Chapter 7
The Ecological Role of Fire

Key Concepts and Questions: This Chapter Explains

- *Why fires are so important in the ecosystem dynamics and structuring of Angola's vegetation.*
- *That fires ignited by lightning are natural and very ancient features of African savannas.*
- *Why fires are considered the greatest consumers of vegetation across African mesic savannas.*
- *Why the grasses of African savannas have been so successful despite hot, dry conditions and repeated fires.*
- *How plants and animals respond both positively and negatively to the impact of fires.*
- *How fires drive the maintenance of alternative stable states between savanna and forest ecosystems.*
- *The importance of an understanding of fire regimes, behaviour and potential impacts as the basis for the development and implementation of fire management systems.*

Context: Fire: Africa's Great Consumer

For the Gondwana continents (South America, Africa, Australia and India) natural fires are the key drivers responsible for shaping savanna ecosystems and limiting the distribution of closed forests. Surprisingly, most textbooks on the fundamentals of ecology have little if anything to say about fire as an ecological driving force, despite the long history of fire research in Africa (Booysen & Tainton, 1984; Phillips, 1931).

In the mesic savannas, fires more than herbivores, are the great consumers of plant biomass. Annually, fires burn over three percent of the vegetated globe. Of this, African savannas contribute 70%. Fires have driven some of the most important ecological adaptations, shaping plant life-forms and animal niche structure. Whole suites of fire adaptations, such as the storage of seed banks in the inflorescenses of proteas and pines (serotiny), the thick corky bark of mesic savanna trees, and the

evolution of C_4 grasses, owe their existence to regular fires. However, for most of the last two centuries, most northern ecologists have attributed savannas to human-driven fires and land transformation. Many followers of plant succession theory have viewed Africa's savannas as artefacts of human-driven fire and deforestation.

The anthropogenic origin of bushfires is not supported by recent research, as comprehensively and elegantly synthesised by South African ecologist William Bond (2019). Based on ecological, paleoecological, phylogenetic and physiological evidence, it has been demonstrated that savannas and their constituent grasslands and woodlands are both natural and ancient features of tropical landscape dynamics. Most importantly, tropical savannas are shaped by fire, natural and human induced.

7.1   The Ancient History of Fire in Africa

Fire in African ecosystems has long been attributed to the activities of ancient hunter-gatherers, burning the savannas to make hunting more efficient. Africa, recognised as the Cradle of Humankind, has had members of the genus *Homo* present for about 2.6 million years, and modern *H. sapiens* has occupied the African savannas for about 200,000 years. But both fire and savannas were dominant features of the African (and global) landscapes, many millions of years before the evolution of modern humans. Lightning strikes, not humans, have been the principal agent for the ignition of fires across the globe. Lightning is a natural phenomenon, with millions of strikes per day. Most of these do not trigger bushfires, but lightning strikes remain important sources of fire ignition over much of Africa, despite the increasing role of humans in setting fires.

Paleoecological studies of charcoal, fossils and carbon isotopes indicate that fire has been a feature of terrestrial ecosystems for 400 million years, appearing at least 100 million years before the first vertebrate herbivores evolved and 300 million years before early angiosperms emerged from forests into more open habitats (Bond, 2019). The arrival of open savanna ecosystems, characterised by a mixture of trees and grasslands, occurred with the resurgence of fire in the late Miocene (ca. 10 Ma), possibly linked to the increased seasonality of rainfall in the tropics and the increasing dominance of C_4 grasses at that time (Box 4.1). Phylogenetic evidence (Fig. 7.1) points to a sharp increase in fire activity in C_4 grasslands within the last 10 million years (Bond, 2015, 2019) providing evidence of the close links between savannas, fires and C_4 grasses. The incidence of fires in global landscapes has increased through human activities during the Holocene, but as extensive agriculture, grazing and human settlements increased, globally, the actual area burnt per year has decreased over the past 150 years (Marlon et al., 2008). However, the ecological role of fire is a deeply embedded and ancient evolutionary force.

As human populations grow and the demands for resources increase in both industrialised and developing countries, conflicts at the urban/wildland interface are reaching serious proportions, as demonstrated by fire events in Australia, Brazil, California, Portugal, Greece and South Africa. The need to understand fire regimes

