A primer on Savanna Ecology

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Preface

The Agroforestry: Southern Africa (AFSA) project is aimed at capacity building in agroforestry training and research. It is a joint project of the Universities of Alberta (UA) and Zimbabwe (UZ), funded by the Canadian International Development Agency (CIDA) of Canada. AFSA is a University Partnership in Co-operation and Development Project (UPCD) managed by the Association of Universities and Colleges of Canada (AUCC). The lead institution at UA is the Department of Rural Economy while at UZ it is the Institute of Environmental Studies. A wide range of other departments are represented on the management committees, reflecting the interdisciplinary nature of the project, including the Department of Agricultural Economics (UZ), the Department of Soil Science (UZ), the Department of Crop Science (UZ), the Department of Public Law (UZ), the Centre for Applied Social Sciences (UZ), the Department of Renewable Resources (UA), and the Forestry Commission (Government of Zimbabwe). The aims of the project include:

- developing curricula materials
- improving the agroforestry knowledge base
- training graduate students
- developing library resources in agroforestry

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A PRIMER ON SAVANNA ECOLOGY

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Introduction

Savanna is one of the world's major biomes (Figure 1). It occupies 54% of southern Africa, 60% of sub-Saharan Africa and 20% of the global land surface (Scholes and Walker, 1993). Furthermore, a large proportion of the world's human population and the majority of rangelands and livestock are found in savannas (Werner, Walker and Stott, 1991).

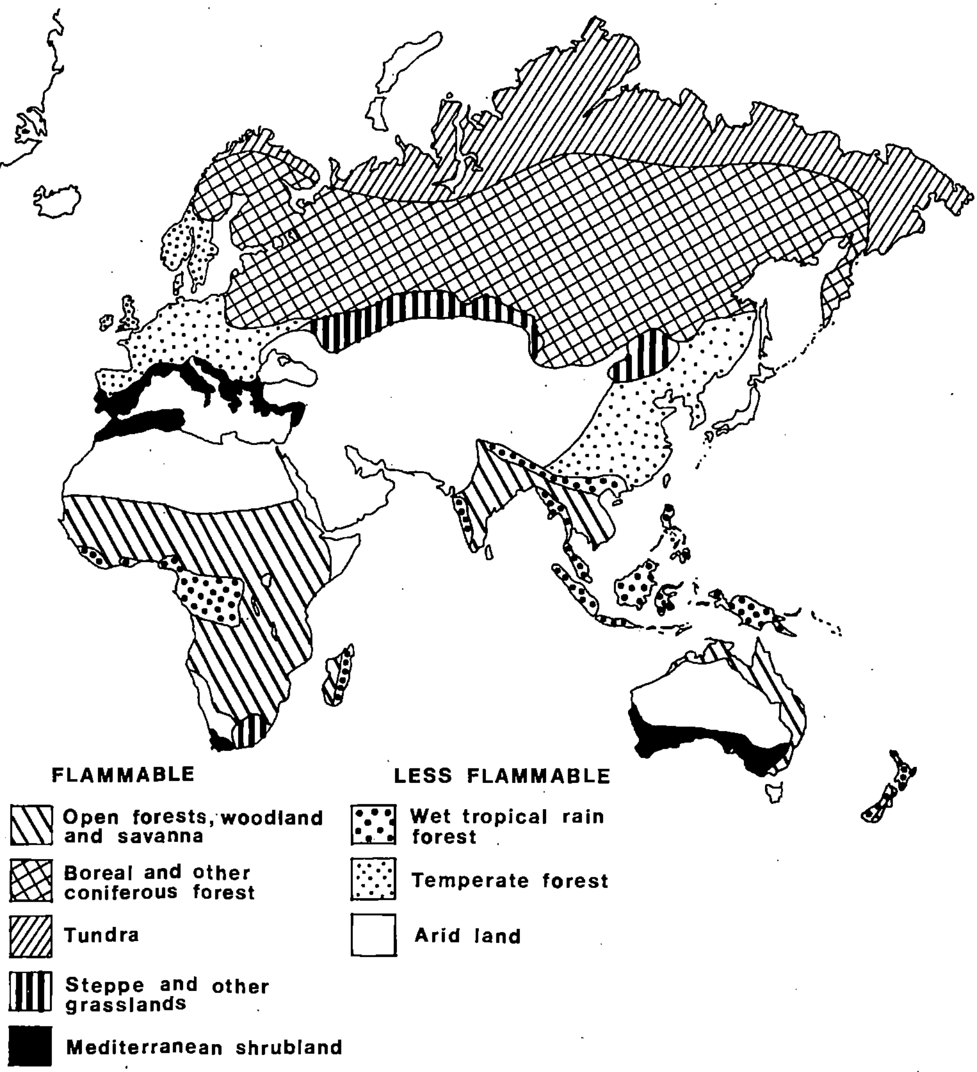
Savannas contribute to both the informal and formal economies of many countries (Campbell, 1996). They supply grazing, fuelwood, timber and other resources to the informal and subsistence economy. Savannas also contribute to the formal economy because they are the main location of the livestock and ecotourism industries. Globally, savannas are important because of emissions of trace gases from fires, soils and animals (Justice, Scholes and Frost, 1994); sequestration of carbon in their soils and biomass; and their biological diversity.

