilis, Balanites angolensis, Boscia albitrunca, B. foetida, Catophractes alexandri, Colophospermum mopane, Combretum apiculatum, Dichrostachys cinerea, Maerua angolensis, Rhigozum brevispinosum, Salvadora persica, Spirostachys africana, Sterculia setigera*, *Terminalia prunioides* or various species of *Commiphora* on shallow, rocky soils and on schist or granite outcrops. Short nutritious grasses include species of *Cenchrus, Enneapogon, Schmidtia, Stipagrostis, Themeda, Tricholaena* and *Urochloa.* Succulents are common, such as

Fig. 15.6 Mixed Namib Savanna Woodlands south of Serra da Neve, which rises to 2489 m. The dark green line of tall trees in the middle-distance marks the Bentiaba river

Fig. 15.7 Namib Savanna Woodlands dominated by *Acacia* species on the Talamajamba plateau, 40 km inland of Benguela. Rich grasslands following summer rain. *Photo* Antonio Martins

Table 15.2 Climatic data for stations within the Namib Savanna Woodland ecoregion

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest Month (°C)	Coldest Month (°C)
Sumbe	Cuanza-Sul	10	389	24.0	27.0	20.1
Baía Farta	Benguela	3	389	22.4	26.3	18.0
Caraculo	Namibe	440	123	22.9	26.4	17.2

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

Aloe littoralis, A. catengiana, Cyphostemma currorii and *Sansevieria pearsonii*, with many succulent arborescent species, including *Adansonia digitata*, *Euphorbia eduardoi, Moringa ovalifolia* and *Pachypodium lealii.*

The deep sands of ephemeral rivers, such as the Curoca, Bero, Giraul and Bentiaba are intermittently lined by tall woodlands of **phreatophytes** (plants using deep water sources) such as *Acacia erioloba*, *Combretum imberbe, Faidherbia albida, Ficus sycomorus, Sclerocarya birrea* and thickets of *Cadaba benguellensis, Cordia ovalis, Euclea pseudebenus, Salvadora persica* and *Tamarix usneoides.*

Typical of arid/eutrophic savannas, this ecoregion has many spinescent trees and shrubs (including species of *Acacia*, *Balanites, Euphorbia, Gymnosporia, Pachypodium* and *Zizyphus*) and even herbs and grasses can be armed with spines. Grasses are generally of high nutritional value through the year, historically supporting large herds of grazers such as Gemsbok and both Plains and Mountain Zebra, and mixed feeders such as Springbok. Most large mammals have been eradicated by humans over the past century and replaced by cattle and goats as the main herbivores.

15.3 Coastal Arid Savannas (Ecoregion 14)

Distribution, Landscapes and Climate

The Coastal Arid Savanna ecoregion includes the coastal lowlands (from sea level to 500 m) where annual precipitation ranges from 350 to 650 mm, from Sumbe in the south to the coast of Cabinda in the north (Fig. 3.32). The ecoregion follows the mostly narrow lowlands of the sedimentary basins of Angola's coastline, a mix of Quaternary and Tertiary marine sediments. Pleistocene sands of former beaches form flat plateaus of red, yellow and grey sands (musseques) which cover earlier Lower Cretaceous to Miocene sediments of clays, limestones, marls, sandstones and conglomerates. The ecoregion extends up the Cuanza valley for 180 km, but is mostly less than 50 km in width.

The cooling and drying impact of the Benguela Current has a profound influence as it moves northwards along the Angolan coast. A narrow belt of low mean annual precipitation, but high relative humidity, creates a climate in which arid savanna elements extend to the mouth of the Congo River where mean annual precipitation is 590 mm. The unusual and dense coverings of the lichenised fungus *Roccella tinctoria* on the trunks of *Adansonia digitata* trees, and tresses of fruticose lichens (*Usnea* spp) hanging from the branches of thicket trees, is at first sight somewhat surprising in this arid environment. High relative humidity, accompanied by coastal fogs and persistent low stratus clouds (*cacimbo*), are accounted for by the presence of a persistent temperature inversion over the cool Benguela Current (Fig. 16.6).