Fig. 7.1 Estimated age and frequency of fire-adapted woody clades from savannas in Africa (black) and Brazil (open). The arrow indicates the surge of fire activity after 10 Ma. After Bond (2015). *Frontiers in Plant Science*, 5, 749. Creative Commons Attribution License (CC BY)
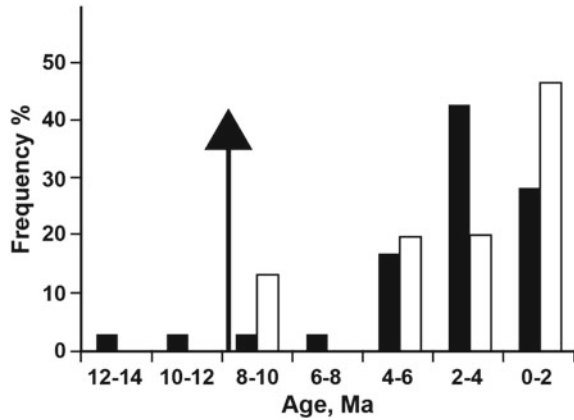
and fire behaviour and to develop fire management strategies has stimulated intensive research programmes on all continents. Fire ecology has become a science in its own right, and southern African workers lead in many aspects of this research (Bond, 2019, and included references). Of particular relevance and value to Angola are the results of long-term fire experiments and fire research projects such as those in Kruger National Park and in Hluhluwe-iMfolozi Park, where for over 60 years, burning trials have been conducted in both arid savanna and mesic savanna (Box 7.1).

The results of both basic and applied research into the role of fire in natural ecosystems have been synthesised within a model (Fig. 7.2) that presents the linkages of biological and geophysical forces and feedbacks over long and short timescales (Archibald et al., 2018). The model provides a useful framework for developing an understanding of the multiple factors involved in fire ecological processes and their evolution, as will be discussed in this chapter.

7.2 Fire Regimes and Pyromes

Fire researchers have recognised distinctive **fire regimes** to describe the repeated patterns of fire at a particular location based on measurable characteristics of individual fires (Bond & Keeley, 2005; Keeley et al., 2012). These characteristics are:

- **Fire frequency** (period of time for plant growth and fuel accumulation between fires),
- **Fire intensity** (rate of energy released by the fire),
- **Fire severity** (the impacts on the affected ecosystems such as biomass consumed, damage to growing points),
- **Fire season** (period of the year during which fires normally occur), and
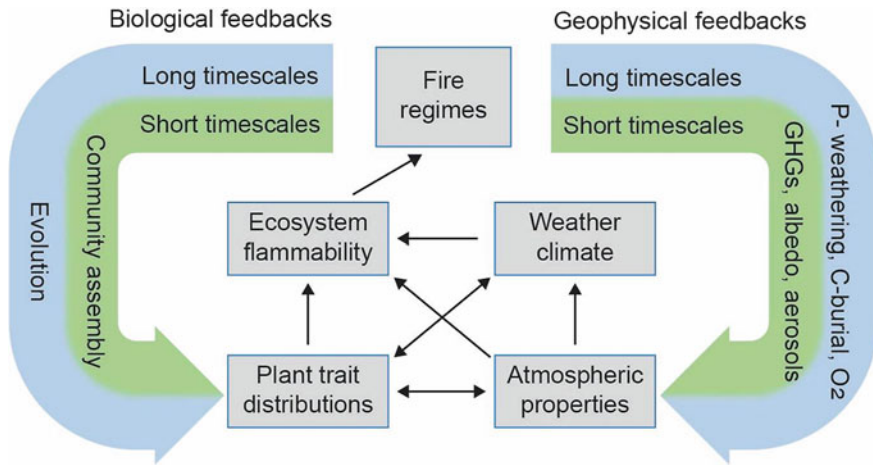- **Fire size** (areal extent of fire impact).

Fig. 7.2 Fire acts through both geophysical processes (exchange of energy and matter between the biosphere and atmosphere) and biological processes (community structure and evolution). Plant innovations that alter the degree to which vegetation is tolerant of fire and the flammability of the vegetation can alter fire regimes, and potentially impact global biogeochemical processes. With both biological and geophysical feedbacks, the type of processes impacted depend on the time scales involved. From Archibald et al. (2018) *Environmental Research Letters*, 13(3):4. Creative Commons Attribution 3.0 Licence

Season, frequency, severity and intensity are interrelated and influence the plant composition (by selecting for fire-tolerant adaptations) and trigger feedbacks between fire and vegetation structure. Fire regimes integrate fire behaviour, climatic, vegetation, faunal and human activities, and are therefore best conceived as emergent properties of a given ecosystem.

In addition to the features of fire regimes, fires are grouped in three **fire types**:

- **Ground fires** (fires that burn in organic layers of the soil, common in the peat of northern **taiga** ecosystems),
- **Crown fires** (fires that burn in the tree canopy, common in Mediterranean-climate shrublands and some confer forests of North America and Eurasia) and,
- **Surface fires** (fires that burn fuels contiguous with the soil). In Angola, surface fires dominate, burning the grass layers below savanna tree canopies with minimal damage to the trees above.

Attempts have recently been made to classify and map fire regimes at a global scale, calling the units **pyromes** (Archibald et al., 2013), analogous to biomes. The system is very generalised, but has some applicability to southern Africa. Three pyromes are important in Angola. The largest, including most of the moist and mesic savannas, are characterised as **FCS** (frequent, cool, small) referring to the high frequency of fires, their low intensity and small patch size. This pyrome is typical of the miombo mesic savannas. The fire patterns of this pyrome have been influenced over the past century by increased shifting cultivation activities. The second pyrome

is the **FIL** (frequent, intense, large) which includes the extensive plains of the Lundas and the Cuando Cubango (Fig. 7.3).