Savannas are, however, experiencing increasing pressures from demographic and economic changes that have increased dramatically over the past few decades. Severe damage to vegetation and soils is evident in several regions (Werner, Walker and Stott, 1991). A further threat to the structure and functioning of savannas is the forecast of global warming and likely changes in precipitation patterns.

Definition of savannas

Savannas are generally defined as tropical and sub-tropical ecosystems characterised by a continuous cover of C4 grasses that show clear seasonality related to water and in which woody plants are significant but form a discontinuous canopy cover (Frost *et al.* 1986; Solbrig, Medina and Silva, 1996; Scholes, 1997). Although the grass layer is often said to be continuous, in general it is highly clumped at the scale of individual tufts (Scholes, 1997). For example, in Zimbabwe, basal cover of grasses is less than 15% in rangeland in good condition.

Figure 1: Major vegetation biomes.



(Source: Bond and van Wilgen, 1996)

An intermediate layer of small trees or shrubs is sometimes present, and the grass layer may be temporarily absent, or replaced by dicotyledonous herbs, during periods of drought or disturbance (Scholes, 1997). Savannas include arid shrublands, lightly wooded grasslands, deciduous woodlands and dry forests.

Height and degree of canopy cover of the tree layer are usually used to classify savannas (Table 1). The different structural types of savanna are not always persistent in time. Natural and human-induced changes in climate, nutrients, fire regime, and herbivory, can displace the borders of the areas occupied by various types of savanna vegetation, and the borders with other types of vegetation such as humid forests and semi-deserts (Solbrig, Medina and Silva, 1996).

Table 1: Different structural types of savannas (Sarmiento, 1984).

1. Savannas with woody species within the herbaceous stratum: **grass savanna** or **grasslands**.
2. Savannas with low (< 8 m) woody species forming a more or less open stratum.
   a) Shrub and/or trees isolated or in groups; total cover of woody species less than 2%: **tree and shrub savanna.**
   b) Total tree/shrub cover between 2 and 15%: **savanna woodland, wooded grassland**, or **bush savanna.**
   c) Tree cover more than 15%: **woodland.**
3. Savanna with trees over 8 m.
a) Isolated trees with less than 2% cover: **tall tree savanna.**
b) Tree cover 2 to 15%: **tall savanna woodland.**
c) Tree cover 15 to 30%: **tall wooded grassland.**
d) Tree cover above 30%: **tall woodland.**
4. Savannas with tall trees in small groups: **park savanna.**
5. Mosaics of savanna units and forests: **park.**

Features of savannas

A key feature of savannas is a climate that has a hot wet season of four- to eight-month duration and a warm dry season for the rest of the year. In southern African savannas the wet season is unimodal, and falls in the summer time, between October and April. The strongly seasonal water availability leads to accumulation of fine dry easily ignited fuels. Regular fires during the dry season are therefore common. Fire frequency ranges from every year in moist savannas to once every ten or more years in arid savannas. The high frequency of grass-layer fires is thus a unifying factor in savannas (Scholes, 1997).

Savannas can also be classified as broad-leafed and fine-leafed. The two broad categories have important features (Table 2). The features relate to differences in soil fertility, annual rainfall, fire regimes, herbivory and tree taxonomy.

Table 2: A comparison of features of two broad categories of African savannas. These are general trends to which there are exceptions.

Feature	Broad-leaved	Fine-leafed
Age of erosional surface	Ancient	Recent
Parent material	Acid crystalline igneous rocks Aeolian sands Sandstones	Basic igneous rocks Mud- and silt-stones Limestones
Phosphorus availability	Low	Moderate
Dominant clays & CEC	Kaolinite, iron oxides (low CEC)	Montmorillonite (high CEC)
Mean annual rainfall	600-1500 mm	400-800 mm
Dominant tree family	Caesalpinoideae (wet) Combretaceae (dry)	Mimosoideae (dry) Burseraceae (v. dry)
Dominant grass subfamily	Panicoideae	Arundinoideae
Mean tree leaf N at maturity	<2.5%	>2.5%
Grass N content at senescence	<1%	>1%
Mycorrhizal associations	Predominantly ECM	Predominantly VAM
N-fixation	Low N-fixation	Moderate N-fixation
Main tree anti-herbivore defence mechanisms	Chemical (mainly polyphenols especially condensed tannins)	Structural (eg. thorns)
Tree leaf size	2-10 cm	0.1-1 cm
Grass growth form	Bunch (caespitose)	Creeping (stoloniferous)
Large mammal herbivory	Low (5-10%)	High (10-50%)
Insect herbivory	Episodic, mostly of woody plants by Lepidoptera larvae	Seasonally recurrent, mostly of grass by grasshoppers & termites, also episodic by locusts
Fire fuel load	High	Low
Fire frequency	Annual-triennial	Quintennial or longer

(Source: Justice, Scholes and Frost 1994).

Dynamics of savannas

Models of savanna structure and function

Many workers (e.g. Walker, 1987; Westoby, Walker and Noy-Meir, 1989; Belsky; 1991; Scholes and Walker, 1993; Jeltsch, Milton, Dean, and van Rooyen, 1996; Scholes and Archer, 1997; Higgins, Bond and Trollope, 2000) reviewed some of the models that explain the coexistence of trees and grasses in savannas. Belsky (1991) divided some of these into global (e.g. Whittaker, 1975) and regional (e.g. Walter, 1971; Walker, Ludwig, Holling and Peterman, 1981; Walker, and Noy-Meir, 1982; Walker, 1987) models.