Floristic Composition and Physiognomy

Due to the erosion and planation of successive marine and terrestrial sedimentary strata, the vegetation cover of Coastal Arid Savanna presents a repeated and predictable sequence of floristic composition and physiognomic structure. Barbosa (1970) recognised nine sub-types within his vegetation type 23. From south to north, one tree species characterises the diverse grasslands, savannas, woodlands, thickets and dry forests of this ecoregion: *Adansonia digitata.* The baobab (*imbondeiro*) has several companion species—*Acacia welwitschii, Euphorbia conspicua* and *Sterculia setigera.*

The fine-scale pattern of communities is reflected in detail in the vegetation map of Quiçama National Park (Huntley, 1972; Fig. 15.8), which includes 28 mapped units over the Park's 9960 km^2. Quiçama plant communities represent the vegetation of the ecoregion, and a few examples will illustrate the diversity of habitats. Grasslands, savannas and woodlands, thickets and dry forests are the main physiognomic types, but closed-canopy gallery forests, floodplain wetlands, mangroves and coastal strand communities, add to ecosystem diversity.

The wide floodplains of the perennial rivers (Cuanza and Longa) that form the northern and southern limits of Quiçama National Park have extensive wetlands dominated by *Cyperus papyrus, Typha capensis* and *Phragmites mauritianus,* with marginal grasslands of *Echinochloa stagnina, E. pyramidalis, Oryza stapfii* and *Vetiveria nigritana* (Fig. 15.9). The escarpment above the floodplain carries deciduous dry thicket (Fig. 15.10).

A rather unique grassland community of this ecoregion is treeless—the monospecific tall grasslands of *Setaria welwitschii* (Fig. 15.11) which occupy the deep swelling and shrinking vertic clays (*terras de Catete*) of Cretaceous marine sediments. On the plateau sands, grasslands are dominated by *Eragrostis superba* and *Digitaria milanjiana*, with tree and shrub clumps associated with termitaria. These grasslands were the richest grazing lands for Quiçama's formerly large herds of Roan Antelope, Eland, Forest Buffalo and Savanna Elephant. Less nutrient-rich grasslands of *Schizachyrium sanguineum, Heteropogon contortus, Andropogon gayanus* and *Pogonarthria squarrosa* form the herbaceous stratum of tree and clump savannas, with the typical mix of tree species already mentioned, plus *Balanites angolensis, Combretum camporum, C. molle, C. zeyheri, Hyphaene guineensis, Maerua angolensis, Strychnos spinosa* and *Terminalia sericea* (Fig. 3.22).

Dense thickets of 5–10 m height are found on plateau red sands with a high clay content (*terras de musseque*) (Figs. 15.12, 15.13, 15.14 and 15.15). These have a mix of deciduous (*Clerodendrum myricoides, Combretum camporum, Grewia*