The arid savannas of the southwest belong to the **RIL** (rare, intense, large) pyrome which relates to the infrequency of fires, often once in 30 years, due to the low biomass of arid savannas, the infrequency of high rainfall events which provide rapid build-up of grass biomass and carry rare but extensive fires. For most years, low rainfall and high levels of herbivory of the palatable grazing and browse reduce combustible biomass to low levels. After episodic, high rainfall events, biomass in arid savannas
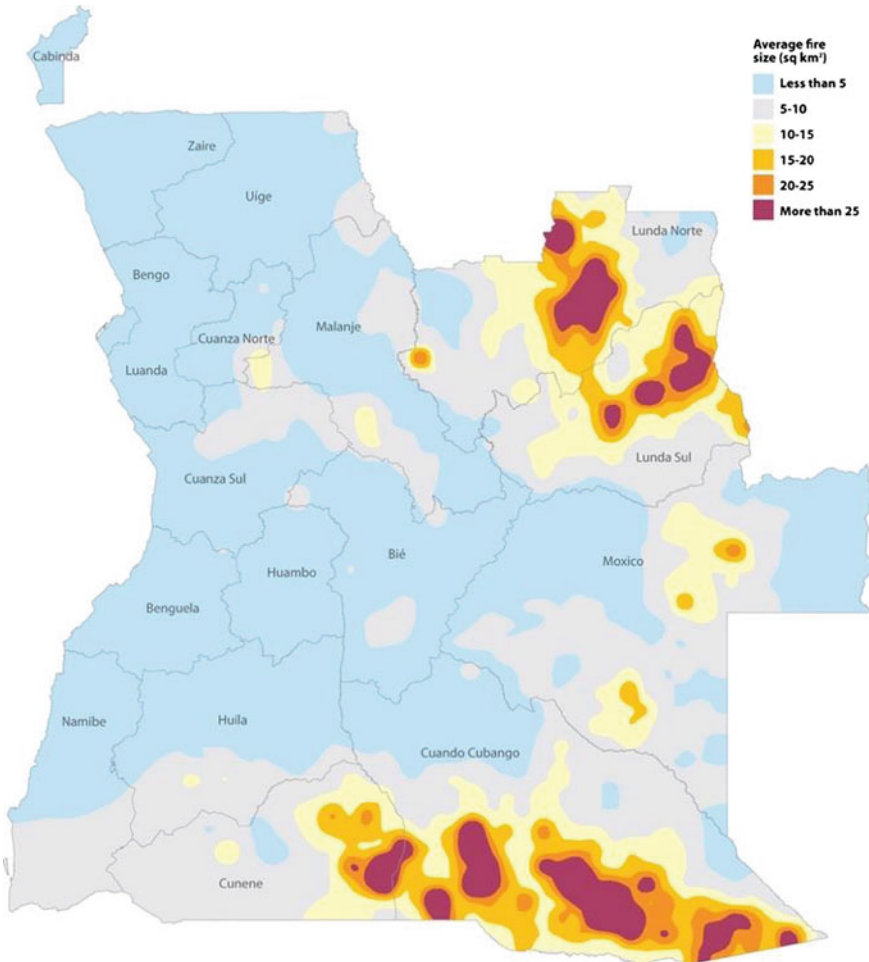

Fig. 7.3 The average size class of fires. Size classes range from less than 5 km^2 (blue) to greater than 25 km^2 (purple). Note the frequent, very large fires in the Lundas and Cuando Cubango. From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.meraka.org.za/products/firefrequency-map

Fig. 7.4 The frequency of fires expressed as the number of years each area of 500 × 500 m burned between 2000 and 2010. Frequency ranges from less than one fire in ten years (white) to fires in every year (purple). Note the absence or low frequency of fires in the coastal belt and arid southwest and the high frequency of fires in Cuanza-Sul, Malange, Lunda-Norte, Lunda-Sul, Moxico and Cuando Cubango provinces. From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.meraka.org.za/products/firefrequency-map
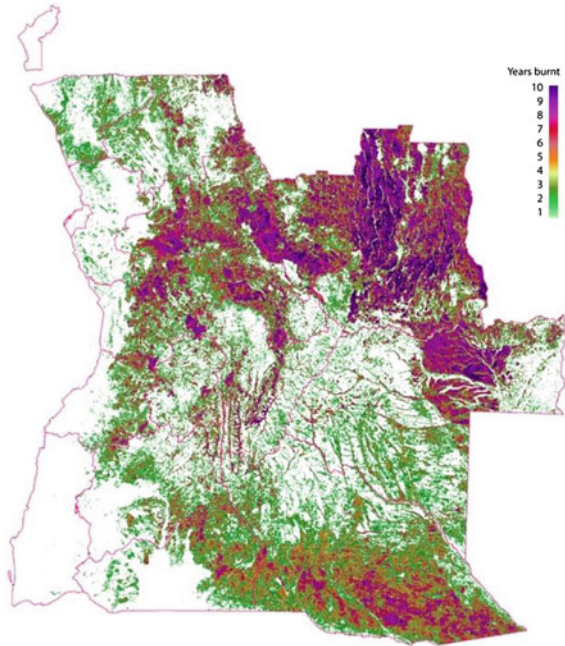
increases to the level at which fires can spread over wide areas. In the last century, indigenous herbivores have been replaced by domestic livestock (cattle, sheep and goats) as the main vertebrate consumers of potential fire fuel, with the consequence that RIL fires are very uncommon in heavily grazed Angolan arid savannas (Fig. 7.4). In northern Angola, high rainfall supports dense tall forests that are too wet to burn under normal circumstances (Van Wilgen et al., 1990).

