RESPONSE OF THREE SEMI-ARID SAVANNAS ON CONTRASTING SOILS TO THE REMOVAL OF THE WOODY COMPONENT

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ABSTRACT

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A three-year study was undertaken in the semi-arid (500mm p.a.) north-eastern lowland area of South Africa. All the woody plants were removed from one-hectare savanna plots on three different soil types, and key hydrological and biological changes were monitored relative to adjacent controls.

Runoff increased initially, but decreased once the grass cover increased. Deep drainage and lateral subsurface flow increased on the sandiest site. Evaporation from the soil surface increased on the heavier textured soils. The duration of plant-available water in the soil increased on all cleared plots.

The pre-clearing woody-plant aboveground biomass was in the range of 5.6 to 11.2 $t.ha^{-1}$, of which 0.66 to 0.80 $t.ha^{-1}$ was leaf biomass. The annual herbaceous production was strongly rainfall dependent, averaging 1 to 1.5 $t.ha^{-1}$, and increased by 0.4-0.6 $t.ha^{-1}$ except on the most fertile site (0.6-2.0 $t.ha^{-1}$). Total available forage increased with clearing, but so did its variability. The observed changes in herbaceous layer palatability could not be attributed to clearing.

Woody plants and grasses were shown to have water-use niche separation in both rooting depth and time of water use. Simulation over forty years of wetting patterns indicated 75 to 85 % niche overlap, with separation on the depth axis more important in sandy sites, and on the time axis in clayey sites. Competition between woody plants and grasses was strongly asymmetrical in favour of woody plants.

Grasslands derived from savannas by clearing are inherently unstable. Maintenance of a treeless grassland by the use of fire is feasible only if herbivory is controlled. Unchecked regrowth will result in reversion to savanna in about 15 years. Clearing is not recommended on sandy upland soils or highly erodible sites.

PREFACE

This study took place in the context of increasing population pressures and land values in the extensive savanna lands of the world, demanding new approaches to their management. There is an ironical opposition in the two major problems in savannas: bush encroachment of grazing lands and tree clearing in centres of rural population. Bush clearing could be an important technique in enhancing production from savannas; however the interactions of trees and grass in savannas are relatively poorly understood.

Conventions

The full naming conventions of plant species mentioned in the text are given in appendix 4. Throughout the text "site" refers to one of the three experimental sites, while "treatment" or "plot" refers to one of the two treatment (cleared or uncleared) plots at a specific site.

Acknowledgements

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The committee of the Klaserie Private Nature Reserve and the landowners upon whose farms I worked, Messrs. Cloete and Lombard, are thanked for their approval. The help and hospitality of the residents of Klaserie P.N.R., in particular Erwin and Jenny Leibnitz and John and Elche Robinson, is gratefully acknowledged. Jackson Mathebula provided faithful assistance in the field.

The most thanks of all are due to my wife Mary, who gave her unstinting help and support at all times.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

Robert John Scholes

28 day of October, 1987

1.0 INTRODUCTION

1.1 THE SAVANNA PROBLEM

Savannas are unusual among the terrestrial biomes in lacking a single dominant plant growth form. Dominance in structure and function is shared by woody and grassy plants, growth forms which in other biomes are mutually exclusive. This is the core of what Sarmiento (1984) calls the "savanna problem": since ecological conditions in savannas allow either form to grow, why does one not predominate, as classical competition theory implies that it should? In semi-arid savannas, which are by definition water limited, the paradox of coexistence under apparently competitive conditions is especially acute.

This problem is a particular case of a general question which has inspired much debate among ecologists: is the structure of a community determined by intrinsic biotic factors such as competition and predation, or is it imposed by extrinsic abiotic factors such as chance fluctuations in the environment?

This study seeks to answer the question "How is the functioning of a savanna altered by a structural modification, namely the removal of woody plants?". In order to do so, it examines the causal links between hydrology, resource partitioning and primary production in semi-arid savannas. These three themes form the focus of the thesis. In elucidating them, some light is also shed on the nature of competitive coexistence in savannas.