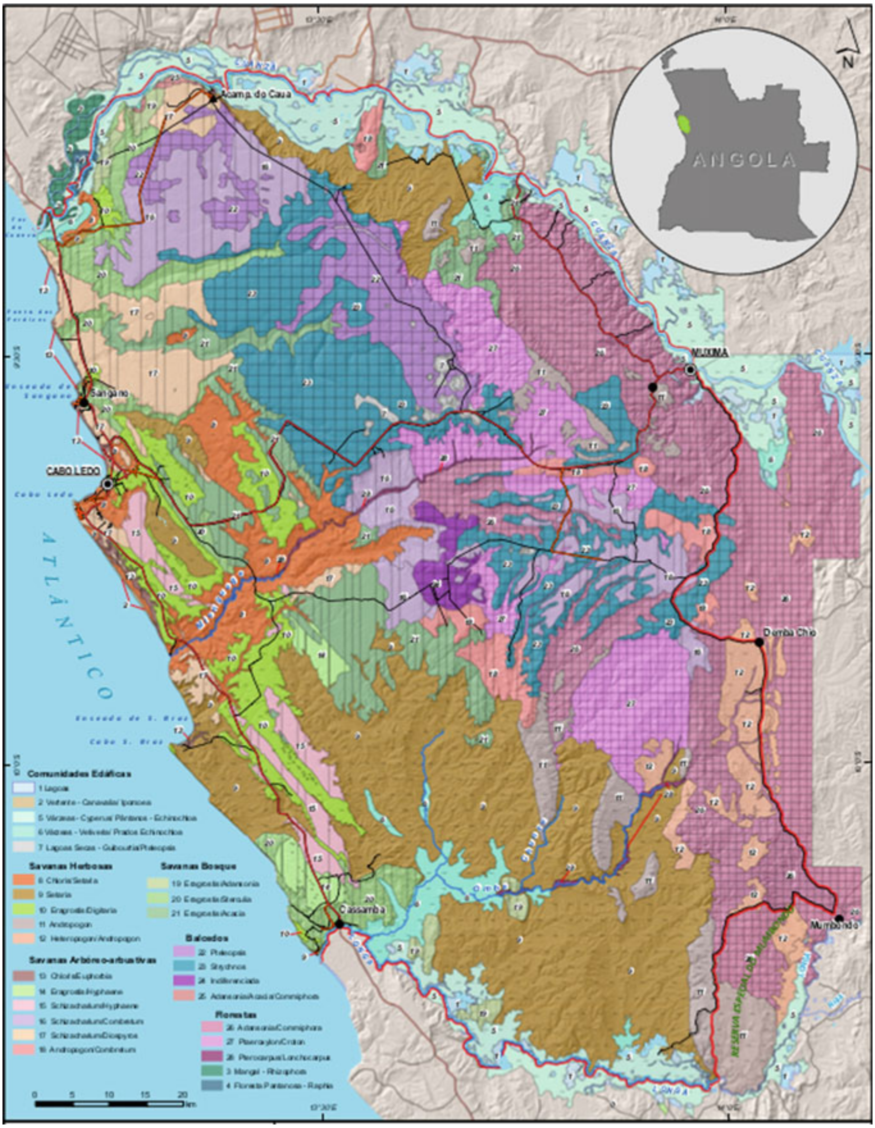

Fig. 15.8 Vegetation map of Quiçama National Park. This 9960 km^2 conservation area has 28 mapped vegetation types, reflecting the diversity of marine and terrestrial sediments on gently undulating landscapes. From Huntley (1972) Parque Nacional da Quiçama. Vegetation Map. Serviços de Veterinária, Luanda

Fig. 15.9 The Cuanza River floodplain below Acampamento da Caua, Quiçama National Park. Dry season deciduous thicket in foreground with grasslands and wetlands on the floodplain. *Photo* Kostadin Luchansky

Fig. 15.10 The Cuanza floodplain, viewed from Acampamento da Caua, Quiçama National Park. Dense dry forest and thicket below the escarpment of the sand plateau, with gallery forest on the margin of the floodplain, lush green during the summer rain season

Fig. 15.11 Tall mono-specific *Setaria welwitschii* grasslands on the deep vertic clays of Quiçama

welwitschii, *Pteleopsis myrtifolia, Strychnos henningsii* and *S. spinosa*) and evergreen (*Garcinia livingstonii*, *Guibourtia carrissoana, Tessmannia camoneana*) shrubs, short trees and emergent succulents (*Euphorbia conspicua*). Grasses (and fires) are rare in the thickets, which are a preferred habitat of Blue Duiker and Bushbuck.

Fig. 15.12 The epiphytic lichen *Usnea* sp. on the branches of *Copaifera coleosperma* in dry thicket

Fig. 15.13 Dry thicket of *Acacia welwitschii, Euphorbia conspicua, Grewia welwitschii* and *Sansevieria cylindrica* on the escarpment slopes above the Cuanza floodplain

Fig. 15.14 Evergreen thicket on deep pale sands of the Quiçama plateau

Dry deciduous forests of up to 15 m height are found on the broken relief of the slightly less arid inland margin of this ecoregion, where it abuts the Angolan Escarpment ecoregion and includes part of Barbosa's (1970) vegetation type 11. Here, on alkaline calcareous soils, the trees, mostly deciduous, include *Adansonia digitata, Acacia welwitschii, Commiphora africana, Croton angolensis, Ptaeroxylon obliquum* and *Pteleopsis myrtifolia.* Where seasonal watercourses cut through the landscape, closed canopy gallery forests of up to 25 m height (*Adina microcephala, Albizia glaberrima, Lonchocarpus sericeus, Millettia thonningii* and *Pterocarpus tinctorius*) are found (Fig. 15.16).