Global model

Whittaker (1975) described the environmental conditions defining and limiting all terrestrial ecosystems (Figure 2). Tropical savannas are characterised by low to moderate annual rainfall (500 1300 mm) and by high mean annual temperatures (18 30° C). Savannas are bounded by woodlands and forests at higher rainfall regimes, by thornscrublands and deserts at lower rainfall regimes, and by temperate grasslands and steppes at lower temperatures. East African savannas fit Whittaker's (1975) model well (Belsky, 1991).

Simple abiotic model

Walter (1971) proposed a two-soil layer model to explain the coexistence of trees and grasses in African savannas. According to this model, in low rainfall areas (<250 mm annually) only grass species which are shallow rooted, receive sufficient moisture to grow, and thus grasslands dominate. Where rainfall is higher (250 - 500 mm annually) trees and grasses coexist since rainfall is sufficient for water to percolate to lower soil horizons, allowing the more deeply rooted trees to survive periods of drought. In areas of high rainfall (> 500 mm annually), woodlands dominate since soil moisture is sufficient to support a closed canopy, which shades out grasses. Walter's (1971) model was developed and expanded by Walker *et al.* (1981) and Walker and Noy-Meir (1982). Walker and Noy-Meir's (1982) model is based on two environmental gradients, rainfall and soil texture (Figure 3). This model predicts an increase in tree density along a gradient of increasing rainfall. However, the model is not valid for East African savannas where shrubs dominate at the lower end of the rainfall gradient (Belsky, 1991). Furthermore, the model does not explain the large variation in the tree:grass ratio within a single climate-soil combination (Belsky, 1991; Archer and Scholes, 1997).

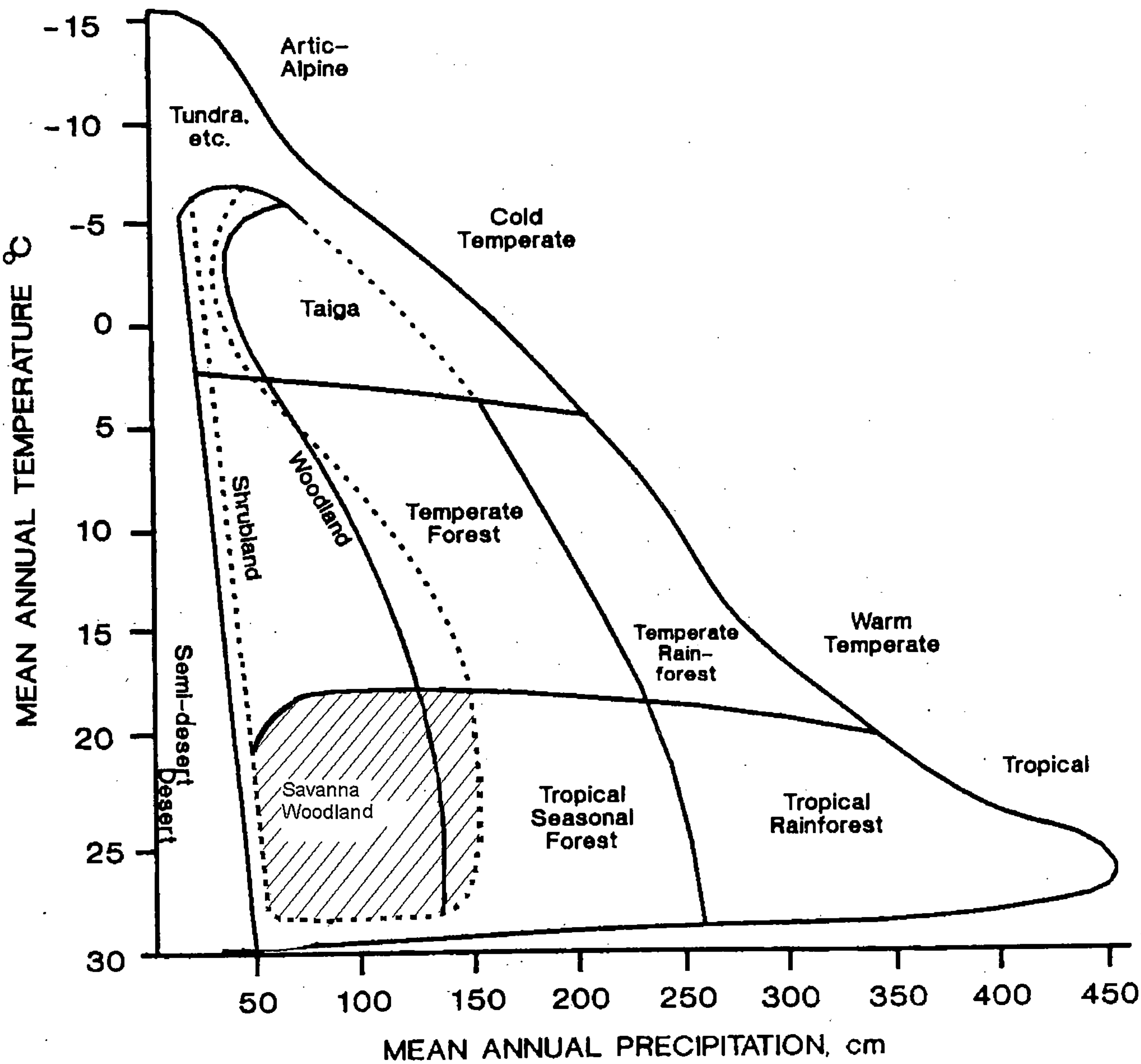


Figure 2: **Relationships of major terrestrial biomes to temperature and rainfall gradients.**

