# Chapter 10
# Ecosystem Processes and Dynamics in Mesic Savannas

***Key Concepts and Questions: This Chapter Will Explain***

- *Why the laws of thermodynamics underpin the processes of energy capture, transfer and loss within ecosystems.*
- *How different photosynthetic pathways have evolved in response to temperate and tropical climates.*
- *How the carbon cycle of a savanna ecosystem is structured.*
- *Why plant biomass production in mesic savannas is higher, but herbivore biomass is lower, than that of arid savannas.*
- *How nutrients are transferred from plants to the soil through decomposition and mineralization processes driven by insects, bacteria and fungi.*
- *Why the rain forests and mesic savannas of Angola can be described as alternative stable states.*
- *How trees and grasses coexist while competing for similar resources.*

## Context: An Introduction to Systems Ecology

One of the unifying concepts in ecology is that of food webs, where energy and nutrients are transferred from one trophic (feeding) level to the next (Sect. 10.1). Ecological research has paid much attention to trophic interactions and structures since the concepts were introduced by Elton (1927) in his classic book *Animal Ecology*. The processes were quantified by Lindeman (1942) for aquatic ecosystems, and later championed by American brothers Eugene and Odum (1953), co-founders of modern integrated whole-ecosystem science. Odum (1983) used general systems theory and the laws of thermodynamics to better understand the flows of energy through ecosystems, and to describe them using conceptual and mathematical models.

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### *Ecosystem Models*

Systems ecologists are largely focused on understanding and managing ecosystems. The functioning of ecosystems is defined by the complex relationships and interactions between living organisms and their physical and biological environments, and the influence of human interventions on these relationships. Systems ecologists attempt to view ecosystems holistically and use models to show how the components within the ecosystem relate to one another. This can be done across a wide range of scales, both spatial and temporal. This is called the **systems approach**—the application of which is not limited to ecology, but also widely used in banking, communications, transport and other sectors.

In ecology the interdependent components of a system are linked through the transfers of energy and matter, as all parts are linked together and affect each other. The similarities, efficiencies and challenges associated with these transfers are what define ecosystems in terms of the growth, development, stability and evolution of the organisms in that system. The systems (or **holistic**) approach simultaneously investigates different components at different spatial and temporal scales. It regards the properties and collective interactions of complex systems to be equal to *more* than the sum of their parts. It contrasts with the **reductionist approach**—which considers that complex systems can be reduced to studies of simpler, individual components and to be *equal* to the sum of their parts.

In systems ecology the emphasis is on how the system operates as a whole and how interactions produce **emergent** properties. An example is the influence of a dense canopy of mixed tree species on the shaded microclimate below it—an emergent property contributed by and exploited by many different organisms.

Given the complexity of ecosystems, models are used to enable scientists to investigate and understand the functional linkages and implications of disrupting any of these linkages. A simple model of a system is given in Fig. 10.1.

Ecosystem models are necessarily far more complex, showing many different storages (boxes), flows between them (indicated by arrows) and the processes (e.g.

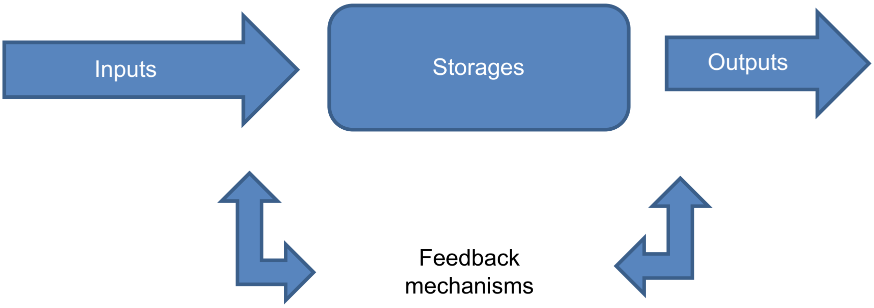

**Fig. 10.1** A simple model of a system. Feedback mechanisms include the interactions between components and processes that maintain system stability, or drive change

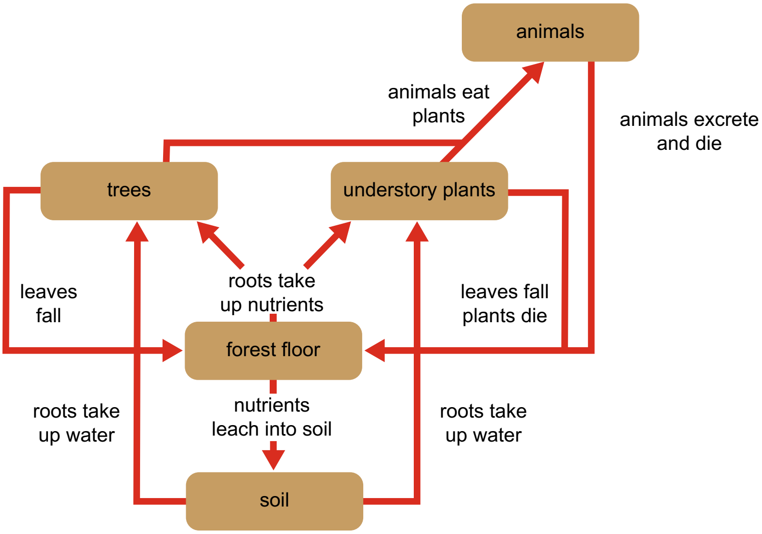

**Fig. 10.2** Pathways and pools of materials in a terrestrial ecosystem. The red arrows indicate transfers of energy, nutrients and water between pools

photosynthesis, herbivory, predation, harvesting, migration) defining the nature of the inputs and outputs. Figure 10.2 shows a more complex, but still simple model.

From the above models, it becomes apparent that two basic processes must occur in an ecosystem for organisms to live. These processes are critical to understanding how and why Angolan ecosystems occur where they do, function as they do and why the plants and animals occurring there are highly adapted to prevailing conditions. There have to be **inputs** and **outputs** of energy and matter (chemical elements). All energy enters ecosystems in the form of sunlight, is converted by photosynthesis into plant biomass and is passed along food chains as it is consumed and eventually leaves the system as heat. The behavior of energy in ecosystems (most importantly, the amount and availability) is determined by two laws of thermodynamics—these govern the flow and storage of energy in a system and the ability to do work.

### *The First and Second Laws of Thermodynamics*

Energy exists in two forms: **potential energy** and **kinetic energy**. The **First Law of Thermodynamics** relates to the **conservation** of energy, and states that energy cannot be created or destroyed, but it can be changed (transformed) from one form to another. For example, when wood burns, stored chemical energy is transformed into heat and light. In photosynthesis, the energy of sunlight is harnessed by the chlorophyll within the plant leaf. No energy is gained or lost to the system in the process. The First Law is important in that it allows ecologists to determine energy transformation efficiencies (how much energy is passed along the food chain) and to determine where energy is lost from ecosystems. Energy is used to do work—in growth, movement, reproduction and in the assembly of complex molecules—all which require energy. Although the total amount of energy in a system does not change (the First Law tells us this) the amount of energy available to do the work does change. Energy available to do work declines along the food chain because of inefficient energy conversions—there is always less usable energy at the end of a transformation that at the beginning. Once energy is transformed into heat, it can no longer be used by living organisms to do work or to fuel the synthesis of biomass. The heat is eventually lost to the atmosphere and can never be recycled. Here the second law of thermodynamics comes into play.

The **Second Law of Thermodynamics** refers to the **transfer** of energy, and states that as energy is transformed, there is a loss of that energy (usually through heat loss) —and in natural systems a point is reached where there is no usable energy. The implication of this is that there has to be a constant input of energy for living things to do work. Energy is derived from the Sun, through photosynthesis, where **light energy** is transformed into **chemical energy**. This chemical energy is stored in plant biomass, eaten by herbivores, which in turn are eaten by carnivores. All living organism will eventually die. At each stage of transformation, less and less energy is available (usually only about 10% at each stage is passed on) and all energy is ultimately lost as heat.

### *Whole Ecosystem Studies in Africa*

During the 1960s and 1970s, an ambitious collaborative scientific initiative, known as the **International Biological Programme** (IBP) stimulated a rapid growth in studies of the structure and functioning of whole ecosystems following Odum's **Systems Ecology** approach. The thinking was that questions relating to the management and sustainable use of the world's biomes and ecosystems could be answered through knowledge of the paths, patterns and processes of **energy flows**, and nutrient and water **cycles,** through ecosystems. The common currency for such transfers of energy is **carbon**, with photosynthesis (**primary production**) as the basic measure of energy entering and being assimilated within communities and becoming available to sustain all ecosystem processes. The amount of energy assimilated (using the surrogate measure of carbon) and transferred as energy in the form of **adenosine triphosphate (ATP)** from one **trophic level** to the next, became a principal focus of the IBP. The quantification of the carbon cycle of ecosystems from tropical rain forests to the arctic tundra was a key output of the IBP. The importance of an understanding of the carbon cycle within ecosystems became increasingly relevant as emphasis on the role of $CO_2$ in **climate change** entered the global environmental policy arena. Carbon also plays a central role in the cycling of other elements such as nitrogen, phosphorus and sulphur, and thus in the growth, survival and reproduction of all organisms in terrestrial ecosystems.

In Africa, two research projects followed the IPB model, the **Lamto Project** in central Ivory Coast and the **Savanna Ecosystem Project** conducted on Nylsvley Nature Reserve in northern South Africa. Both projects have high relevance to the understanding of Angolan mesic savannas. The Lamto Project is located in the transition from Guinean Rain Forest to the Guinean Forest/Savanna Mosaic, similar to much of the tallgrass savannas of northern Angola. Nylsvley is located at the floristically depauperate southern extension of mesic/dystrophic savannas, with a structure and function very similar to that of the dry miombo of Angola. The dominance of trees such as *Burkea africana*, *Ochna pulchra* and *Terminalia sericea* reflect this similarity, as do the leached, infertile and sandy soils of the Nylsvley ecosystem.