Apart from its theoretical implications, the question is of fundamental importance to the management of savannas. The production of grass in savannas is controlled by rainfall, soil type, the density of woody plants and the grazing regime. The first two are beyond the practical control of the manager, but the last two can feasibly be manipulated. An alteration in structure may in itself be a desirable end, since in savannas it is one of the factors influencing the herbivore species composition. Bush clearing has been recommended as a management technique by many authorities, and is increasingly widely practised in savannas. A knowledge of the limitations and consequences of bush clearing would be of great practical value.

1.2 STRUCTURE AND FUNCTION IN SAVANNAS

1.2.1 DEFINITION OF TERMS

Savanna is here used in its biome sense, as neotropical ecosystem types occurring under a strongly seasonal moisture regime in which C4 grasses and woody plants both provide significant contributions to the primary productivity. So defined, they may be further subdivided on functional grounds into **semi-arid savannas**, in which annual primary production correlates strongly with annual precipitation, which has a mean value in the range 250-700 mm (Rutherford & Westfall 1986), and **moist savannas**, whose stucture and dynamics are less dominated by moisture supply, and more by nutrient status and fire. This scheme is in some ways conceptually similar to the eutrophic-dystrophic split proposed by Huntley (1982), except that semi-arid savannas as defined here includes both dystrophic ("moist") and eutrophic ("arid") members. Semi-arid savannas must further be established on well-drained soils, so that direct precipitation is the only source of moisture. This study is exclusively concerned with semi-arid savannas, which for the sake of brevity will simply be referred to as savannas. The area of relevance of this study should be considered to be the semi-arid savannas of sub-Saharan Africa, although the principles may be applicable elsewhere. Such savannas occupy an area of 959 000 km^2 in Africa south of 22°S alone.

The distribution of savannas is well correlated with the occurrence of the so-called **savanna climates** (Koppen 1931, Walter 1975, Phillips 1983, Nix 1983), the single most important feature of which is the strongly seasonal rainfall. The bulk of the rain falls in the wettest six months, which occur in summer. Rainfall in the driest three months is less than 50mm (Nix 1983). The coefficient of variation of mean monthly rainfall exceeds 75%. The mean annual temperature exceeds 20° C, with the mean minimum of the coldest month exceeding 13° C. Frosts are rare and the diurnal temperature fluctuation exceeds the range of mean monthly maximum minimum temperatures. Radiation is very high (160-190 $kcal.cm^{-2}.yr^{-1}$) and the annual potential evapotranspiration greatly exceeds annual precipitation. Savannas are further characterised by having frequent occurrences of fire, and a high ratio of below- to above-ground biomass.

The dominant growth forms in savannas are the woody plants and the grasses. **Growth form** refers not only to the location of the perennating organ as in Raunkiaer's (1934) life form classification, but to the entire complex of genetically-determined phenological, morphological, physiological and reproductive characteristics which together translate into a fairly distinct ecological grouping. This coincides with Grime's (1979) definition of **strategies**, although finer variations of strategy can be discerned within the broad categories of growth form applied here. The three-way categorisation of strategies proposed by Grime (1979) is not very useful in savannas, since most of the species tend to be stress-tolerant competitors. A comparison of the "grass" and "woody plant" growth forms is presented in Table 1.1.

Trees (>3m tall, few stems) and shrubs (<3m tall, multi-stemmed) are functionally equivalent unless the effects of fire and browsing are restricted to a certain height range. In this study "trees" will be used as shorthand for "woody plants".

A third growth form, **forbs** (the non-graminoid component of the herbaceous layer) may periodically be conspicuous in savannas and are mostly cryptophytes. They are particularly prevalent following episodes of drought and heavy herbivory and may constitute an important component of ungulate diets at certain times of the year (Owen-Smith 1982).

Table 1.1 A comparison of key features of the "grass" and "woody plant" growth forms in semi-arid savannas.

Feature	"Grasses"	"Woody plants"
Taxonomic group	Poaceae & Cyperaceae	Various Dicotyledonae
Raunkiaer's life form	Therophytes & hemicrypyophytes	Phanerophytes
Typical height	<1m	1-6m
Typical canopy spread	<1m	1-10m
Lifespan	Annual to shortlived	Longlived
Photosynthetic pathway	Mostly C4	C3
Reproductive strategy	Vegetative and sexual with a single large investment per ramet. investment per ramet.	Largely sexual, with repeated small investments.
Response to herbivory	Regrows. Meristem protected by position.	Chemical & structural deterrents.
Response to fire	Little mortality.	Mortality of young plants.