Fig. 15.15 Deciduous thicket on the plateau 'musseque' red sands of Quiçama

Fig. 15.16 Open woodland of *Adansonia digitata* on the margins of the Cuanza floodplain, Quiçama National Park

15.4 Faunal Composition of Arid Savannas

The Arid Savannas of Angola (Ecoregions 12–14) have a distinctive mammalian fauna compared with that of the Mesic Savannas. Typical of arid/eutrophic savannas, many of the herbivores form large herding populations that can number several hundred individuals where they occur in untransformed landscapes. The largest, nomadic herds are formed by Springbok, Gemsbok and Blue Wildebeest. While the first two species are limited to the arid savanna of the southwest, Blue Wildebeest were once numerous in Bicuar, Cuando Cubango and the grasslands of Cameia. Other herding species that occur in the arid savannas and drier limits of mesic savanna include Plains Zebra, Hartmann's Zebra, Cape Buffalo, Red Hartebeest, Common Impala, Topi, Greater Kudu and Giraffe. Black-faced Impala, Black Rhino and African Elephant, once common in the southwest, are now extinct in the area.

Three mini-ungulates, Kirk's Dik-dik, Klipspringer and Steenbok, well-adapted to survival in the absence of free water, were once common in the southwest. Forest Buffalo, Savanna Elephant, Eland and Roan Antelope were once abundant along the northern Coastal Arid Savanna of Quiçama, but were decimated during the civil war.

Many carnivore species, from African Lion to Cape Fox, occur in the arid savannas of southwest Angola. These include African Lion, Leopard, Cheetah, Brown Hyaena, Spotted Hyaena, Aardwolf, Black-backed Jackal, Bat-eared Fox, Meerkat and Honey Badger. Table 15.3 provides a shortlist of typical vertebrate species of the Arid Savanna Biome (Fig. 15.17 and Table 15.4).

Table 15.3 Climatic data for stations in Coastal Arid Savanna

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month (°C)
Luanda	Luanda	44	405	24.3	27.0	20.1
Nzete	Zaire	15	381	24.2	26.8	20.1
Dondo	Cuanza-Norte	38	614	26.2	28.5	21.4
Soyo	Zaire	10	590	25.9	28.2	21.2

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

Fig. 15.17 Forest Buffalo (*pacassa*) in dry thicket on the margin of the Cuanza River, Quiçama National Park. This once abundant emblem of Quiçama is now extinct in the Park. *Photo* Merle Huntley

Table 15.4 Vertebrate Species Typical of the Arid Savannas of Angola

- **Amphibians**: Dombe Toad, Grandison's Pygmy Toad, Marbled Rubber Frog, African Bullfrog
- **Reptiles**: Leopard Tortoise, Ansorge's Leaf-toed Gecko, Angola Banded Thick-Toed Gecko, Huntley's Sand Lizard, Sundevall's Writhing Skink, Horned Adder, Western Banded Spitting-Cobra
- **Birds**: Ostrich, Secretary Bird, Monteiro's Hornbill, White-tailed Shrike, Benguela Long-billed Lark, Rockrunner, Benguela Long-tailed Starling, Rufous-tailed Palm Thrush, Cinderella Waxbill
- **Mammals**: Black-backed Jackal, African Hunting Dog, Bat-eared Fox, Cape Fox, Cheetah, Caracal, Lion, Leopard, Spotted Hyaena, Brown Hyaena, Aardwolf, Common Impala, Black-faced Impala, Red Hartebeest, Springbok, Common Wildebeest, Tsessebe, Roan Antelope, Common Waterbuck, Kirk's Dik-dik, Klipspringer, Gemsbok, Steenbok, Cape Buffalo, Common Eland, Greater Kudu, Giraffe, Common Warthog, Plains Zebra, Hartmann's Mountain Zebra, Black Rhino

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