The results of the 16-year Savanna Ecosystem Project (1974–1990) were synthesised by Scholes and Walker (1993) and provide a detailed account of the structure and functioning of the *Burkea* savanna. The results of the 30-year Lamto Project have been comprehensively synthesised by Abbadie et al. (2005). The Lamto and Nylsvley syntheses, together with that of Frost (1996) on the miombo of Zambia and Zimbabwe, remain the most important reviews of the subject and form the basis of the present outline. Here we will examine components and interactions in the creation, transfer and cycling of energy and nutrients in mesic/dystrophic savannas as quantified at Nylsvley, also referencing data from miombo sites in Angola, the Democratic Republic of the Congo, Ivory Coast, Zambia and Zimbabwe.

This chapter will commence with an outline of food webs and trophic levels in nature, then follow the pathways of primary production, consumption and decomposition, and conclude with a discussion on concepts of tree-grass dynamics in African savannas.

## 10.1 Food Chains, Food Webs and Trophic Levels

Before considering the processes of ecosystem energetics and nutrient transfers, an understanding of the framework of ecosystem structures is necessary. The interspecific interactions within ecosystems described earlier—(Sect. 9.6 on herbivory, predation, parasitism, and mutualism)—evolved for the acquisition of energy and nutrients for growth and ultimately, reproduction. These relationships, between the various species in an ecosystem, form **food chains**, and the collective interactions (**links)** form **food webs**. Savanna ecosystems such as those that dominate Angolan landscapes have two food chains—a grazing food chain and a detrital food chain, as illustrated in Fig. 10.3.

The successive levels in a food web are called **trophic levels**. The feeding relationships are classified into **autotrophs** (primary producers—which receive their energy directly from the Sun via photosynthesis) and **heterotrophs** (consumers of plant and animal tissue). **Primary consumers** comprise **herbivores** which feed on plants, **secondary consumers** comprise **carnivores** that feed on herbivores, and **omnivores** that feed on both plants and animals. The relationships are popularly compared to a pyramid. Topping the trophic pyramid are **apex predators**, which feed on lower trophic levels but are not themselves eaten. In addition to the contributors to the pyramid, **decomposers** (detritivores) consume dead organic matter and convert it into energy and nutrients, which become available for plant growth and therefore to the cycling of materials through the ecosystem. The movement of mineral nutrients is cyclic, whereas the movement of energy is unidirectional and noncyclic.

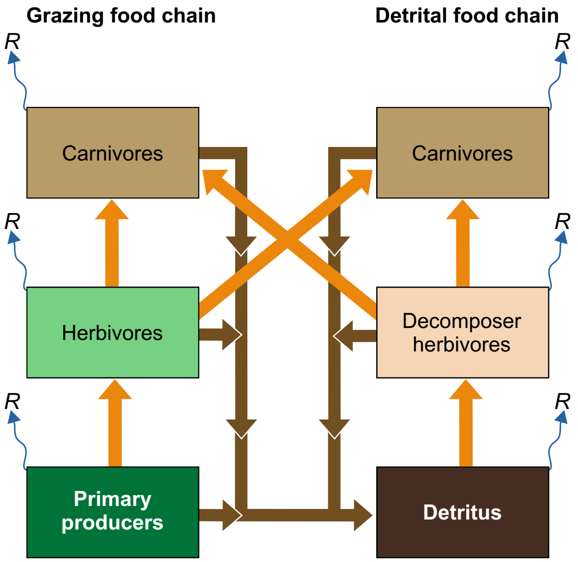

**Fig. 10.3** Generalised grazing and detrital food chains. Orange arrows linking trophic levels represent the flow of energy associated with ingestion. The blue arrows represent the loss of energy through respiration (*R*). The brown arrows represent a combination of dead organic matter unconsumed biomass) and waste products (faeces and urine). From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

Once the structure and quantification of food chains has been achieved, an immediate observation will be the rapid loss of energy transferred from one trophic level to the next. In grazing food chains, this is approximately one order of magnitude per step. In crude terms, in a food chain of four levels, for every 1000 kg of grass produced by primary production and consumed by antelope, only about 100 kg of animal tissue is produced, sufficient to support 10 kg first-level predators, and 1 kg of second-level (apex) predators. This explains why there are so few predators compared with herbivores, and why food chains seldom have more than three or four levels.

An important concept relating to food chains and food webs is that of bottom-up and top-down controls. **Bottom-up controls** are those that limit the productivity and abundance of populations in the trophic level above them. Thus grass productivity places limits on the biomass of herbivores that they support, which in turn controls the numbers of predators that feed on them. Conversely, predators can control herbivore population size, which in turn can control grass and tree biomass by defoliation. These are **top-down controls**.

Against this framework of food chains, food webs and trophic levels, the successive steps in the functioning of savanna ecosystems can be summarised, starting with the basis of life on Earth—the capture and synthesis of solar energy, carbon dioxide and water into organic matter through photosynthesis.

## 10.2 The Photosynthetic Pathways of Angolan Plants

Plants have evolved three photosynthetic pathways (known by the abbreviated forms **$C_3$, $C_4$ and CAM**). The earliest pathway, $C_3$, evolved 2800 Ma in a $CO_2$-rich atmosphere, while the $C_4$ pathway evolved much later, about 30 Ma when atmospheric $CO_2$ had decreased to one eighth of the concentration during the Paleozoic. $C_4$ grasses dominated open landscapes by 8 Ma. Today, $C_4$ plants make up less than 3% of the world's flowering plant species, yet because of their high productivity, they account for about 25% of primary productivity on the planet, including such crop species as maize, sugarcane, sorghum and millet (Sage, 2004). Of the 7500 species of $C_4$ plants, 4500 are grasses. Within the grasslands of the world, $C_3$ grasses dominate in temperate climates and $C_4$ grasses are dominant in the open (non-forested) ecosystems of the tropics. Of the world's 16,000 species of CAM plants, most are succulents, adapted to hot, arid climates.

*$C_3$ Photosynthesis*

Globally, the most common photosynthetic pathway is $C_3$, used by more than 95% of plant species (trees, shrubs and herbs), and particularly those grasses that occur in regions of moderate sunlight intensities and temperatures, humid soils and an absence of fires. The term $C_3$ refers to the fact that the first carbon compound produced during $C_3$ photosynthesis contains three carbon atoms. The $C_3$ photosynthetic pathway is less efficient than $C_4$ in terms of water use and growth, especially in warmer climates and at lower concentrations of atmospheric $CO_2$. $C_3$ grasses are rare in Angola. Unlike $C_4$ grasses, $C_3$ grasses are tolerant of shading and the few Angolan $C_3$ grass species such as *Olyra latifolia* are found in the shady environment of forests.

*$C_4$ Photosynthesis*

A defining characteristic of tropical savannas is the prominence of fire-tolerant but shade-intolerant $C_4$ grasses as the dominant ground stratum (Huntley, 1982). Over 95% of Angolan grasses are $C_4$ species. It is therefore useful to understand what is special about the $C_4$ photosynthetic pathway as it relates to the success of $C_4$ grasses in savanna ecosystems.

Over evolutionary time, many plant lineages have evolved specialised anatomical and biochemical mechanisms that have given competitive advantages to plants growing in the tropics, in regions with high temperature and light, with soil moisture limitations, and especially in fire-prone environments such as the savannas (Sage, 2004). The $C_4$ pathway first evolved in grasses in the Oligocene (about 34–24 Ma) during periods of global cooling, aridification and declining atmospheric $CO_2$. It is important to note that during the Triassic, Jurassic and Cretaceous periods, atmospheric concentrations of carbon dioxide were four to eight times greater than during the Oligocene and Miocene and through to the present time. During the late Miocene (8–5 Ma), there was a massive increase in the dominance of $C_4$ over $C_3$ grasses according to records determined by the carbon isotope ratios of fossil soils. This was the age of speciation of $C_4$ grasses, the expansion of savannas and, especially in

Africa, the diversification of antelope and other mammal herbivores. The dicotyledons (trees and forbs) evolved the $C_4$ path later than the grasses, about five million years ago. The $C_4$ path evolved independently over 45 times, in 19 families of angiosperms, providing a remarkable demonstration of convergent evolution.

At the biochemical level, $C_4$ plants operate the full $C_3$ process, but add on an additional layer of metabolism, in effect supplementing rather than replacing the $C_3$ pathway. The unique leaf anatomy and biochemistry of $C_4$ plants enables them to concentrate carbon dioxide around the carboxylating enzyme **rubisco**, producing a 4-carbon compound. Further, by suppressing photorespiration, the plant's photosynthetic and water use efficiency is improved. **Photorespiration** is the metabolic process where rubisco takes up oxygen during the day and releases some carbon dioxide, wasting some of the energy produced by photosynthesis. As a result, in high light and temperature environments, by supressing photorespiration, $C_4$ plants tend to be more competitive and productive than $C_3$ plants while using less water (Edwards et al., 2010).

*CAM Photosynthesis*

CAM is the acronym for **Crassulacean Acid Metabolism**, a photosynthetic pathway first discovered in species of the succulent family Crassulaceae. Evolved for life in arid environments, CAM plants have a very interesting adaptation to increase water use efficiency involving closing the leaf stomata during the day, and opening them at night. This behaviour reduces moisture loss by evapotranspiration via the stomata on hot sunny days. $CO_2$ is collected by opening the stomata at night, when the air is cooler and more humid. The $CO_2$ is stored overnight as malic acid in vacuoles of the leaf mesophyll cells, and during the day, the malic acid is transferred to the chloroplasts, converted back to $CO_2$, and used in photosynthesis. In Angola, typical CAM plants include *Euphorbia conspicua* and *Aloe littoralis*, both common along the coast.