A detailed study of the spatial and temporal trends of fire across Angolan landscapes from 2001 to 2019 (Catarino et al., 2020) showed that ca. 30% of the country's area burned each year, with the highest percentage burnt being in the northeast and southeast, as reported earlier in the studies of Archibald et al. (2010), Fig. 13.3. Increasing frequency of fires followed trends in human population growth and small-scale subsistence agriculture in the miombo ecoregions of central Angola, with the conversion of forests and woodlands into grasslands and shrublands. Catarino et al. (2020) record an increasing incidence of fire across 23% the area of Bicuar National Park between 2001 and 2019.

7.3   Fire Intensity

Fire intensity is a function of fuel load, heat yield and rate of spread. Rate of spread is influenced in turn by wind speed: the stronger the wind, the more intense the fire. The impact on tree recruitment or mortality increases as the grass cover (**fuel load**)

accumulates and dries towards the end of winter, due to the decrease in the moisture content of leaves, from 88% in summer to 28% in the late dry season. Fuel load does not build up linearly but increases for the first three to four years post-burn, after which decomposition reduces the rate of increase in combustible material.

Build-up of fuel is rapid on nutrient-poor soils such as those of the Angolan miombo, where grasses are of low palatability and herbivores are scarce. Mesic savannas generally experience low intensity fires once every one to three years, both trees and grasses surviving due to their fire-tolerant adaptations. In arid savannas, grazing and browsing by herbivores removes much of the biomass, and reduces the potential of fires spreading from the point of ignition. Fires are infrequent and usually of low intensity in arid savannas, except after high rainfall events with subsequent rapid fuel accumulation.

Fire intensity is measured in **kW/m**—the energy released at the fire front per unit area as it moves across the landscape. Fires in African miombo and Brazilian cerrado have similar fire intensities, at between 2000 and 15,000 kW/m. Fires of 3000 kW/m are sufficient to result in **top-kill** of 90% of tree saplings of 1 m tall, but only 40% of those 2 m tall. Top-kill is the destruction of the growing tips of young trees, leading to stem death. Trees that survive the top-kill **fire trap** of high intensity fires, which are typical of late winter burns, can grow to maturity. Fire, through its control of tree growth, determines the density of trees in savanna systems. The inability of fire to penetrate closed-canopy forests determines the distribution of savanna or forest in tropical landscapes where climatic conditions do not limit forest growth (Sect. 10.7).

Experience in southern Africa indicates that closed forests are especially vulnerable to damage during firestorms, through the simultaneous combination of three weather factors that increase fire intensity—air temperature above 30 °C, relative humidity below 30%, and a wind speed of over 30 km/h. Such **firestorms** can generate their own weather conditions by creating a convective column of scorching, rising air above the fires (Archibald et al., 2017). The heat and smoke generated by firestorms can be enormous. The local formation of cumulus clouds above the Cuanza floodplain, as heat rises off burning swamplands, and cools and condenses, is a familiar sight in Quiçama National Park during the dry 'fire season'. Similarly, the flamboyant sunsets over Angola during the fire season, created by the scattering of the sun's rays by smoke particulates in the lower atmosphere, are indicative of the vast extent of bush fires (*queimadas*) over the Angolan interior from April to October.

7.4 Fire Season

In Angola, fire seasonality varies from early-season burns (May–June) in the north to late-season (July–September) in the south (Fig. 7.5).