(Source: Whittaker, 1975)

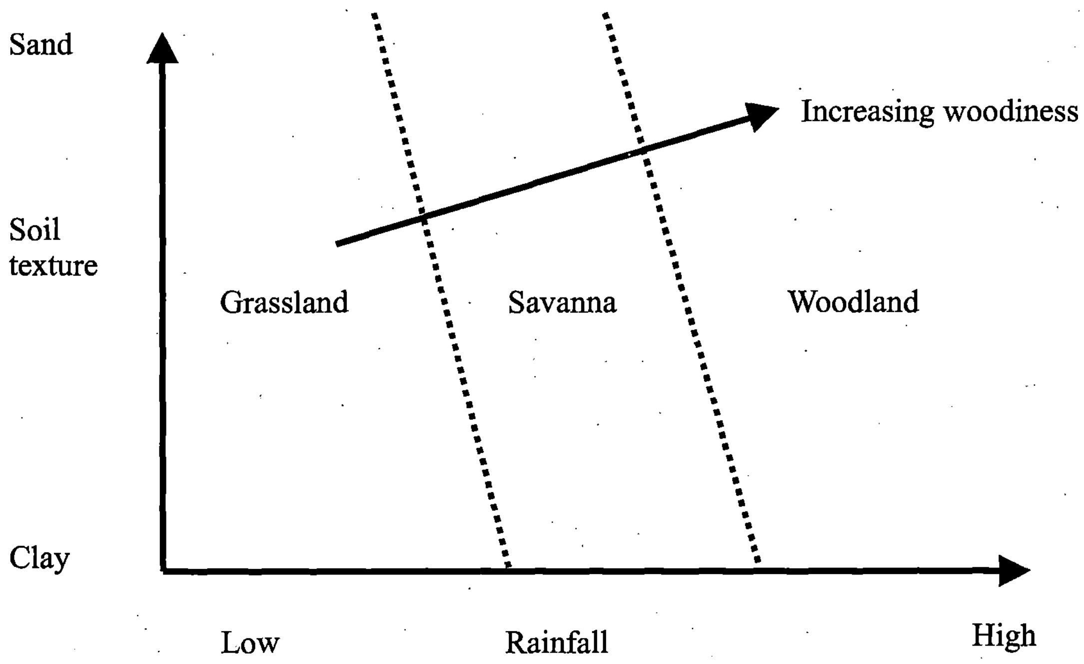


Figure 3: The Walter/ Walker model of tropical savannas.
(Source: Walker and Noy-Meir, 1982).

Multi-factor model

Walker (1987) developed a model incorporating important environmental factors influencing vegetation structure of savannas. Soils, rainfall, predators, herbivores and fire interact in complex ways to influence vegetation structure and functioning (Figure 4). The relative influence of each factor varies temporally and spatially.

Functional model

Frost *et al.* (1986) developed a functional model of tropical savannas. The model is based on plant available moisture (PAM) and available nutrients (AN). Rainfall, water infiltration, evapotranspiration and soil texture are integrated into a single measure of soil moisture available to plants. Available nutrients are a measure of the nutrients available to plants during their growth. This model is novel since it substitutes biologically meaningful measures (PAM and AN) for purely physical measures (Belsky, 1991).