## 10.3 Primary Production in Mesic Savannas

The study of ecosystem energetics has introduced many key terms to the science. As we have seen, photosynthesis is the process of converting carbon dioxide and water into organic compounds using the energy of solar radiation. The result is referred to as **primary production (PP)** and the **rate** is **gross primary productivity (GPP)**. Some energy is lost through **respiration (R)** before storage. The rate of storage of energy after respiration is **net primary productivity (NPP)**. The amount of accumulated organic matter at a given time is called the **standing crop biomass**.

*Solar Radiation and Precipitation*

Solar radiation drives all life on earth, but only a tiny fraction of incoming radiation is assimilated by terrestrial ecosystems (Sect. 5.1). The solar radiation reaching the upper atmosphere over the tropics is reduced by 40% due to reflection and absorption by clouds. A further 13% is reflected by the canopy of vegetation and soil, while most of the remaining 47% is used up in evaporating the moisture, or warming the surface of the soil and vegetation. Less than 1% of the incoming solar radiation is used in photosynthesis, indicating that primary production is not limited by solar radiation. Water, not energy, is the key constraint on primary production and the carbon flows and nutrient cycles of savannas.

Climate, but specifically mean annual temperature (MAT) and mean annual precipitation (MAP), and soil nutrient status (especially nitrogen, phosphorus and sulphur) determine NPP of Angolan savannas. The relationship between mean annual precipitation and the peak of above ground herbaceous biomass is illustrated in Fig. 10.4. The actual rate of photosynthesis in savannas is controlled by evapotranspiration which is the combined value of plant transpiration and surface evaporation. On soils of similar fertility, the maximum canopy photosynthesis of African savannas has been shown to increase exponentially with mean annual precipitation (Merbold et al., 2009). Primary production also varies through the course of a year. In the tropics, the length of the growing season is determined by rainfall rather than by daylength or temperature. By way of contrast, in temperate regions, day length and temperature are key determinants of plant growth activity.

### *Quantification of Energy Pools and Fluxes*

An early objective of many ecosystem studies was to quantify the flow of energy (using carbon as a surrogate) through the system. In the systems ecology tradition, the quantification of interactions between organisms and the environment is usually presented as **'box and arrow'** models (Fig. 10.5) where boxes represent the **pools** of materials (carbon, nutrients, water) and arrows indicate the direction and quantity

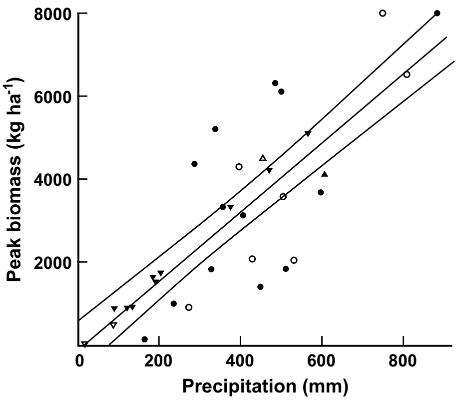

**Fig. 10.4** The relationship between mean annual rainfall and peak above-ground herb biomass, for sites in East and southern Africa. (Symbols indicate sample sites across the region). The significant linear regression predicts a biomass increase of approximately 800 kg ha$^{-1}$ for every 100 mm increase of precipitation. From Shorrocks (2007) *The Biology of African Savannahs*. Oxford University Press, Oxford

of transfers (**fluxes**) of energy and matter. Primary production is usually quantified as grams of dry matter (DM) produced by plants per square metre per year (g DM $m^{-2}$ $y^{-1}$). One gram of dry matter contains about 0.45 g carbon, or 20 kJ of energy. It should be noted that measures of net primary productivity are usually given as grams carbon per square metre per year (g C $m^{-2}$ $y^{-1}$), or in g dry weight (DW) per square metre per year (g DW $m^{-2}$ $y^{-1}$) while standing crop biomass is given in Mg $ha^{-1}$, equivalent to 100 g DW $m^{-2}$. Comparisons of data sets on primary productivity and biomass should take the large differences between measures of dry matter and carbon into account.

Very few studies of whole ecosystem energy flows have been undertaken in African savannas due to the cost and complexity of such research projects. One such attempt was that of the South African Savanna Ecosystem Project. Figure 10.5 presents the carbon budget for Nylsvley *Burkea africana* savanna woodland, representing mesic/dystrophic savanna at the southern limit of the biome's rainfall and productivity gradient. The total standing biomass for the *Burkea* savanna ranged from 10–35 Mg $ha^{-1}$, significantly less than that of mature miombo in Angola, which reaches 100 Mg $ha^{-1}$. For comparison, Rain Forest averages about 440 Mg $ha^{-1}$, while at the opposite extreme, the standing biomass of desert shrubland is about

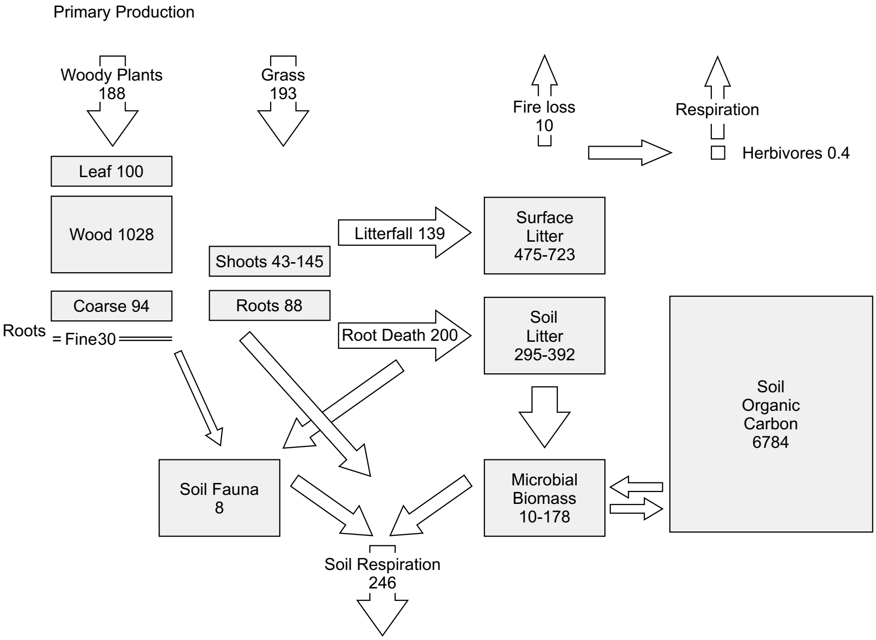

**Fig. 10.5** The mean annual carbon cycle in the *Burkea africana* broad-leafed savanna at Nylsvley in northern South Africa. The values in the pools (boxes) are in g C $m^{-2}$; the fluxes (arrows) are in g C $m^{-2}$ $y^{-1}$. The total ecosystem carbon stock of 9357 g C $m^{-2}$ includes two-thirds as soil organic carbon. From Scholes and Walker (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge

7 Mg ha$^{-1}$. The Nylsvley carbon budget and profile of annual primary production provides an illustration of the components of energy flowing through a woodland and its allocation to different plant parts.

### *Allocation of Primary Products*

In savannas, grasses have a higher relative Net Primary Production than trees. **Relative NPP** is the NPP relative to the standing biomass. This reflects the higher relative growth rate of grasses compared to trees. Tree saplings might allocate 50% of energy to leaves, but as they increase their biomass with age, this might drop to only 5% going to leaves, with the major share of energy going to support structures (stems and branches) and for maintenance (respiration). The allocation of fixed carbon to different plant parts (leaves, shoots, stems, roots) varies considerably in different ecosystems and also in terms of light conditions (full sun or shade). The **root to shoot ratio** (R:S) ranges from 0.2 in tropical rain forest to 1.2 for arid savannas to 4.5 in desert. Rain forests have most of their carbon stock located in their above ground organs, with relatively little below ground in their shallow roots systems. Savannas and especially grasslands have their carbon stores below ground. This gradient relates to declining rainfall, net primary production and standing biomass. As a general observation, as aridity increases, investment in underground storage organs also increases. However, some mesic savannas have ‘underground trees’ which have extensive lignotubers and branching structures below the soil surface (see Box 14.2). Angolan plant ecologist Amândio Gomes and colleagues found that *Parinari* grassland geoxyles on arenosols had a belowground biomass of 16 Mg ha$^{-1}$ while in *Brachystegia* grasslands on ferralsols the biomass averaged 44 Mg ha$^{-1}$ (Gomes et al., 2021). They found that the below-ground biomass of the geoxyle grasslands almost equalled that of the above-ground biomass of neighbouring miombo woodland.

### *Net Primary Production in the Nylsvley* Burkea *Savanna*

The net annual primary production for the Nylsvley study site was 950 g DW m$^{-2}$ y$^{-1}$, using about 0.3% of radiant energy received by the ecosystem, with NPP about equally contributed by trees and grasses. The contribution of different plant parts to the total annual primary production of dry matter in the *Burkea africana* savanna (in grams Dry Matter per square metre per year (g DM m$^{-2}$ y$^{-1}$) was estimated as follows (Scholes & Walker, 1993):

- *Woody plants*—total 468 (wood growth 89; current twigs 27; leaves 156; flowers and fruit 10); coarse roots 11; fine roots 175 g;
- *Herbaceous plants*—total 482 (leaf and culm 157; roots 325).

Grazeable grass production (that available to herbivores) at Nylsvley was 157 g DM m$^{-2}$ y$^{-1}$ of a total grass NPP of 482 g DM m$^{-2}$ y$^{-1}$.

Basal area of woody plants in the study population (4.2 m$^{-2}$ ha$^{-1}$) increased at 6% per year. A maximum basal area level of ca. 10 m$^{-2}$ ha$^{-1}$ of trees was measured on an adjoining site that had been protected from fire for 30 years. Here competition with other trees had stabilised the tree growth rate in the absence of fire and other disturbances. Increases in the basal area of mature trees in both Wet and Dry miombo approximates 3% per year, but with several-fold higher total NPP and standing crop biomass than the Nylsvley *Burkea* broadleaf savanna, as discussed below.