Structure refers to the distribution of the various growth form components in space, within a given plant community. Vertical space is subdivided into strata or layers, and horizontal space is expressed as percentage cover per stratum. A savanna has a relatively continuous herbaceous layer consisting mostly of grasses, with a discontinuous woody plant layer above. The latter may be subdivided into a shrub and a tree layer, or alternatively a regenerative and a mature plant layer. The proportion of trees to grass varies widely within savannas, which intergrade continuously with grasslands on the one hand and woodlands on the other. Structural classifications erect arbitrary criteria to delineate these formations (Pratt, Greenway & Gwynne 1966) and may discard the term savanna entirely. No precise functional boundary exists.

1.2.2 DETERMINANTS OF SAVANNA STRUCTURE

The first comprehensive treatment of savanna ecology was by Walter (1939,1971), and the first research synthesis was by Bourliere & Hadley (1970). The determinants of savanna structure and function are extensively discussed in four recent texts: Huntley & Walker (1982), Bourliere (1983), Sarmiento (1984) and Tothill & Mott (1985). A succinct summary is provided by Frost *et al* (1986).

The current consensus, as drawn from the above references by Frost *et al* (1986), is that there are four determinants of savanna structure and function. Soil moisture regime and nutrient status are ranked as "primary" determinants because they tend to constrain the modifying influence of the "secondary" determinants, fire and herbivory, whose effect can nevertheless be profound. In a practical sense only the secondary determinants are amenable to management, although management actions can lead to changes in the primary determinants as well. It is believed that if the influence of fire and herbivory is removed, the savanna structure will tend towards a unique basic structure determined by moisture and nutrient availability. Thus a savanna maintained in a grassy condition by repeated fires may be referred to as a fire sub-climax grassland. Should the structure not respond to an alteration in one of the determinants it is inferred that a threshold has been crossed to a system governed by a different set of determinants. A proposed example of this (Walker *et al* 1981) is when heavy grazing results in a dense, low-statured woody vegetation known as a thicket, which effectively excludes grass, grazers and fire.

In addition to influencing savanna structure *via* primary and especially secondary determinants, man can also alter savanna structure directly, by land clearing and wood collecting. Grasslands created from savannas in this way are known as "anthropogenic". The history of man in Africa is so long that his influence cannot in many cases be termed unnatural.

The four determinants tend to be mutually correlated and interactive. For instance, low soil moisture is often associated with high nutrient status; however, nutrients are unavailable in the absence of water. Therefore the outcome of these four factors is only deterministic at a broad scale. The intensities of the four determinants vary independently (and usually unpredictably) over time. Structure at a given site may therefore be determined by the coincidence of two or more individually rare (episodic) events at some time in the past. Dynamics of this type are more appropriately viewed as probability distributions than as strictly deterministic events.

The discussion of the effects of the individual determinants which follows concentrates on a single structural parameter: the woody plant biomass. Use of the woody : grass ratio (Walker *et al* 1981) is conceptually attractive, since it reduces the number of variables under consideration and removes the distortion due to the increase in biomass of all components with increasing rainfall, but in practice is difficult to apply due to the enormous seasonal variability of grass biomass. Furthermore, the strong asymmetry in competition between mature trees and grass, implied by Knoop & Walker (1984) and quantified in this study, means that grass biomass is strongly dependent on woody biomass, but not *vice versa*, which reduces the utility of the index. Most field workers express the degree of woodiness in terms of tree density, basal area or canopy cover. These are rough and site-specific indices of the woody-plant green leaf biomass. Since leaf biomass controls transpiration, photosynthesis, interception of light and rainfall and litterfall, it is probably the best single parameter to express the functional effect of woody plants in savannas.

Persistence of savannas as a structural formation suggests that some process of equilibrium operates and that for a given set of ecological circumstances an expected degree of woodiness exists. The woodiness of savannas is variable, both in space and time. Some broad trends are discernable and are indicated in Figure 1 on page 7 .