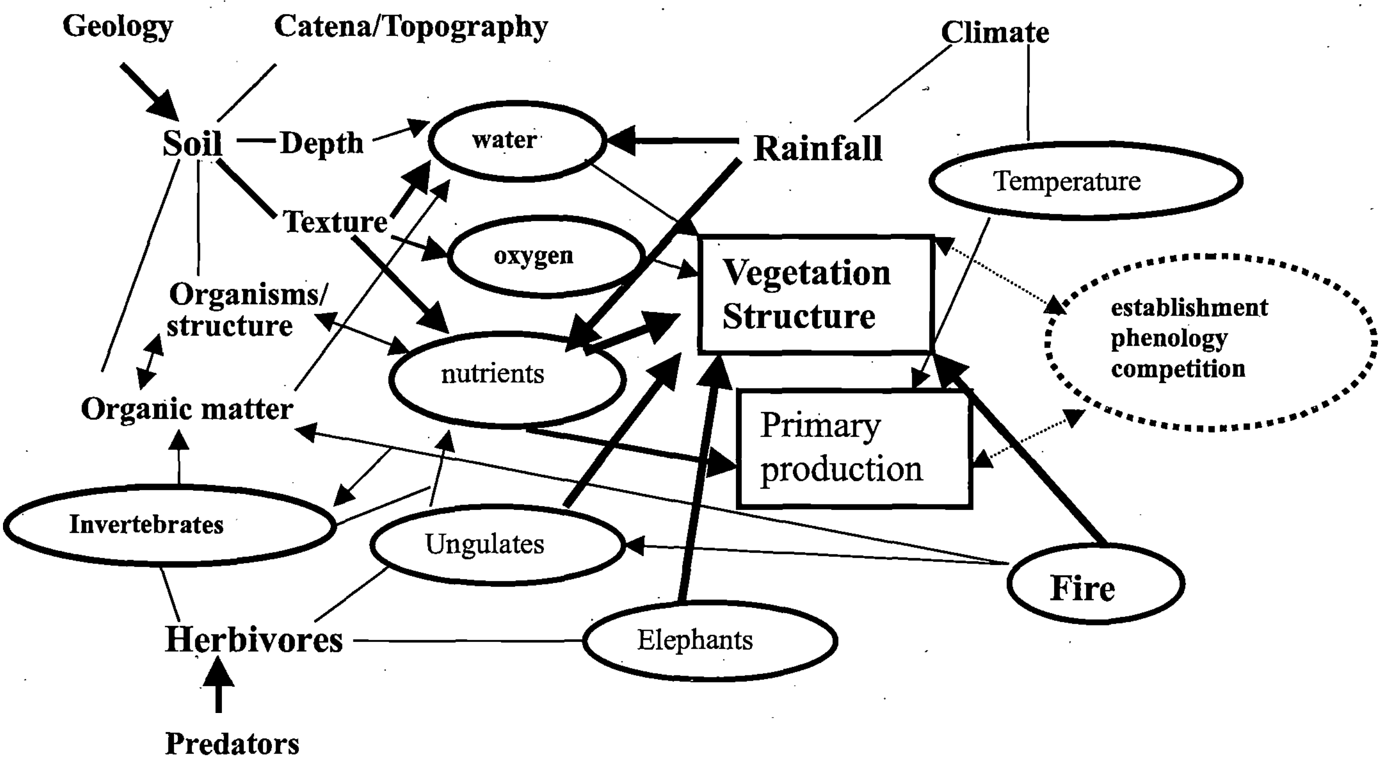


Figure 4: Walker's multi-factor model of the determinants of African savannas. The breadth of the arrow indicates the relative importance of a factor. Some interactions have been excluded to keep the diagram simple.
(Source, Walker, 1987).

The axes of Frost *et al.*'s (1986) model have not yet been well defined and therefore placement of savannas and community types within the model (Figure 5) can only be approximate (Belsky, 1991). Another limitation of the model is that the two axes are not independent (Scholes, 1991). First, high rainfall areas tend to have weathered and infertile soils. Second, in dry climates, soils with a high clay content are both more fertile and drier than sandy soils receiving the same rainfall, since more water is lost by runoff and evaporation from heavier textured soils.

Plant-available moisture (PAM), available nutrients (AN), fire and herbivory are major factors that explain some of the common features and differences in savanna structure and function. These factors interact at all ecological scales from landscapes to local patches, but their relative importance differs with scale (Scholes, 1991; Solbrig, 1993).