Frost (1996) indicates that annual leaf and twig growth in miombo amounts to about 5% of total woody biomass, with young trees adding proportionately more per unit biomass than older trees. Much of this growth is lost annually through litter fall.

## 10.4 Standing Crop Biomass and Canopy Cover in Mesic Savannas

The above-ground biomass of mature stands of miombo woodland increases following a precipitation gradient from about 20–30 Mg $ha^{-1}$ at Nylsvley to 55 Mg $ha^{-1}$ in Dry Miombo to over 100 Mg $ha^{-1}$ in Wet Miombo. Total biomass of old-growth miombo in Zambia was calculated as 106 Mg $ha^{-1}$, of which 63% was aboveground and 37% belowground (Chidumayo, 1995; Chidumayo & Frost, 1996). The ratio of aboveground to belowground biomass tends to decrease with decreasing rainfall, due possibly by the need for more extensive water-harvesting root systems in drier sites such as Nylsvley (Frost, 1996).

The total woody plant canopy cover at Nylsvley was 32%, biomass was 16.2 Mg $ha^{-1}$, with a tree basal area of 4.2 $m^{-2}$ $ha^{-1}$. Grass canopy cover was 33% and basal cover 5.5% with 1.6 Mg $ha^{-1}$ above ground biomass. The dominance of three tree species (*Burkea africana, Ochna pulchra, Terminalia sericea*) is illustrated by their contributing, collectively, 78% to woody plant biomass, to leaf area index and to primary production.

In the miombo of Shaba, DRC, Malaisse et al. (1975) recorded basal area of trees as 13.5 $m^{-2}$ $ha^{-1}$, increasing by 2.9% per year. Herbaceous standing crop biomass of grasses and forbs ranges from 1.5 Mg $ha^{-1}$ in Dry Miombo to 3.3 Mg $ha^{-1}$ in Wet Miombo. Grass biomass contributes only 2–5% of total aboveground biomass in woodlands. The biomass of grasses on the moist valley grasslands (locally called *mulolas*, *chanas* or *dambos*) is much higher, in the absence of trees and shrubs.

## 10.5 Herbivory and Primary Consumption in African Savannas

The next step in the energy budget of savannas will now be considered—the transfer of energy from the primary producer component to the primary consumption component. Measures of biomass (usually live weight) is often used as a surrogate for energy in studies of large mammals. An example of the pathways and partitioning of plant material into the herbivore component at Nylsvley, northern South Africa, is given in Fig. 10.6. Scholes and Walker (1993) synthesised field data from several studies in the Nylsley *Burkea* ~~savanna~~ woodland, which illustrates that most above ground primary production is consumed by decomposers and fire in this mesic/dystrophic system. Herbivores such as Impala use only a small fraction of the primary production component. Most of the material ingested (I) passes out as excretion (E) or respiration (R). Very little goes to production (P). Grasshoppers, although more efficient at assimilating energy than impala, are wasteful feeders, with much of the material removed from plants falling to the ground during feeding.

*Relationship Between Mean Annual Precipitation and Herbivore Biomass*

Coe et al. (1976) presented a close correlation between mean annual rainfall, predicted primary production, and mammalian herbivore biomass (as a surrogate

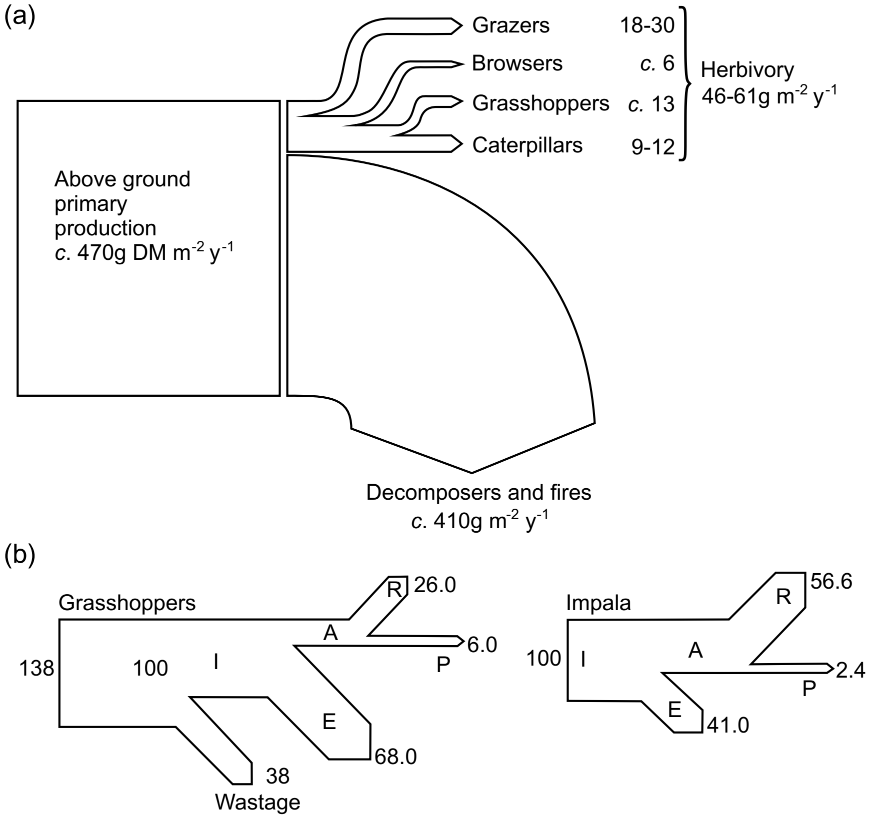

**Fig. 10.6** Primary consumption at Nylsvley, a mesic savanna in northern South Africa. **a** Pathways showing the fate of primary production, with the major portion going to decomposition and fires. **b** Partitioning of energy consumption by two herbivores into intake (I), excretion (E), production (P) and respiration (R). The fraction not excreted is assimilated (A), by the digestive system. The ratio of intake to assimilation indicates that grasshoppers (4%) have a higher assimilation efficiency than impala (2.4%). From Scholes and Walker (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge

for primary consumption) in African savannas. However, this relationship differs between the savannas of high and low nutrient soils (Bell, 1982). The mammal biomass of Africa's arid/eutrophic savannas increases with increasing mean rainfall. In the heavily leached moist/dystrophic miombo ecosystems, at some sites, the higher the rainfall, the lower the mammal biomass (Frost, 1996). The relationship between herbivore biomass (for herbivore species with an adult live mass of more than 15 kg) and mean annual precipitation, in three soil nutrient availability groups has been presented by Fritz and Duncan (1994) for African savannas. They found that for a given rainfall the herbivore biomass on high nutrient soil is significantly greater (2–3 times) than savannas on low nutrient soil (Fig. 10.7). They also found that mammal species richness had a significant but very small effect on the biomass-rainfall relationship, indicating that carrying capacity is limited at the community rather than the species level in African savannas.

Mammals in particular are scarce in miombo, with low biomass and low densities. Several antelope species are endemic to, or have their primary range, in miombo. These include Sable Antelope, Roan Antelope and Lichtenstein's Hartebeest. These are large-bodied, coarse-grass grazers, which are very selective in seeking out herbage at its optimal nutrition stage, or by moving through their home range which includes some diversity of forage through the seasons. Selective feeding in nutrient-poor habitats requires relatively large home ranges, and miombo ungulates occur at low densities, when compared with the large herds of Wildebeest, Zebra, Gemsbok and Springbok in arid savannas. The net result is that the mammal biomass that can be carried by miombo ecosystems, even at high plant biomass, is much less compared to that carried by rich arid/eutrophic savannas such as the acacia savannas and short grasslands of volcanic soils of East Africa.

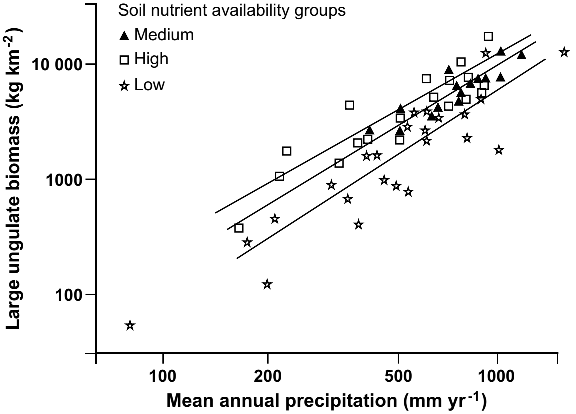

**Fig. 10.7** Relationship between mean annual precipitation and large herbivore biomass. Regression lines for soil groups: Top—high nutrients (squares); Middle—medium nutrients (triangles); Bottom—low nutrients (stars). Note that herbivore biomass is 2–3 times higher on high nutrient than on low nutrient soils at the same precipitation level. From Owen-Smith and Danckwertz (1997) In Cowling et al. *Vegetation of Southern Africa.* Cambridge University Press, Cambridge

While the arid/eutrophic savanna grasslands of Serengeti have 50–80% of their annual grass primary production removed by herbivores (McNaughton, 1979), the use in mesic/dystrophic savannas such as miombo probably lies between 5% (Shaba, DRC: Malaisse et al., 1975) and 10% (Nylsvley: Scholes & Walker, 1993). This is a consequence of the low nutrient value and rank nature of miombo grasses, the rapid loss of nutrient status at the onset of the dry season, and the poor browse quality of trees and shrubs. All this relates to the poor nutrient status of miombo soils.