Fire experiments are lacking for Angola, but studies in similar ecosystems in Zambia, Zimbabwe and the Ivory Coast demonstrate the effects on trees of annual fires. Distinct patterns of impact of fires in the early dry season, late dry season, and with total fire exclusion (Fig. 7.6) have been recorded in fire experiments initiated in
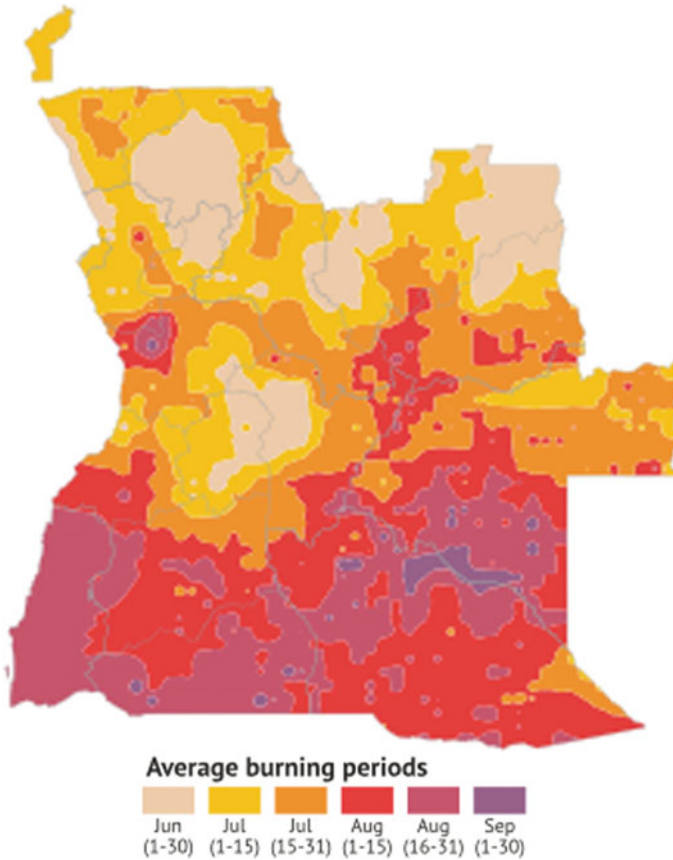
Fig. 7.5 Seasonality of fires in Angola. First early-season fires commence during May in the north (yellow), with late-season fires commencing from July to September in the south (red). From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.mer aka.org.za/products/firefrequency-map

1936 in the Ivory Coast (Laris & Wardell, 2006). After 60 years, an open savanna had developed on the late season site, where high intensity fires prevented tree growth in all but the most fire-adapted species. On the early season site, where fire intensity was mild, a dense woodland had established, of mixed species more typical of mesic savannas. On the site from which fire had been excluded, a closed canopy of rain forest trees had established. Similar long-term experiments in South Africa found that trends towards forest establishing on sites from which fire was excluded were only observed at sites receiving over 700 mm rainfall per annum (Bond et al., 2003). Fire, herbivory, rainfall and season all interact to determine fire impact.
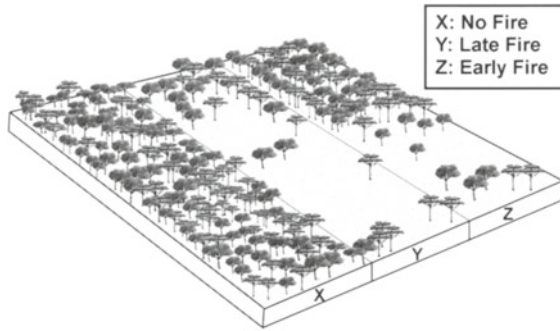
Fig. 7.6   The layout of the burning experiment at Lamto, Ivory Coast. A 'late' fire is more intense than an 'early' fire due to greater biomass accumulation and drier fuel load. Today, the 'no fire' block has returned to a moist forest, the 'late fire' is open savanna. From Laris and Wardell (2006) *Geographical Journal*, 172(4): 271–290, based on Louppe et al. (1995)

7.5   Fire Frequency

Fire-free periods of more than four years are rare in mesic savannas such as the miombo of Angola. Researchers estimate that for mesic savannas, fire-free intervals of nine years might occur once per century. Human activities make such events highly unlikely in Angola. Conversely, in Gabon, attempts to re-establish open savanna communities within forest reserves (to provide open habitats for tourists to view Forest Elephant and Forest Buffalo) have been frustrated by the rapid re-colonisation of sites by forest trees, unless hot dry-season fires are applied annually. Once forests have established in the moist tropics, return to an open savanna is extremely rare without human intervention.

7.6   Impacts of Fire on Soils

Over most of Angola, with the exception of the Congo forests and the arid savanna, fires are a frequent phenomenon. Hot fires often result in the loss of nitrogen, phosphorus and organic carbon, although cooler fires can facilitate the release of nutrients from plant matter into the soil. Loss of nitrogen and sulphur is particularly high (90% and 60% respectively) through **volatilization** (vaporization) when a fire reaches temperatures above 700 °C. Cation loss from volatilization is not as high. Despite these losses, the main effect of fire is a short-term increase in the availability of almost all inorganic nutrients, which are added to the soil as ash.

The passage of heat during a fire also stimulates biological **mineralisation** in the organic layer, due to the increase of pH resulting from the added ash. A nutrient pulse might occur for several months following a fire, with dramatic increases in plant growth rates and higher nitrogen concentration in leaves. Fires can thus favour

grasses such *Panicum* species, which have high light and nitrogen requirements, and which are also greatly preferred by grazers. The green flush following fires, and the mineralisation of soil nitrogen and the increase of the protein content of leaves, is attractive to all herbivores, with corresponding movement of grazer populations from unburnt to burnt areas. The nutrient pulse following **slash and burn** agriculture, which lasts for two or three years before the nutrients are exhausted, is the basis for this subsistence farming practice across Africa.