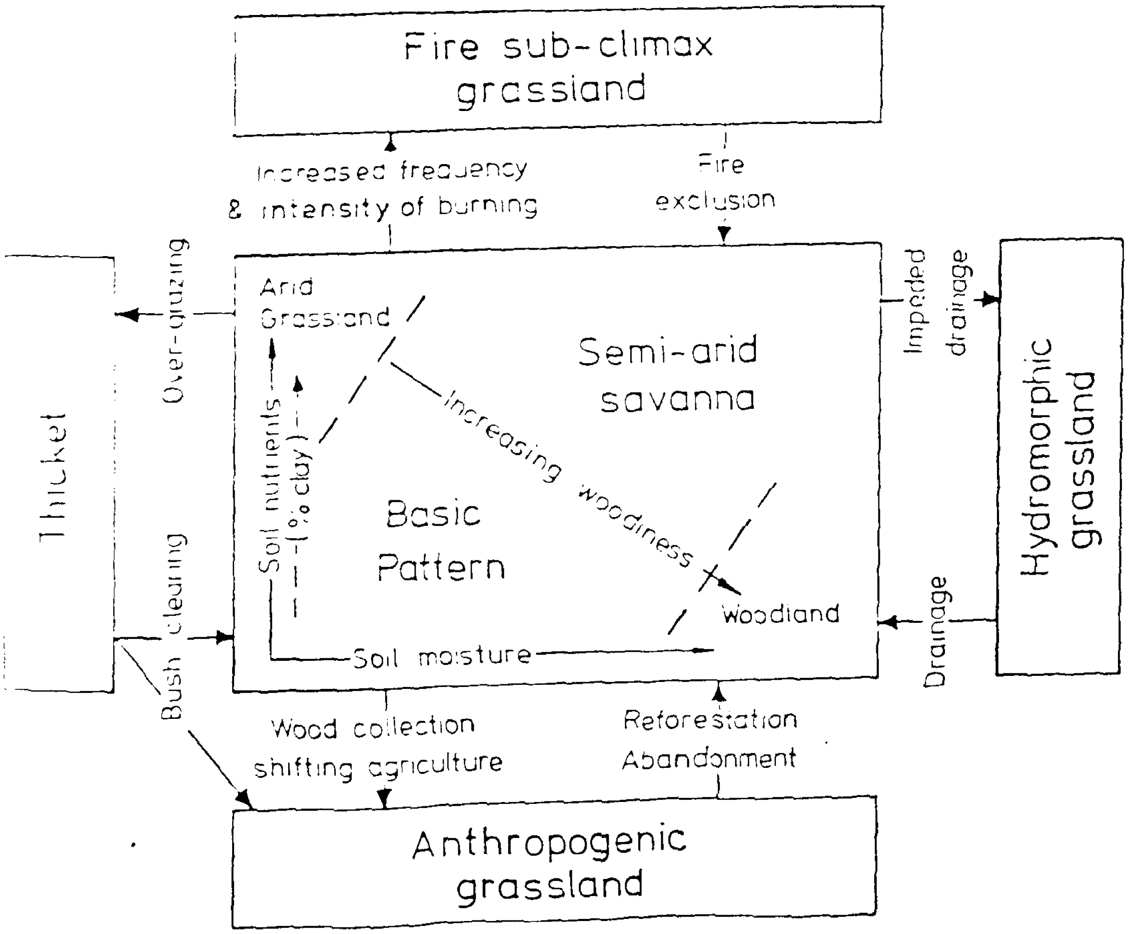

Figure 1. Structural trends in semi-arid savannas: basic pattern follows Walker (1985).

1.2.2.1 Soil moisture regime

There is a tendency to higher biomasses of both trees and grass with increasing soil moisture availability (Walter 1971). This trend is stronger in the woody plants than in the grasses, possibly due to the simultaneous shading of the grasses by trees. The result is *increasing dominance* by trees with increasing moisture. Soil moisture status is determined by precipitation and is modified by soil texture and topographic position.

Rainfall is highly variable at all spatial and temporal scales, and this variability increases disproportionately as mean annual rainfall decreases (Green 1969b).

The finer-textured ("heavier") soils, i.e those with higher proportions of clay- and silt-sized particles, have a higher water holding capacity but a lower hydraulic conductivity than those dominated by sand-sized particles. Thus a given amount of rainfall penetrates more deeply on coarse- than on fine-textured soils. Walter (1971) suggests that the ability of relatively deep-rooted trees to utilise water from the subsoil means that the woody-plant biomass on sandy soils is higher than on clayey soils receiving the same rainfall.