### *Nutritional Quantity and Quality*

The nutritional quality of grasses, measured in terms of nitrogen content (essentially a surrogate for protein content), at ca. 2% N at the early growing season, drops to ca. 0.8% as the young leaves expand, decreasing further to 0.5% during early dry season. Given that the N level required to maintain ungulates on natural range in Africa is 0.8%, it can be recognised that the nutrition value of miombo grasses and woody plants is very poor, accounting for the very low herbivore biomass carried by miombo woodlands. This low herbivore biomass results in less than 2% of available browse in miombo being consumed, as reported from a study in Zimbabwe, and 4% consumed in the *Burkea-Ochna* savanna of northern South Africa (Scholes & Walker, 1993). Even bulk-consumers such as elephant are very selective in their feeding habits in miombo. In Malawi, only 13 out of 35 woody species eaten by elephant were rated as their preferred food.

As a general rule, mammal herbivore productivity in arid/eutrophic savannas is limited by food quantity, which is in turn limited by rainfall, which limits primary productivity. In mesic/dystrophic savannas, primary consumption is limited by food quality, which is limited by soil nutrients. Furthermore, Owen-Smith (1982) recorded that browsers face an **energy** (**quantity**) shortage during the dry season (when many deciduous trees have lost their leaves) while grazers face a **protein** (**quality**) shortage at that time. As a consequence, in miombo, nutrient cycling does not pass through large herbivores, but through two other consumer pathways—fire, as discussed earlier, and termites, as discussed below. In Angola, domestic livestock is most productive in the arid southwest, and almost absent in the north, due not to the quantity of grass, but due to its quality.

### *Herbivory by Invertebrates*

While termites have very visible roles in the miombo decomposer component (Sect. 10.6), the impact of other invertebrates, both as consumers and pollinators, needs mention. In Zimbabwean miombo, invertebrates consumed up to 30 kg $ha^{-1}$, double the value eaten by mammals (Martin, 1974). In the moist miombo of Shaba, Zaire, lepidopteran larvae were found to feed on 80% out of 159 plant species studied. Selection of plants by moth larvae was very focused for most species. Of 153 lepidopteran species recorded as feeding on miombo trees, 75% fed on only one or two plant species. An exception was noted in the ubiquitous miombo dominants—*Brachystegia spiciformis* and *Julbernardia paniculata*—which hosted 16 and 30 lepidopteran species respectively (Malaisse, 1983). Defoliation of trees by invertebrates occurs during the wet season, and is normally not very conspicuous. However, in some years outbreaks of moth and beetle populations can defoliate broad areas of *B. spiciformis* and *J. paniculata,* their faeces (frass) providing a shower of nutrients to the litter layer and triggering microbial decomposition. At Nylsvley, periodic outbreaks of defoliating caterpillars (*Cirina forda* and *Sphingimorpha chlorea)* removed up to 33% of leaf production of the dominant tree *Burkea africana.*

*Assimilation, Production and Consumption Efficiency*

Primary consumers (herbivores) vary in efficiency of food use after ingestion. **Assimilation efficiency** is the ratio of assimilation to ingestion. Of the energy assimilated, some goes to respiration and some to production (building new tissue and reproduction). **Production efficiency** is the ratio of consumption to assimilation. Endotherms (mammals, birds) have higher assimilation efficiencies than ectotherms (insects, reptiles), and predators are more efficient than herbivores. Production efficiency is lower in vertebrate endotherms than ectotherms, because endotherms have to expend energy to maintain a constant body temperature. They typically convert only 2–4% of assimilated energy into production. African ungulates are near the bottom of the production efficiency scale, at about 2% (Fig. 10.6b). Most invertebrate ectotherms have low assimilation efficiencies but high production efficiencies, on average around 40%. Measurements for mesic savanna at Lamto, Ivory Coast, found grasshoppers had a production efficiency of 42% (Gillon, 1973). The ratio of ingestion to production at the next-lower trophic level is termed **consumption efficiency**. These ratios are derived from measures of the energy transfers from one trophic level to the next along the food chain, from primary producers (plants) to primary consumers (herbivores) to predators and to detritivores and decomposers.

## 10.6 Decomposition and Nutrient Cycling

Scholes and Walker (1993) in discussing nutrient cycling in the Nysvley savanna, make the important observation: "Building nutrients into organic molecules is one half of the cycle of life; disassembling the molecules is the equally important other half."

A generalised model of nutrient cycling in woodland ecosystems is presented in Fig. 10.8. Solar radiation drives primary production, synthesizing carbon, water and nutrients into living organic matter. The balance of production after respiration and other metabolic losses is net primary production, represented by the trees, shrubs and grasses of the savanna community. Some nutrients in the vegetation are retranslocated within the canopy. Even before leaves fall to the ground, nutrients are withdrawn from them. The carbon to nitrogen ratio of leaves prior to leaf fall is 50:1, dropping to 20:1 before they enter the litter layer of the woodland floor. Dead leaves, twigs, branches and trunks contribute to the build-up of dead organic matter through litterfall. Decomposer organisms break down and mineralise the organic matter, releasing nutrients which together with atmospheric and soil mineral sources, are incorporated into new plant growth.

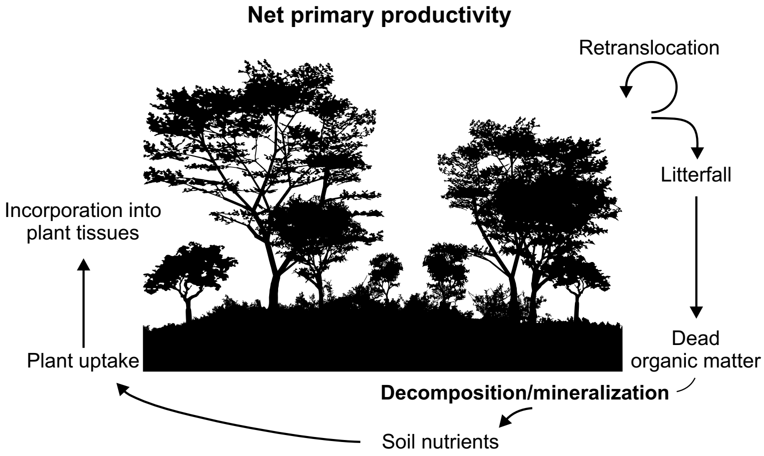

**Fig. 10.8** A generalised model of nutrient cycling in a terrestrial ecosystem. Plants take up water and nutrients from the soil, these are used in the process of photosynthesis within tree and grass leaves, some nutrients are retranslocated prior to litterfall, whereafter the accumulated litter is decomposed and mineralised, releasing nutrients for uptake by plant roots. At the ecosysystem level, inputs are also received from the atmosphere (oxygen, nitrogen) and from the weathering of rocks and minerals. Outputs from the ecosystem include nutrients released from the decomposition and mineralization of dead organic matter and from soil nutrients leached from the system. Redrawn after Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

### *Nutrient Cycling in Mesic/Dystrophic versus Arid/Eutrophic Savannas*

The nutrient cycling processes of mesic/dystrophic and arid/eutrophic savannas differ in fundamental ways. In mesic savannas, it is the rate at which organic compounds can be **disassembled** (releasing nutrients by decomposers) which limits primary production, not the rate at which they can be **assembled** (forming carbon compounds through photosynthesis). These contrasts are summarised in Fig. 10.9, developed as a general model of nutrient cycling (Chapin, 1980). The model can be adapted to summarise the different processes, transfers and feedbacks of nutrient-rich and nutrient-poor ecosystems, such as the mesic/dystrophic and arid/eutrophic savannas of Angola. In short, low nutrient soils result in low rates of net photosynthesis, producing plant tissue of low nutrient content. The litter falling from plants with low nutrient levels result in slow rates of mineralization, and higher rates of immobilisation by the decomposer organisms, thus releasing low amounts of nutrients into the soil for plant uptake. As Smith and Smith (2015) state: “Low nutrient availability begets low nutrient availability (Fig. 10.10).”

### *Decomposition, Mineralisation and Carbon: Nitrogen Ratios*

Organic compounds produced by photosynthesis and held in plant tissues are ultimately consumed by herbivores or become litter, and are gradually transformed into minerals in the process of **decomposition**. The product of the decomposition process is called humus, the main component of **soil organic matter**, which in turn is an

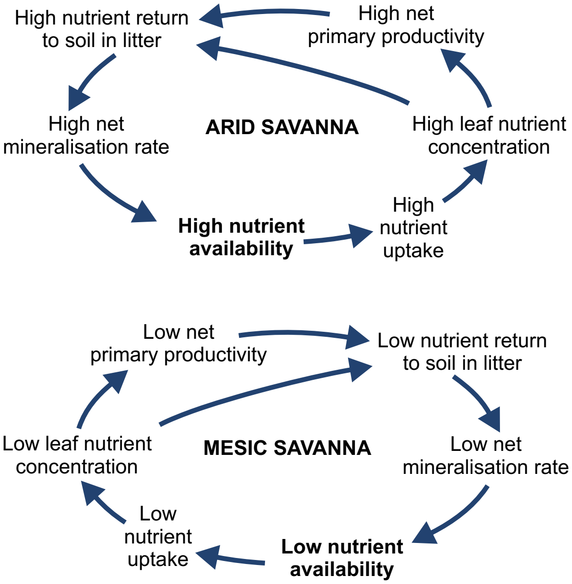

**Fig. 10.9** Feedbacks that occur between nutrient availability, net primary productivity, and nutrient release in decomposition for initial conditions of low and high nutrient availability. Adapted from Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