One of the few fire studies conducted in Angola, in open and dense woodland near Savate in Cuando Cubango, found much lower nutrient levels in the open than in the dense woodland soils. This difference was probably a consequence of the open areas being burned often and intensely, while the dense woodlands were seldom burned (Stellmes et al., 2013; Wallenfang et al., 2015).

Fires leave distinctive pale, sandy, and sparsely wooded margins around savanna woodlands in eastern Angola (Fig. 7.7). The processes involved have not been researched. However, several factors might be important. The shading by large trees on the outer margin of wooded clumps might favour short, sparse, shade-tolerant grasses, which form an effective apron as a fire break. A second possibility is that the woodland trees might produce an **allelopathic** chemical substance that suppresses grass growth around their perimeter. Third, the band of sandy soil might result from soil–water processes, such as on the 'seep-line' in the typical catenas of miombo
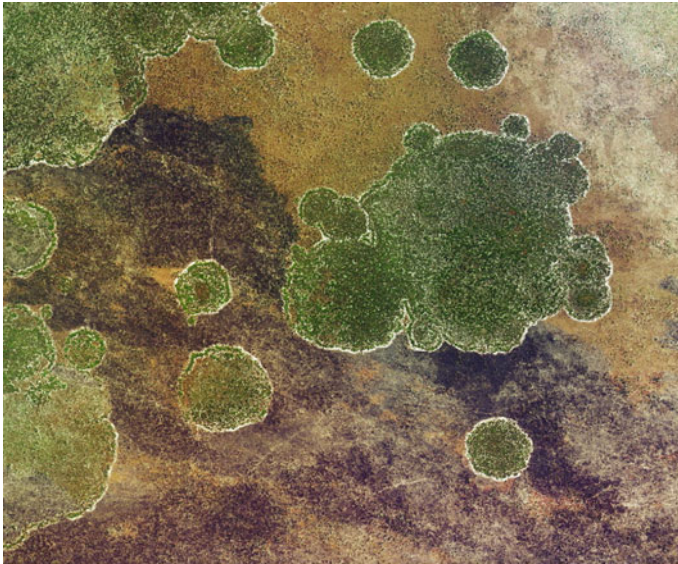

Fig. 7.7 'Fairy forest circles' in Angola. The two circles at the top of the image are each about 700 m in diameter. The bare, whitish rings around the fairy forests and larger rounded blocks of forest are clear of vegetation. The dark area across much of the lower part of the image was recently burnt. The centre of the image is at 15.587 South and 19.3435 East, some 60 km SSE of Cuito Cuanavale. Image from Microsoft's Bing aerial imagery. From Mendelsohn et al. (2022)

ecosystems. Finally, the accumulation of litter around the forest margin promotes slow, smouldering fires that kill plant growth in a narrow belt, depositing a fine ash apron which might also be allelopathic. This is but one of Angola's many ecological phenomena that deserves further research.

7.7   Plant Responses to Fire

Fire is a very strong selective pressure in fire-maintained ecosystems. It is a consumer of vegetable matter and it behaves like a herbivore in that it consumes plant organic compounds and converts them into by-products. But unlike herbivores, fire is an unselective consumer, it is not controlled by predators, nor does fire avoid plant material high in cellulose and lignin nor low in nitrogen. The responses of plants to fire are simple—survival or death. Plants fall into one of two categories—**pyrophilic** (fire-tolerant) or **pyrophobic** (fire-intolerant). The adaptations of plants to fire vary with fire frequency, intensity and season. Grasses, forbs, shrubs and trees respond in different ways to fire, resulting in a gradient of physiognomic structures from open grassland to grasslands with scattered trees and shrubs, to woodlands with open crowns, to closed-canopy forests. Savannas depend on fire for their existence, whereas forests depend on their ability to exclude fire.

To survive recurrent fires, savanna trees have evolved five key adaptations—**thick bark**, deeply embedded **epicormic buds**, underground **lignotubers**, **self-pruning** and **hydraulics**. The first four traits have been known for over a century. These traits protect the tree stems against direct fire damage and allow rapid sprouting of woody shoots after the passage of fires. They also provide underground storage of water and nutrient reserves. Further, by regularly dropping old twigs and branches (**self-pruning**), savanna trees prevent fire from climbing into the tree canopy. Forest trees, however, do not possess such adaptations, and post-fire mortality is very high where fire breaches the forest margin.

Tree mortality following the passage of fire has been attributed to the destruction of the **cambium** (growth tissue) and **xylem** (water transfer tissue) of trees, but South African researchers (Midgley et al., 2011) have suggested that the sudden death of forest trees is caused by '**hydraulic death**'. The heat pulse from a fire causes the blocking (**cavitation**) of xylem vessels by air bubbles—similar to an **embolism** (the blockage of an artery by a blood clot) in humans. Savanna trees have seemingly developed greater resistance to cavitation and suffer lower mortality than forest trees.