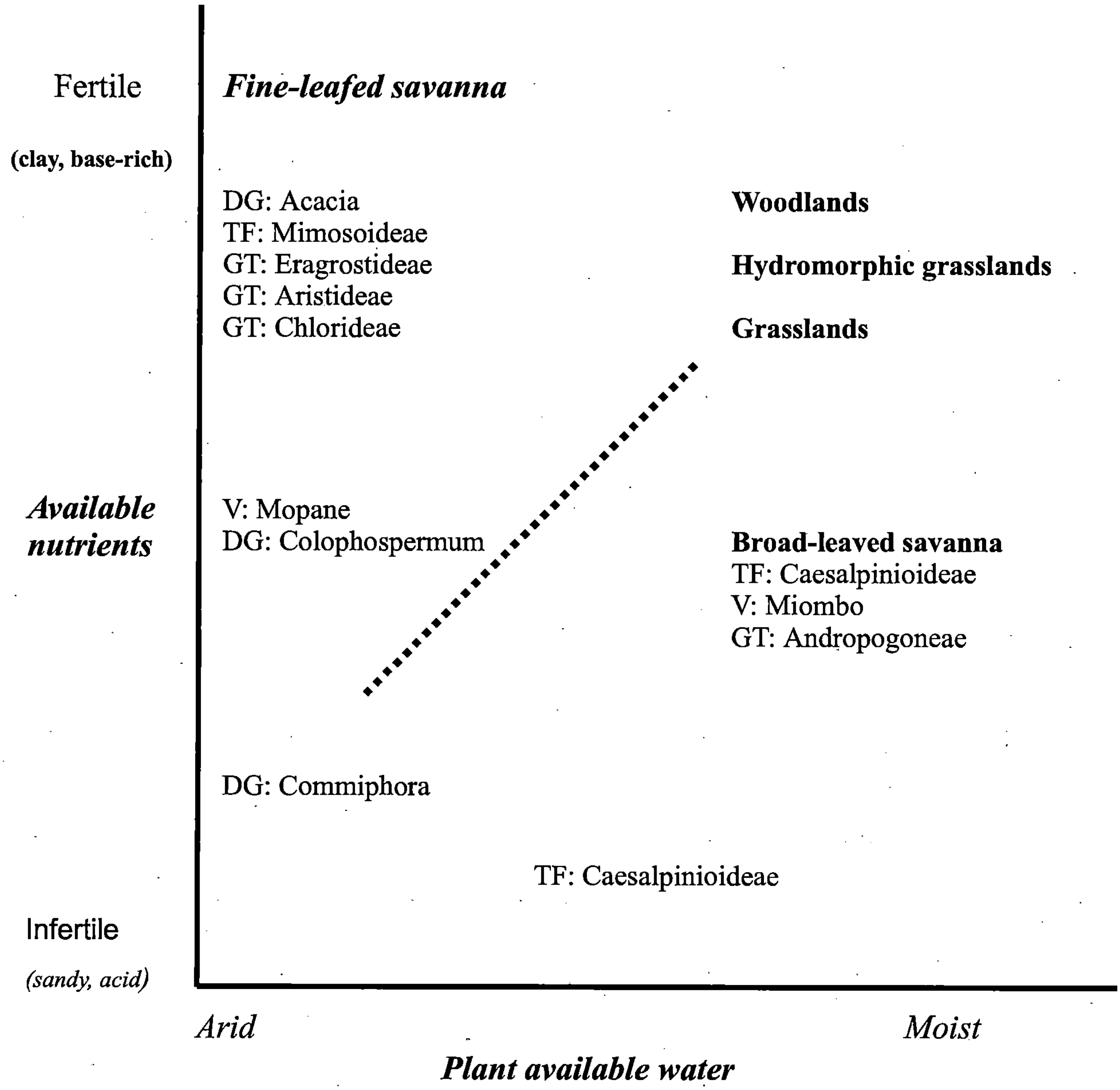


Figure 5: **The association between environmental factors and floristic and structural characteristics in southern African savannas. DG, dominant tree genus; TF, dominant tree family; GT, dominant grass tribe; V, vernacular name.**
(*Source: Scholes, 1997*).

Plant-available moisture and available nutrients are primary determinants of savanna structure and function at higher scales. Where PAM and PAN have high values, woody elements dominate, and as PAM and /or PAN increase, savanna gives way to moist forest. When PAM and/or PAN have low values, plants tolerant of dry conditions become abundant, and if values of the PAM-AN plane get very low, a semi-desert replaces the savanna. Between these extremes of moisture and nutrients, several types of savanna are encountered (Solbrig, 1993).

At a local scale, the patchy distribution of soil types and topographic features modify PAM and AN, and together with fire and herbivory, determine the density of the tree layer, the productivity of the system, and the rates of nutrient and water flow through the system (Scholes, 1991; Solbrig, 1993). Factors that influence each of the four determinants are described below.

Soil moisture

African savannas are usually divided into dry and wet forms, in the belief that significant ecological differences exist between the two types (Scholes, 1991; Scholes and Walker, 1993). A useful dividing limit is annual rainfall at which the strong linear dependence of annual herbage production on annual rainfall in dry savannas begins to level off. This occurs between 700 and 900 mm mean annual rainfall, with the lower limit occurring on sandy substrates and the higher on fine textured soils.

The strong seasonality in available soil moisture is a key determinant of savanna structure and functioning (Werner, Walker and Stott, 1991). It sets a limit on maximum plant productivity and a constraint on types of plants that can survive alternating periods of drought and favourable water relations. Total productivity is also constrained by availability of nutrients. Nutrient availability is partly dependent on precipitation and past vegetation history and partly dependent on other factors such as parent material.

Several factors influence the amount of soil moisture (Bell, 1986; Frost *et al.*, 1986; Solbrig, 1993). These include:

i) quantity and seasonal distribution of annual rainfall and the proportion of this rainfall that enters the soil;
ii) water holding capacity of the soil, which is a function of soil texture and depth; and
iii) amount of evapotranspiration that is related in complex ways to climate, soil texture, soil surface characteristics and type of vegetation at a site.

Soil nutrients

Savanna soils vary widely in texture, structure, profile and depth reflecting the geology, geomorphology and climate, and the influence of topography, relic features of past landforms, the kind and exten-t of vegetation cover, and animal activity of the particular savannas (Frost *et al.*, 1986). Physical characteristics and the underlying geological formation determine both the nutrient content and the water and nutrient retention capacity of a soil.

Three main factors influence the availability of nutrients. These are: parent geology, rate of weathering and transport of material into and out of an area by water (Bell, 1986). Basic igneous rocks (e.g. basalts, dolerites, gabbros) and sedimentary rocks derived from organic or fine alluvial deposits (e. g. limestones, shales, mudstones, siltstones) are rich in nutrients (Bell, 1986).

For example, the East African basic volcanics produce some of the most fertile soils on earth. In contrast, acid igneous rocks (e.g. andesites and granites) and sedimentary rocks derived from coarse alluvial fractions (e.g. gneisses, sandstones, quartzite) are poor in nutrients. Precambrian metamorphic rocks of the central African basement produce generally poor soils.

Water availability and temperature influence the rate of weathering. Weathering in warm and wet areas is faster than in dry and cool ones. In sloping areas, soil profiles are drier, weathering is slower and erosion may exceed deposition.

Soil fertility is inversely related to rainfall. In high rainfall areas nutrients are lost through leaching. This negative correlation between rainfall and soil nutrient availability is the basis for the distinction between moist-dystrophic savannas and arid-eutrophic savannas (Huntley, 1982). Soil nutrient availability also tends to be negatively correlated with water permeability. Permeable soils are usually sandy and have a low cation exchange capacity (CEC), while impermeable soils are usually clayey or have some other mineral concretion and have a high CEC (Bell, 1986).

Fire

Fire is common in savannas (Bond and van Wilgen, 1996). Although lightning was and occasionally still is a source of spontaneous fires, today humans cause most fires. Fire has a profound effect on savanna structure and growth of vegetation (Frost and Robertson, 1987; Bond and vanWilgen, 1996). Fires reduce standing biomass and litter, and may kill individual organisms, seeds, seedlings and unprotected plant tissues. Fire also changes the energy, nutrient and water fluxes between the soil and atmosphere. The nutrient status and productivity of savannas are determined in part by the frequency, timing, and intensity of burning.