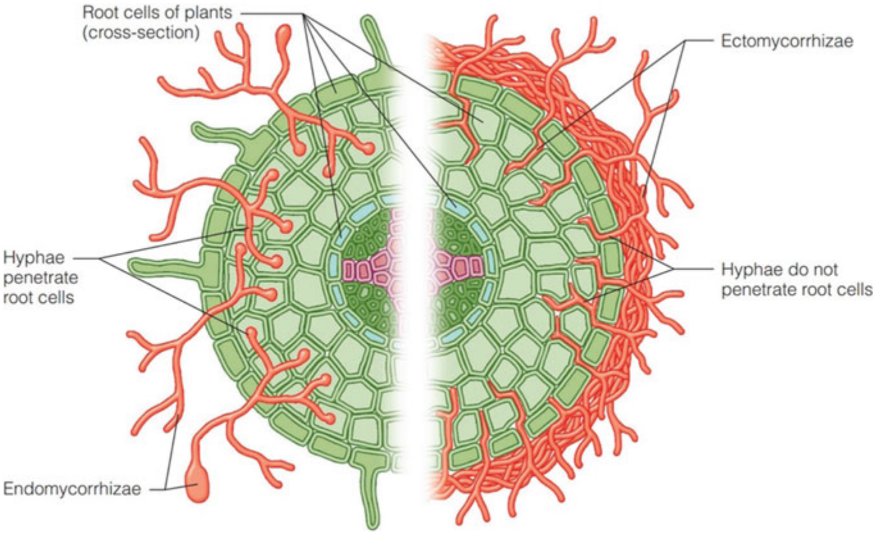

**Fig. 10.10** Mycorrhizal structures. Left: Endomycorrhizae grow within tree roots, and fungal hyphae enter the cells. Right: Ectomycorrhizae form a mantle of fungi about the tips of rootlets; their hyphae invade the tissues of rootlets between the cells. From Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

important constituent of the rooting zone (**rhizosphere**) where most root growth, and water and nutrient uptake, occurs. The chemical bonds holding together organic compounds such as the carbohydrates of leaves and twigs must be broken to release essential macronutrients such as nitrogen, phosphorus and sulphur into their inorganic form, for uptake once again by plants. The process is called **nutrient mineralisation**. Some of the released nutrients are taken up again by decomposer organisms, resulting in **nutrient immobilisation**. A wide range of organisms (decomposers) are involved in the fragmentation, digestion and excretion processes of mineralisation, including termites, woodlice, dung beetles, earthworms, nematodes, bacteria and fungi.

The rate of breaking down organic matter varies according to chemical composition and nutrient content. Glucose and other simple sugars are easily broken down, but cellulose and lignins are more difficult. An important consequence of the decomposition process is the change in the **carbon to nitrogen (C:N) ratio** in soils as decomposition proceeds. As decomposer organisms use up the high energy carbon of litter, there is an increase in the proportion of nitrogen. This nitrogen is incorporated into complex lignin-based compounds and is thus not available to plants. Gradually the quality of the litter is degraded into a form where decomposition proceeds very slowly. As in most biological processes, temperature and moisture influence the rate of microorganism activity and therefore of decomposition. Warm, moist conditions favour microorganism activity; cool, dry conditions do not.

### *The Role of Fire in Mesic Savanna Nutrient Cycling*

It must be remembered that in savannas not all mineralisation occurs through the activity of decomposer organisms. Decomposition includes the microbial oxidation of litter—microbial digestion in the gut of herbivores by microbes (Box 8.1) —or combustion by fire. Fire is a significant contributor to the nutrient cycle of mesic savannas where very little of the products of photosynthesis are consumed by herbivores. At Nylsvley only about 50 g C $m^{-2}$ $y^{-1}$ out of 950 g C $m^{-2}$ $y^{-1}$ primary production is consumed by above-ground herbivores. By far the major portion is transferred directly from the primary producer component to the decomposer component. About 5% is consumed by herbivores, 15% is oxidised by fires, and 80% is broken down by decomposer organisms. Mineralisation rates are fastest by fire, intermediate by passing through a ruminant gut, and slowest by microbial decomposition in the leaf litter layer or soil. Releases of nutrients from decomposing organic material, and the nutrient cycle as a whole, are driven by rainfall and fire and therefore occur as pulsed events, not as smooth and continuous processes.

### *Decomposition Rates*

Litter decay is as much as 90% in the first year in Wet Miombo, where termites account for 40% of litter decay. Decay rates are much slower (40% in the first year) in Dry Miombo, where termites are less active. Litter decomposition in the mesic savanna of Nylsvley is even slower, with a mean turnover time of five years. Termites and ants process less than 5% of this—the major role in decomposition is that of microorganisms. The seasonality of decomposition in mesic savannas is complemented between microorganisms that are active in the warm moist summer and the incidence of fires in the cooler, dry winters.

### *Mycorrhizal Mutualisms in the Nutrient Cycle*

Perhaps the most common, but least recognised, mutualistic interactions in nature are those between mycorrhizas, rhizobia and the roots of vascular plants. Without the nutrient capture and nitrogen-fixing roles of these soil microorganisms, plant life as we know it could not exist. The relationship is so profound that some authors have commented that most higher plants do not have roots: they have mycorrhizae.

**Mycorrhizae** are mutualisms comprising networks of fungal hyphae that capture nutrients (including phosphorus and nitrogen) from the litter layer and transport these to the roots of plants in exchange for carbon. Three types of mycorrhizae are recognised:

- **Vesicular–arbuscular endomycorrhizae** (VAM: nitrogen-fixing) that are found in over two-thirds of plant species.
- **Ectomycorrhizae** (ECM: non-N-fixing) that are particularly common in nutrient-poor miombo woodlands and are found in 10% of plant species.
- **Ericoid mycorrhizae** found in nutrient-poor heathlands.

The structural distinctions between endo- and ectomycorrhizas are illustrated in The hyphal sheaths surrounding the roots of ectomycorrhizal hosts do not penetrate root cells, while the hyphae of endomycorrhizae penetrate root cells

Endomycorrhizae have tiny, below-ground fruiting bodies. Ectomycorrhizae produce large above-ground fruiting bodies (such as mushrooms, Fig. 10.11), which release vast numbers of wind-borne spores. The mutualistic association of termites and fungi in the decomposition of plant material is especially well illustrated by the association of mycelial gardens of the litter-feeding termite *Macrotermes falciger* and the mushroom *Termitomyces reticulatus* (Fig. 10.12). The association is described in Box 14.2.

A unique feature of miombo woodlands among tropical woodlands and forests is the number of tree species having ectomycorrhizal rather than endomycorrhizal associations. In miombo, the canopy dominants—*Brachystegia, Julbernardia, Isoberlinia, Marquesia, Monotes*—all have non-N-fixing ectomycorrhizas. Endomycorrhiza are associated with *Albizia, Erythrophleum, Pericopsis* and *Pterocarpus,* which also have root nodules of N-fixing rhizobia. Globally, leaves of trees with nitrogen-fixing root nodules (rhizobia) normally have 40% higher N content than non-N-fixing species.

In Angola, ectomycorrhizae might be particularly important in mobilising nutrients (particularly phosphorus) in the inherently nutrient-poor soils of the miombo. Frost (1996) suggested that the success of *Brachystegia* and other detarioid legume species on the infertile soils of the miombo is due to their having extensive ectomycorrhizas. This suggestion is supported by recent studies by Gomes et al. (2021) of the plant functional traits of trees and geoxyles of the very acid (pH 3.3) and very low plant-available phosphorus soils of the Angolan Wet Miombo ecoregion. The study concluded that key traits such as specific leaf area, and leaf phosphorus content,

**Fig. 10.11** *Termitomyces titanicus*, the world's largest edible mushroom, symbiotic with *Macrotermes* termites. Mushrooms are a significant food source for rural communities in miombo. *Photo* Pedro Vaz Pinto

were highest in detarioid Fabaceae when compared with other legume lineages. The ectomycorrhizal associations of the dominant Detarioideae trees (e.g. *Brachystegia, Julbernardia*) were found to produce higher nutrient levels than the endomycorrhizae of non-Detarioid and non-Fabaceae trees of miombo landscapes (Gomes et al., 2021).

### *Rhizobia*

While nitrogen is the most abundant constituent of the atmosphere, contributing 79% of atmospheric gases, it is not directly available to plants. Atmospheric nitrogen is broken into a soluble form by lightning, and carried to earth by rain. Nitrogen from the gaseous form is also made available to plants by nitrogen-fixing bacteria of the genus *Rhizobium*. Here it is relevant to emphasise the importance of nitrogen to all living things. Nitrogen is a major part of amino acids, the building blocks of proteins and of nucleic acids such as DNA, which transfers genetic information to subsequent generations. It is a major component of chlorophyll, the substrate for photosynthesis. It is also the key component of adenosine triphosphate (ATP)—the energy-carrying molecule found in the cells of all living organisms.

While the main source of nitrogen is via atmospheric precipitation, the role of nitrogen-fixing bacteria is critical in the nitrogen cycle. In rhizobial mutualisms, soil-living bacteria come into contact with the root hairs of host plants, enter the root

**Fig. 10.12** *Termitomyces reticulatus*, cultivated by the termite *Macrotermes falciger* in miombo woodland, DRC. *Photo* Andre De Kesel

hair via an infection thread which stimulates the root cells to divide and to form a nodule. The bacteria have the ability to absorb atmospheric nitrogen and convert it to plant-available nitrogen in the form of ammonia. Rhizobia are mostly associated with members of the legume family Fabaceae.

## 10.7 Savanna/Forest Dynamics: Fire as the Driver of Alternative Stable States

### *The Process of Plant Succession*

In most of the ecological literature of the twentieth century, especially that of colonial botanists working in Africa, the savanna landscapes of the tropics were considered the result of human influences. The perception was based on prevailing concepts on the processes of vegetation change, where developing communities passed through a series of stages (or **seres**). It was suggested that tropical savannas were **seral** communities, retarded in their development towards a climax forest by human activities, including fire and deforestation. In the early twentieth century, British and American ecologists (Clements, 1916, 1936; Tansley, 1935) had developed the concept of **plant succession**—whereby plants of **pioneer** species colonise open sites (coastal sand dunes, landslides, volcanic lava flows) and gradually build soils and initiate a **primary succession** of simple plant communities.