A further advantage to tree survival, growth and reproduction in savanna trees is the ability of tree saplings to emerge rapidly above the '**fire-trap**' of repeated fires, typically by reaching over 2 m in height before the next fire season. Below 2 m height, saplings are vulnerable to topkill. The presence of large underground storage organs (lignotubers) plus other fire-resistance adaptations, allows some saplings to survive successive fires until they emerge above the flame zone, especially during extended fire-free periods. An extreme fire adaptation is that of **geoxyles** (also known

as geoxylic suffrutices)—trees and shrubs that have very limited aboveground growth except during the immediate post-fire period (Box 14.3).

Among savanna grasses, species of the Andropogoneae (which dominate Angola's moist and mesic savannas) are the 'fire grasses'. These burn regularly, are typically intolerant of shading, and which accumulate tannins, which in turn discourage herbivory and retard decomposition. In summary, the grasses of mesic savannas grow rapidly following a fire, accumulating a fresh load of combustible material that cures rapidly and creates an aerated fuel bed that enables rapid spread. The grasses of arid savannas are less well adapted to fire, but well adapted to grazing.

7.8 Responses of Animals to Fire

Studies on the responses of animals to fire are far less common than studies on the responses of plants. However, comprehensive syntheses of knowledge on animal responses to fire in African ecosystems are provided by Bigalke and Willan (1984), Frost (1984), Smit and Coetsee (2019) and Nieman et al. (2021a). A few generalisations can be made.

Contrary to popular opinion, high rates of mortality are uncommon in most animal groups during fire events. Most animal species respond to fires by avoidance or immediate dispersal. Many insects flee in advance of the flame front, and most vertebrates are able to move faster than fires. Exceptions, such as reptiles, amphibians and small mammals, survive in refuges within the habitat matrix that do not burn. Examples are termitaria, underground rodent holes, bush clumps, rocky outcrops or bare overgrazed patches. Some invertebrates, such as ticks, can sense the volatile substances released by approaching fires, and drop to the ground to take refuge in cracks in the soil surface.

The heat pulse from savanna fires seldom exceeds a few centimetres depth, making escape possible for many soil-dwelling animals (Frost, 1984). Studies in the mesic savannas of Ivory Coast found low mortalities in soil organisms. Insects survived in trees and shrubs above the fire killing zone of ca. 2 m. The majority of mobile insects fled before being consumed by fire, with only 5% of grasshoppers being killed, 7% surviving in situ, and 88% dispersing away from burned areas in the Ivory Coast study (Gillon, 1973).

Fires attract numerous species of birds (storks, kites, hornbills, drongos) to feed on the fleeing insects, causing a higher mortality to their prey than that caused directly by fire. In the short term, rodents and other small mammals disperse from burned areas, as do many larger species, returning once the first shoots of recovering grasses and woody plants appear. For many small mammals, cover and refuge from predators might be more important than food limitations in determining a return to areas recovering after a fire. Ground-nesting birds, such as pipits, larks and plovers generally nest after the fire season.

Following fires, the recovery of the vegetation triggers the return of herbivores, with population density often greatly exceeding pre-fire levels. Fire effects differ

in terms of fire intensity, frequency, seasonality and the spatial extent and pattern of burned and unburned areas. Furthermore, the recovery rate of vegetation structure influences the species composition and biomass of the surviving or colonising animal populations. A rapid turnover of animal species often occurs, with the immediate increase of predators (especially insect-feeding birds) during fires, followed by grazers, then browsers, as the grass cover and woody plants recover. Mammal predators take advantage of the high densities of prey species that converge on the rich grazing and browsing available in post-fire areas.

Studies on the behavioural patterns of various small mammals (rodents and shrews) suggest the existence of pre-adaptations for population recovery on burns (Bigalke & Willan, 1984). These include non-territorial sociability, a broad non-specialist feeding niche, nocturnal activity, and tolerance of low cover.

In a synthesis of studies on 51 species of larger mammals (body mass greater than 5 kg) of African savannas and grasslands, Nieman et al. (2021b) found a strong correlation between body size and response to fire. The vast majority of studies were conducted in arid/eutrophic savannas of protected areas such as the Serengeti and Kruger National Park. Grazing species were more likely to respond positively to fire (showing a preference for burned over unburned areas) than browsing species. Very large species of roughage feeders such as buffalo and elephant, were found to be ambivalent in their responses to fire. Nieman et al. (2021b) suggest that smaller-bodied herbivores (5–200 kg) require more energy and nutrients relative to their body mass, and are thus more influenced by the nutrient increases found on recently burned areas. As described in Box 8.1, larger-bodied herbivores have greater gut capacity and retention time, and can thus extract nutrients from lower-quality forage on unburned areas.