The fire regime of an ecosystem has four components (Scholes and Walker, 1993). These are: 1) frequency, the reciprocal of the mean time between fires; 2) intensity, the rate of energy release ("hotness"); 3) season of burning, and 4) type of fire (surface, canopy, backfire or headfire).

Fire frequency

Natural fire frequencies in moist savannas are thought to be about once every 1-2 years, decreasing to once every 3 or more years. In general, more frequent fires suppress woody biomass. Hence, less frequent fire leads to higher woody biomass.

Fire intensity

Fire intensity is expressed as the rate of energy release per metre of flame front. It can be calculated as the product of rate of spread and energy content of material burned. The energy content of material burned is calculated from the fuel load, its energy content and the proportion of available fuel that is actually burned. The fuel load includes litter. High intensity fires are effective for bush control. However, fires of lower intensity can damage seedlings and small saplings within the grass layer.

Fire season

Most fires in savannas occur in the dry season when grass fuel is dry. It is argued that fires that occur in the early dry season when fuel is moist are generally less intense than those occurring in the hot dry season. Thus fires in the late dry season tend to be more destructive than in the early dry season.

Herbivory

Biomass and type of herbivores

African savannas are famous for the diversity and abundance of large mammalian herbivores that they support (Owen-Smith, 1982; du Toit and Cumming, 1999; Illius and O'Connor, 2000). Species range in body mass from a 4 kg dik dik to a 5 000 kg elephant. Some 44 large herbivore species of 29 genera frequent African savannas (Owen-Smith, 1982). Twenty species are classified as grazers (animals that feed mainly on herbaceous plants), 13 as browsers (animals feeding mainly on woody plants), 10 as mixed feeders and 1 as an omnivore. The browser-grazer dichotomy seems to be a special feature of the African savanna (Owen-Smith, 1982; du Toit and Cumming, 1999).

The high faunal diversity and herbivore biomass density has been attributed to the high spatial heterogeneity of African savannas (du Toit and Cumming, 1999). Several authors (e.g. Coe, Cumming and Phillipson, 1976; Bell, 1982) have described the distribution of herbivore biomass in relation to rainfall and soil type (Figure 6). Herbivore biomass tends to increase with rainfall up to about 700 mm per year and then levels off or declines at higher rainfall (Bell, 1982). However, at any given rainfall level, herbivore biomass is related to soil fertility. Herbivore biomass on fertile soils is considerably higher than on infertile soils. The difference is marked at higher rainfall levels.

High	**Low quality woodland and forest:** *Very low biomass selective feeders incl. smaller antelopes and primates*	**High quality woodland and forest:** *High biomass of mixed range of herbivores:* ***elephants, rhinos, giraffe, kudu, nyala, buffalo, zebra, hartebeest, etc.***
Soil water	**Low quality woodland** ***Low biomass of tolerant herbivores i.e. elephants, buffalo, zebra, etc.***	**High quality fine-leafed woodland and short grassland:** ***High biomass of selective browsers and grazers i.e. giraffe, impala, kudu, gazelle, wildebeest, springbok***
Low	**Low quality grassland** ***Low biomass of medium tolerant grazers & mixed. feeders: eland, zebra, roan reedbuck.***	
	Low — **Soil nutrients** — **High**	

Figure 6: Distribution of large herbivore biomass in relation to soil moisture and rainfall.
(Source: Bell, 1986)

Megaherbivores (animals exceeding 1 000 kg in adult body mass i.e. elephant, black rhino, white rhino, hippo and giraffe) make up 50-70 % of herbivore biomass in most savannas. There are four exceptions to this general rule (Bell, 1986) as follows:

1. Areas where man has eliminated some or all larger herbivores (megaherbivores);
2. The East African volcanic short-grass plains;
3. The Central-Southern African basement highland sour grasslands; and
4. High rainfall low-nutrient woodland and forest (i.e. northern Angola, central Democratic Republic of Congo) but not in the high-nutrient volcanic forests.

Feeding ecology of African ungulates

The range of food quantity and quality over which an animal can survive is the key factor in the feeding ecology of herbivores (Bell, 1986; du Toit and Cumming, 1999). As a rule of thumb, the productivity of large mammalian herbivores in fertile savannas is limited by food quantity especially during the dry season while that in infertile savannas is limited by quality (Scholes and Walker, 1993).

Most herbivores select for high quality green leaves but differ in their ability to tolerate diets that depart from this. Tolerance of low quality plant material (low protein to fibre ratio) in the diet increases with increasing body size. This is attributed to the fact that large animals have relatively low metabolic rates and maintenance requirements per unit weight and to the fact that lower quality foods require relatively large gut volumes (Bell, 1986).

Dietary tolerance also varies in relation to the structure and physiology of the digestive system. African ungulates can be divided into ruminants and non-ruminants. Ruminants ferment plant fibre in the complex multi-chambered fore-gut while non-ruminants have a simple stomach and ferment fibre in the hindgut and caecum. Ruminants have a higher digestive efficiency than non-ruminants because of a lower rate of passage of food through the rumen (Bell, 1986). Food retention time increases as food quality falls. In contrast, non-ruminants process food rapidly and the rate of passage is unaffected by food quality.

The ability of different types of African herbivores to tolerate plant secondary compounds is unclear (Bell, 1986). Secondary compounds that deter herbivores include digestibility reducers (e.g. tannins) and toxins (e.g. alkaloids, cyanogenic glycosides).