The process of plant succession results in floristic and structural changes to the community, as richer organic soils, and more moderate microclimates, develop. These **seral stages** support shrubland, then woodland, then forest systems, each forming part of a slowly changing continuum. The **climax community** (forest) was considered the ultimate reflection of vegetation potential within a particular climatic zone. In Clements's view, for each climate, there was a single, stable vegetation state—the climax. Clements likened communities to organisms, each species being part of an integrated, interacting whole. His **organismic community** concept was challenged by another American ecologist, H.A. Gleason. Gleason (1939) considered each species in a community to have independent responses to the environment. The mix of species across a landscape represent a **continuum** of **individualistic** responses, not interdependent clusters. Today, ecologists increasingly view communities as manifesting characteristics of both concepts. Emphasis is now placed on how the adaptations and life history traits of individual species determine species interactions and distribution patterns under changing environmental conditions (Smith & Smith, 2015).

In particular, ecologists working in southern African and Brazilian savannas have challenged the traditional successionist view, demonstrating that very different vegetation states, such as forests and savannas, can share the same landscapes and the same climate. The convergence of ecological characteristics of the cerrados of Brazil and of the mesic savannas of Africa described by Huntley (1982) is well illustrated by their dynamics relative to fire in the maintenance of **alternative stable states**. Indeed, tropical savannas and forests have evolved in parallel over many millions of years, characterised by distinctive physiognomic and floristic structures, endemism and responses to fire. Savannas, such as miombo and cerrado, are not, in the language of twentieth century ecologists, '**early successional**', '**secondary successional'** or '**fire sub-climaxes'**, but are alternative stable states living in a dynamic relationship with adjacent closed forests under the same climate. As has been repeated in previous chapters, savannas are ancient ecosystems—not human-induced artefacts.

### *Equilibrium, Resilience and Feedbacks*

To understand the theory of alternative stable states, it is necessary to introduce the concept of ecosystem equilibrium. Natural ecosystems are considered to be in a state of **equilibrium** when the system may be subject to slight fluctuations of energy and matter but where there are no sudden changes in the system's structure and function. Observed fluctuations tend to occur within defined limits. They are considered to be in a steady-state equilibrium where there are no (or very slow) changes in the long term, even though there are oscillations in the short term (e.g. due to rainfall variability). Systems in a steady state equilibrium usually return to the steady state following a **perturbation** (a disturbance such as a fire or drought). The ability to return to equilibrium after a perturbation is referred to as an ecosystem's **resilience**. The maintenance of a steady state equilibrium is through the mechanisms of feedback loops. There are two types of feedback—negative feedbacks and positive feedbacks. A **negative feedback counteracts** the change in input or impact, tending to **maintain** the system in its current state. A **positive feedback amplifies** the change in input or impact, pushing the system toward a more pronounced change and sometimes leading to another state.

### *Instability and Tipping Points*

Change at geological or evolutionary time scales allows plants and animals to adapt to new conditions, whereas rapid change (such as current global warming) may be too rapid for species to adapt, resulting in declining habitat conditions and ultimately, species extinctions. If a system is altered, with such change leading to additional or accelerated change, the system might move away from its original equilibrium past a **tipping point**. The system will have been pushed towards a new **stable state**. If this happens the system is said to have been subject to **positive feedback**. The feedback is *positive for change* and the system may be considered to be **unstable**. A negative feedback counters any change away from the equilibrium and contributes to system **stability**. Ecosystems that have not been transformed by human activities are normally in a stable equilibrium because of the multiple stabilizing **negative feedback** loops that drive the system back to the steady state equilibrium.

### *Alternative Stable States*

The theory of **alternative stable states** (ASS) suggests that each state is maintained at equilibrium by negative feedbacks. Much of the evidence for the ASS theory comes from tropical savannas. The crux of the ASS theory is that ecosystems can switch to an alternative state through what is termed a **regime shift**. A regime shift might occur when there is a major shock to the system, such as a fire storm penetrating a forest, opening the canopy and allowing fire-tolerant grasses to establish and result in a change from a closed canopy forest to an open canopy savanna. A regime change can also be more gradual, as through longterm fire exclusion in savanna, where forest species gradually establish in the savanna. As the canopy of woodland closes, a moist, cool, forest microclimate develops, where low biomass and low fuel-load of shade-tolerant but fire-intolerant grass and ground cover is established, supressing fire entry.

Hoffmann et al. (2012) present an elegant model of alternative stable states involving the complex interaction of fire, climate and species traits that maintain the structure of cerrado and closed forest in central Brazil. The model is highly relevant to miombo, despite Angola's mesic savanna having a totally different species composition to that of the mesic savannas of the Brazilian cerrado.

### *Thresholds: Fire-resistance and Fire-suppression*

Fire-tolerant (**pyrophilic**) savannas are maintained by fire as grasslands and woodlands, and have done so for millions of years. However, under an unchanging climate, but with the sustained absence of fire, the transition to a different state, such as a fire-intolerant, (**pyrophobic**) forest, is possible. Such regime change results in a mosaic of bi-stable states, such as the moist savanna/forest mosaics of Zaire, Uíge and Malange provinces in the Congo basin (Figs. 2.2 and 12.5). Disturbances such as hot fires along a forest margin, might change the vegetation structure by opening up the canopy and allowing shade-intolerant grasses to establish. But unless followed by successive fires, the forest margin will recover, returning to its former state.

Hoffmann et al. (2012) describe two critical ecological thresholds involved in the resistance to change or the transition of savanna to forest.

- Savanna trees cross the **fire-resistance threshold** once individual trees have accumulated sufficiently thick bark to avoid stem mortality due to fire and to attain sufficient height to escape top-kill by frequent fires. Adaptive traits in plants are critical. Savanna trees accumulate bark thickness faster than do forest trees. They also have other adaptations to fire such as epicormic buds and relatively larger investments in underground storage organs. The open canopy of mesic savannas maintains a light and flammable $C_4$ grass layer, sufficient to support low intensity fires that do not damage trees, but sufficiently hot to kill the seedlings of fire-intolerant forest species.
- Forest communities cross the **fire-suppression threshold** when they have developed enough canopy cover to suppress fire by excluding shade-intolerant, highly flammable savanna grasses. Forest tree species accumulate leaf area and canopy density more rapidly than savanna trees, thus shading out shade-intolerant savanna grasses, accelerating the transition to forest. The dense forest canopy creates a cooler, more humid microclimate that supports a light, poorly combustible ground cover, including forbs and $C_3$ grasses.

### *Regime Shifts and Feedback Mechanisms*

In the savanna/forest mosaic example, both states are stable until a particular ecological threshold (such as regular fires or total fire exclusion) is crossed. The passage across the thresholds (tipping points) result in substantial changes in the structure and function of the system. The shift from one regime to another might be sudden, such as when the feedbacks that usually maintain the system are overwhelmed by a firestorm, or gradual, such as the drying out of a wetland and its replacement by a thicket. Evidence for grasslands changing to forests as a consequence of fire exclusion come from many experiments in southern, central and west Africa (Fig. 7.6). Similarly, the conversion of forest into grassland from increased frequency of fires along the forest margin and penetration of fire into forests, has happened in many of the Afromontane forests of Angola. Once the regime shift has occurred, it might take centuries to revert back to a former state.

The interactive geophysical and biological processes and feedbacks that operate within the mesic savannas of Africa are comprehensively synthesised by Archibald et al. (2018) as illustrated in Fig. 7.2. Plants create feedbacks to flammability through their structure and the microclimate that they create. **Flammability** is the property of an ecosystem to ignite and propagate a fire, if a source of ignition is present. Tall, shade-intolerant $C_4$ grasses of the Andropogoneae dominate the most flammable fire regimes of Angola. In the humid, cool microclimate of forests, $C_4$ grasses are physiologically incapable of out-competing $C_3$ shrubs and shade-tolerant, slender $C_3$ grass species, which produce little flammable material. Most undisturbed closed-canopy forests have very little ground vegetation and thus minimal fuel for combustion, so even when fires penetrate the forest margin, they do not advance very far into the forest. In the arid savannas, the shorter Chloridoid and Aristidoid grasses are palatable to grazing herbivores, and thus do not accumulate much fuel. Mammal grazers and browsers thus regulate vegetation structure. The responses to disturbance pressures, such as fire and herbivory, are evolutionary feedbacks demonstrated by features of plant morphology and physiology, and community emergent properties such as structure and microclimate.

### *The Influence of Spatial and Temporal Scale*

Spatial scale influences the pace of change. A small patch of grassland in the middle of a forest might be too small to be ignited by lightning strikes that are the main trigger for natural fires. In the absence of fire, the fire-suppression threshold will be crossed and forest trees will close over the site, shading out any flammable grass species and thus preventing further fire ignition or spread. At the forest margin, grassland fires normally die as the architecture, microclimate and flammability of the vegetation changes. However, as the ratio of perimeter to surface area increases as forest patch size decreases, smaller forest patches become highly vulnerable to fire. In the mountains of Cuanza-Sul, Bié, Huíla and Huambo, the ratios of forest margins to forest canopy of remaining forest fragments have increased due to human-induced pressures such as frequent fires and timber extraction. Single fire events can now sweep through a forest and eliminate the shade-tolerant grasses, which are rapidly replaced by sun-loving flammable species, resulting in hotter and more damaging fires in following years. The once stable state of forest is then replaced by an alternative stable state of savanna, maintained by fire-resistant grasses, shrubs and trees. Finally, it should be recognised that human-driven disturbances (fire frequency, invasive species, charcoal production, deforestation) have accelerated these processes over much of Angola. The forest patches of the Angolan highlands can well be described as rapidly vanishing forest islands in a sea of grassland fires.