Mammals, like other animals, may be killed or injured by fire during the fire event, but otherwise respond by dispersal. Over longer periods, both grazing and browsing herbivores respond by concentrating on burned areas as the regrowth of grasses and woody plants progresses, resulting in changes to the vegetation structure.

Herbivores are attracted to the burned vegetation due to the increased nutritive quality of young regrowth, especially in areas where old, moribund and low-value herbage has accumulated in the absence of fire. Many savanna antelope species drop calves in the late winter following an autumn fire season, benefiting from the increased forage quality for the nutrition needs of rapidly growing calves. Although increased concentrations of game provide greater opportunities for predators, the open habitats following fires also provide greater visibility of predators by their prey. There are clearly trade-offs between advantages and disadvantages for predators and prey.

African mammals appear to be well adapted to fires, and many derive benefits from fires. Despite the expectation that fires could cause high mortalities among mammals, reports on fire-induced mortalities are rare. In an isolated case, following eight fire-free years, an extensive hot fire in Kruger National Park spread over 25% of the Park, and led to death or injury in nine mammal species, including lion, elephant and antelope (Brynard, 1972). In general, mortality in larger mammals is very low, except where barriers, such as rivers or fences, prevent escape to refuges.

Box 7.1 Human–Environment Interactions: Fire Impacts and Ecosystem Management

Fire is a key driver of natural ecosystems in Africa. However, human activity and climate change have altered fire frequency and severity, with negative consequences for biodiversity conservation. Angola ranks among the countries with the highest fire activity in sub-Saharan Africa. (Catarino et al., 2020)

Wildfires, especially extensive fires that can threaten human settlements and livelihoods, are popularly and justifiably regarded as negative environmental forces. However, natural, lightning-ignited fires have existed on the planet for hundreds of millions of years, reaching their current importance in the savannas of the seasonally dry tropics about ten million years ago. *Homo sapiens* thus evolved in the fire-adapted ecosystems of Africa, and soon learned how to ignite and manage fire as a useful tool. As the 'Cradle of Humankind', it is not surprising that Africa has long been known as the 'fire continent', and today has the highest incidence of fires, natural and anthropogenic, on Earth. At the human–environment nexus, fire is both a useful tool and a dangerous force, depending on how it manifests.

In Angola, the rate of loss of forests and woodlands to charcoal production, and through short-term subsistence agriculture, is among the highest in Africa. Fire is a key element in the land transformation process. A detailed analysis of moderate-resolution imaging spectroradiometer (MODIS) satellite data by Catarino et al. (2020) indicates that annually, up to 30% of the Angolan landscape is burned. The extent and frequency of bush fires varies for one ecoregion to another, but over most of the country, the impacts of fires caused by human activity far exceeds that of natural (lightening ignited) fires. The negative impacts of uncontrolled bush fires are particularly serious along the margins of the isolated remnant patches of Guineo-Congolian, Afromontane and Mangrove forests. These rich centres of biodiversity are critically endangered by repeated fires. Similarly, the extensive mesic savannas of the planalto—the bread-basket for many rural communities—are also under threat over the vast area occupied by the miombo woodlands of central Africa.

The increasing incidence and intensity of fires over much of Angola coincides with the rapid increase in both urban and rural populations since Independence, with human populations increasing from 6.5 million to 32 million between 1975 and 2022. The problem is double edged. The majority of the rapidly increasing urban population cannot afford fossil-fuel based energy sources and are dependent for their domestic needs on charcoal and firewood imported from rural areas. In response to this demand, charcoal has replaced fruit and vegetables as the key cash crop produced by rural communities. Traditional, ecologically sustainable systems of shifting agriculture, where fields were rested after four or five years of cropping, allowing fertility to recover over perhaps 30 years before the next cycle of use, have been abandoned. The

notoriously poor soils of the planalto are soon depleted of their nutrients, and new fields cleared through deforestation and fire. Traditional systems have not been replaced by modern systems of fire management.

In some African conservation areas fire has been used to manage ecosystems in favour of selected habitats, rare species or the protection of infrastructure. Modern fire management systems are complex and expensive to implement. They require advanced knowledge of fire behaviour and habitat responses based on many years of research. Few African countries can today afford the investment needed to implement controlled, rotational burns over large areas. For this reason, learning from the experience of other countries, such as Namibia, South Africa, Tanzania and Zimbabwe is the most pragmatic approach. General principles and guidelines for fire management have been developed for the arid and mesic savannas of Kruger National Park, which ecosystems are similar to those in many Angolan national parks. The findings of these studies are of use to fire managers in Angola's protected areas (Archibald et al., 2017; Bond & Van Wilgen, 1996; Govender et al., 2006; Van Wilgen et al., 2007). As a guiding principle, more frequent fires, early in the dry season, and therefore less intense, are recommended for mesic savannas.

It is wise to remember that fire must be respected for both its positive and negative attributes. The words of pioneer African ecologist, John Phillips (1965) "Fire: a good servant but a bad master", are pertinent when considering fire management options.

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