Bell (1986) predicted that species with a wide tolerance of dietary quality (i.e. larger species, especially non-ruminants) tend to produce unstable plant herbivore interactions. He gave the following four reasons. First, because of their wide dietary tolerance, they are capable of using a higher proportion of the vegetation and so leave a smaller unusable reserve. Second, larger species are less vulnerable to environmental fluctuations because since their dietary tolerance is high, they are better able to wait out dry spells than more selective species by switching to very poor quality material. Third, large animals are less vulnerable than small animals to predation. Fourth, since reproductive rates are inversely scaled to body size, populations of larger species cannot respond as rapidly to improved conditions by rapid recruitment as those of smaller species.

Storage effect model

Some authors (e.g. Warner and Chesson, 1985; Higgins, Bond and Trollope, 2000) proposed the storage effect model to explain the coexistence of trees and grasses in savannas. It is a non-equilibrium model that emphasises differences in demography rather than physiology in explaining coexistence of potential competitors. The storage effect model depends on the occurrence of overlapping generations and fluctuating recruitment rates. Thus, the reproductive potential is 'stored' between generations allowing populations to recruit when conditions are favourable (Higgins *et al.*, 2000).

Higgins *et al.* (2000) demonstrated that the storage effect model operates in savannas because of the following three reasons. First, seedling establishment rates depend on rainfall which is highly variable. Second, grass fires which vary appreciably in intensity in savannas, can prevent tree recruitment. Third, savanna trees are long-lived. Higgins *et al.* (2000) have therefore hypothesised that grass-tree coexistence is driven by limited opportunities for tree seedlings to escape both drought and the flame zone into the adult stage.

Equilibrium and non-equilibrium dynamics

It is usually assumed that natural ecosystems are in equilibrium. This means that if not interfered with by humans, they will persist in their present state for long periods of time (Solbrig, 1993). However, natural ecosystems are affected by different natural disturbances such as frost, drought, floods and fire (e.g. Frost *et al.*, 1986; Walker, 1987; Westoby *et al.*, 1989; Higgins, Bond and Trollope, 2000). Equilibrium hypotheses predict that the system will return to its previous state once the source of disturbance has disappeared.

Equilibrium hypotheses imply that there are negative feedbacks in the ecosystem that control the behaviour of the various elements (Solbrig, 1993). So, for example, plant growth is supposedly controlled by herbivore pressure, and by decomposition rates that control nutrient availability in the soil; herbivores in turn are supposedly controlled by the availability and quality of plant biomass, and by predation rates, and so on (Solbrig, 1993).

Theories about the optimal way to manage ecosystems have been dominated by this way of thinking (Behnke, Scoones and Kerven, 1993). For example, introduction of domesticated herbivores is thought to move the system away from equilibrium, resulting in reduced availability and quality of feed. To compensate for this situation an effort is made to eliminate wild herbivores (which are seen as competitors) and to "improve" the quantity and quality of the vegetation through artificial means such as fertilisation, control of stocking rates and periods of grazing (Solbrig, 1993).

Increasingly a different sort of thinking is influencing the way ecosystems are perceived. This new thinking is represented by the so-called "non-equilibrium" hypotheses (Westoby *et al.*, 1989; Behnke, Scoones and Kerven, 1993). These hypotheses maintain that natural ecosystems are not in equilibrium but instead are the result of various historical and chance factors, and that a system such as savanna can be present in multiple states. Studies with non-equilibrium systems indicate that their behaviour is very different from that of equilibrium systems. Most notable among the characteristics of their dynamics is the existence of more than one equally probable and equally stable state. Non-equilibrium systems are therefore inherently non-predictable. The same disturbance can create one state in one instance and a very different one in another case. If this is true then the existence of a savanna in any one of a multitude of states may indicate that it is being managed sustainably. This considerably complicates management. It requires a much more careful analysis than what has been undertaken in most instances to determine which model is best suited for a particular system. One important consideration is the relative importance of internal biotic factors such as negative feedbacks between plants and herbivores, and external factors such as drought.

Variation in annual rainfall imposes an additional stress. The variance in interannual precipitation is inversely related to total rainfall. Furthermore, the lower the average rainfall, the more extreme the effects of drought years on the flora and fauna. Consequently, dry savannas are almost certainly non-equilibrium systems (Ellis and Swift, 1988), while it is less certain of wet savannas. Illius and O'Connor (2000), however, have challenged the assumption that semi-arid savannas are non-equilibrium systems where herbivores have minor impacts on the vegetation.

What are the ecological and management implications of non-equilibrium systems? According to Westoby *et al.* (1989) savanna dynamics can be described by a set of alternative stages of the vegetation and a set of discrete transitions between states. Consequently, they recommend that the manager make an inventory of the possible alternative states of the system and of the possible transitions from one state to another, remembering that there is more than one possible transition. This knowledge will allow the manager to develop adequate responses for each state and possible transition.

Threats to savannas

There are several threats facing African savannas. These include global climate change and an increase in human population. The major threat is the increase in human population density. The increase in human populations in turn leads to increased pressure on the land. The increased pressure on the land is characterised by an increase in deforestation and conversion of grazing land to arable leading to overstocking. Furthermore, du Toit and Cumming (1999) argue that overgrazing by livestock coupled with episodic droughts is causing widespread rangeland degradation and loss of both floristic and faunal diversity.

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