### *Paleo-ecological Evidence of Regime Change*

While field observations of regime changes are difficult because of the long timeframes of the processes, paleo-ecological studies are providing valuable evidence of regime changes of African vegetation. Carbon isotope studies measure the proportions of $C_4$ grasses and $C_3$ trees and shrubs found in samples extracted from soil profiles. Studies in southern and western Africa provide evidence of both rapid regime change, and stability, in savanna/forest dynamics. Paleo-ecological evidence indicates that since the end of the last Ice Age, approximately 12,000 years ago, the grasslands of many African savanna ecosystems have persisted against conversion to forest cover (Bond, 2019). In other areas, forests have replaced savannas (Maley et al., 2018). The alternative stable state concept has recently been applied to biogeographical models of Africa's forest and savanna biomes, using extensive site-based lists of tree species (Aleman et al., 2020). The results demonstrate the wide divergence of tree species between the two biomes, but also the broad areas in which both formations occupy similar climates. The forest/savanna transitional mosaics (Ecoregions 2 and 3) at the interface between the Guineo-Congolian Rain Forests and Mesic Savannas of northern Angola represent distinctive alternative stable states that have existed for millennia within the same climatic zone.

### Box 10.1 Tree—Grass Coexistence: The 'Savanna Problem'

Savannas are neither grasslands nor forests, but integrated mixes of grass and tree life forms within a co-dominant continuum of both grassland and woodland physiognomies. Both trees and grasses influence and are influenced by the availability of light, water balance, water cycle, primary production and the accumulation of fuel for periodic fires. But how do tropical savannas achieve the coexistence of grasses and trees without one displacing the other? The Venezuelan ecologist Sarmiento (1984) described the phenomenon as the 'savanna problem'. The topic has attracted the attention of many researchers and resulted in numerous papers describing alternative causal mechanisms. Here some of the explanations for tree/grass coexistence will be summarised to provide an introduction to one of the most debated features of savanna ecology.

The first and classic model explaining the relationship between trees and grasses in savannas was that of German ecologist Heinrich Walter (1898–1989). The '**Walter Hypothesis**' was based on field work undertaken in Namibia in the 1930s. The hypothesis presented a vertical niche-partitioning model where grass roots are more successful competitors for water in the surface horizons of soil than are trees (Walter, 1971). In contrast, tree roots access water from both the surface and from the deeper horizons that are inaccessible to grasses. Walter argued that deep-rooted savanna trees can use subsoil water throughout the year, including during the dry season, while grasses use their dense, shallow root system in the topsoil to rapidly take up water after infrequent rainfall events. The two life forms can therefore coexistence at equilibrium. Walter confined his hypothesis to arid savannas. He presciently considered that nutrient-deficient mesic savannas are controlled by biotic and disturbance factors. He also emphasised the important difference in the superior water use efficiency of grasses over trees as the ultimate cause of vertical partitioning.

Walker and Noy-Meir (1982) tested the Walter hypothesis in the *Burkea africana* mesic savanna of Nylsvley and simplified Walter's arid savanna model to a generalised 'two-layer' hypothesis (Fig. 10.13), extending the original arid savanna hypothesis to a mesic savanna at the dry, southern limit of the biome's distribution.

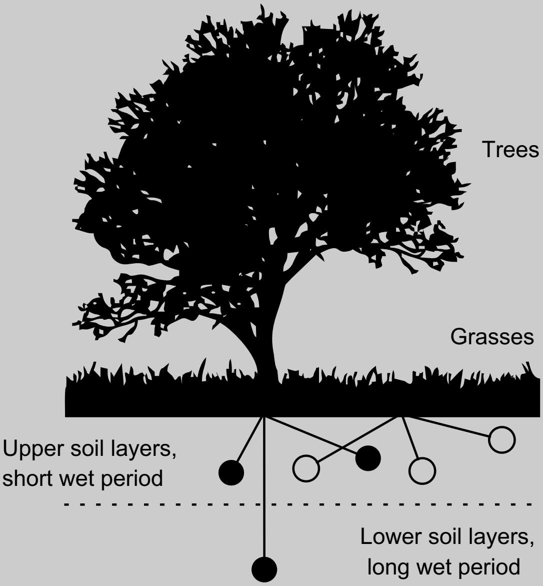

**Fig. 10.13** The simplified 'two-layer' model of vertical resource partitioning. Filled circles represent tree roots, open circles grass roots. Note that competition only occurs in the upper soil layer, where water is available for a short period prior to evaporation. Redrawn after Walker and Noy-Meir (1982) *Ecology of tropical savannas.* Springer, Berlin

The 'savanna problem' discussion was taken further by Scholes and Archer (1997) who presented a detailed global review of the complex interactions between trees and grasses in savanna ecosystems. They describe four models: niche separation by depth; niche separation by phenology; spatial separation, and balanced competition.

- **Niche separation** by depth has been discussed above (the Walter hypothesis).
- **Phenological partitioning** can be illustrated in mesic savannas such as Angola's miombo, where trees come into full leaf before the onset of rains, using resources stored since the previous rainfall period. Grasses, however, have very limited water and carbohydrate storage capacities and therefore have to slowly build up photosynthetic capacity as the rain season proceeds. There is thus a clear temporal (phenological) separation in the root and shoot

activity of trees and grasses, the trees using the earliest rains and the grasses only becoming competitive later in the season.

- Besides vertical partitioning in soil and seasonal partitioning in root activity, a third dimension is that of **spatial partitioning** across the savanna landscape. Trees create their own microenvironment of increased fertility and a milder microclimate below their canopies from litter fall and shading. Their roots also expand into the adjacent grassland by up to seven times their canopy radius. Inter-specific as well as intra-specific competition increases as the biomass and density of trees increase, up to a level at which competition between trees limits their density and biomass.
- **Balanced competition** models argue that intra-specific competition for resources is stronger than inter-specific competition. In this case the dominant species becomes self-limiting at a biomass insufficient to eliminate the weaker competitor. In miombo woodlands, certain species tend to dominate over selected areas, with a limit to their density and biomass, and with a sparse under-storey of grasses.

All these mechanisms could lead to stable coexistence between trees and grasses. Scholes and Archer (1997) concluded that no single model can account for the variety of phenomena at all savanna locations. They noted that climate is as important as competition in mediating these interactions.

Building on the discussions of Scholes and Archer (1997), Sankaran et al. (2004) provide a synthesis of hypotheses that seek to explain the coexistence of trees and grasses in savannas drawing on the different processes occurring in arid and mesic savannas. They identify two classes of models: first, competitive interactions that maintain coexistence and second, demographic bottlenecks to tree establishment and persistence in savannas. The competitive interaction models have been discussed above. Here the second approach—**demographic-bottleneck** models—provide another approach to the 'savanna problem'. Here the critical challenge for savanna trees is not on fine-scale effects of resource competition but relates to the recruitment and persistence of trees in the face of climatic variability and/or disturbance (Higgins et al., 2000; Osborne et al., 2018). The emphasis is placed on the success or failure of tree germination, sapling growth and adult tree establishment (Fig. 10.14). Several steps are involved:

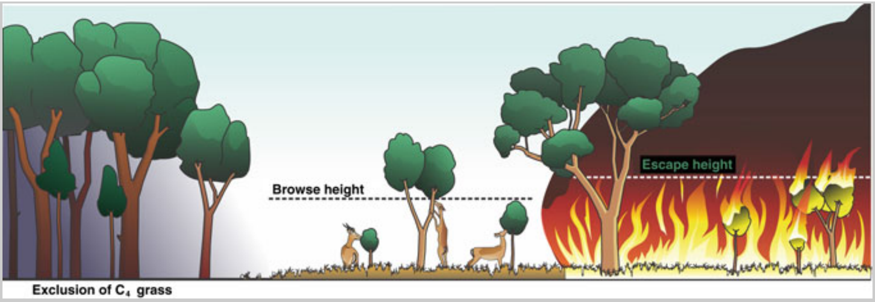

**Fig. 10.14** The mechanisms of tree-grass coexistence in savannas. Fire and browsing cause demographic bottlenecks for tree recruitment into the grass layer, leading to the emergence of 'escape heights' in each case. When trees surpass these heights they are no longer suppressed by fire or browsing, and may reach mature sizes. Most $C_4$ grasses are excluded under closed canopies because they are intolerant of shading, a mechanism which suppresses fires. Each of these feedbacks is positive, leading to the emergence of tipping points beyond which the ecosystem transitions rapidly to an alternative stable state. From Osborne et al. (2018) *New Phytologist*, 220: 10–24

- Tree recruitment in savannas can be slow, due to drought, herbivory and/or fire. Initial recruitment is controlled by rainfall, for successful germination, and for growth to seedling stage.
- Thereafter, fires and herbivory may hold sapling growth below the '**fire escape**' height for many years.
- Fluctuating recruitment and overlapping generations 'store' the reproductive potential of the trees (known as the '**storage effect**') until they can escape above the fire trap and progress to mature adult stature.
- Having established, trees may persist for long periods, until extended droughts, or high rainfall periods followed by intense fires, change the patterns of mortality and regeneration.

Savanna grasses live in a mix of microhabitats, each with differing light, soil nutrient and moisture conditions, and varying degrees of disturbance from mammals and fire. But grasses and forbs, despite their humble stature compared with trees, exert powerful interactions with tree populations. The accumulation of grass biomass, providing fuel for fires, regularly impacts on tree sapling recruitment. But equally, the shading of grasses by trees and suppression of $C_4$ grass growth and fuel accumulation prevents grass fires from killing the mature trees of woodland. Disturbance from wind, fire, and by burrowing, grazing, browsing or trampling mammals—from porcupines to elephant—results in a non-equilibrium grass-tree situation. Fire prevents woodlands developing into forest and also maintains open grasslands within the savanna matrix. The savanna ecosystem is under continual but subtle change. Individually, disturbance factors such as wind, herbivory and fire might have limited critical impacts, but in combination, the chance occurrence of discrete, often rare events can result in the shift to alternate stable states of savannas as illustrated below (Fig. 10.13).

In recent years, the competition-based hypotheses have lost support to the demographic bottleneck hypotheses. Both approaches await greater clarity on grass demography to conclude the discussions on the 'savanna problem'.

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