The deeper penetration and shallower capillary fringe on coarse-textured soils conserves moisture by protecting it from evaporation. Furthermore, almost all the soil water is available to plants, while on finer-textured soils a considerable proportion is held at tensions exceeding the plant wilting point, but nevertheless still susceptible to evaporation. Therefore evaporation from the soil surface is higher on clayey soils than on sandy. Runoff loss is also higher on clays. In the semi-arid rainfall range deep leaching losses on sands are insignificant. The net result of these factors is that in the semi-arid rainfall range sites with a high clay content are more xeric than sandier sites receiving the same amount of rain. This accounts for the extension of savannas into lower rainfall areas on sandy than on clayey soils, and the upper rainfall threshold of semi-arid savannas being higher on clays (Walker 1985, Figure 1 on page 7). The geographical distributions of savanna woody plant species also extend into drier areas when on sandy substrates (Huntley 1982).

At the low end of the semi-arid rainfall range clay sites produce less grass annually than sandy sites since they have less available water. At higher rainfalls, however, the superior nutrient status which tends to be associated with clays permits greater grass production per unit moisture transpired, resulting in greater grass production than on sands. Under the fluctuating rainfall regime typical of semi-arid savannas clay sites have in general a higher but more variable annual production of grass (Dye & Spear 1982, O'Connor 1985).

At rainfall levels above the semi-arid limit clay sites are moister than sandy sites during the rainy season due to their poor drainage. Shallow or otherwise impermeable soils may experience seasonal waterlogging and be devoid of trees. Such hydromorphic grasslands are excluded from the savanna definition applied here.

Ridge crests tend to have shallow sandy soil and bottomlands to have clayey, deep soils due to the process of illuviation at a landscape level, as discussed in more detail in chapter 2. Bottomlands are therefore intrinsically more xeric, but may receive extra water inputs in the form of runon and subsurface lateral flow from upslope.

Vertisols, (soils with more than about 35% 2:1 clays, usually smectite or illite) may support a lower tree biomass than an equivalently clayey soil dominated by 1:1 clays (usually kaolinite) and probably do not fit easily into the four-determinant system. It is suggested that the repeated shrinkage and swelling on these "cracking clays" under seasonal rainfall is injurious to tree roots, but less so to grasses due to their higher rate of root turnover.

1.2.2.2 Soil nutrient status

Plant production on eutrophic soils is higher than that on dystrophic soils with the same moisture availability. However, eutrophic savannas tend to have a lower standing crop of grass and fewer trees than a dystrophic savanna receiving equal rainfall (Bell 1982). The mechanism for this phenomenon probably operates through the higher herbivory levels and more frequent and intense fires on the former. The effect of nutrient status is also difficult to separate from that of moisture regime, since both are strongly influenced by the clay content of the soil and landscape position.

The nutrient status of a soil refers to the flux rate of nutrients to the plants relative to their growth requirements. It is determined both by the size of the nutrient pool and its rate of turnover, as well as the numerous factors relating to plant demand and ionic movement in soils. The pool size is ultimately determined by the mineral content of the parent material and the rate and duration of the pedogenic processes which have operated on it. The ability of the soil to retain nutrients against leaching (its ion exchange capacity) is determined by its clay type, clay content and organic matter content, the last two being highly correlated. Therefore, soils on old surfaces (such as the African shield), derived from acidic parent materials such as granites, quartzites and sediments have low-activity clays and tend to be dystrophic, whereas those on actively eroding surfaces (such as major river valleys), derived from basic igneous rocks (such as basalts) have high-activity clays and tend to be eutrophic Huntley (1982). Bottomland soils are enriched by nutrients leached from the ridgetops, and have more high-activity clays. Since plant production and consumption on the eutrophic soils is high, the rate of turnover of organically bound nutrients is also high.

1.2.2.3 Herbivory

Herbivory and fire both act to reduce plant biomass, and are important tools for the modification of savanna structure since they can be managed relatively easily. South and East African savannas support unusually high levels of mammalian herbivory, both of grazers and browsers. Grasses are tolerant of moderate levels of herbivory, which may even stimulate their growth (McNaughton 1983). At low levels of herbivory the vigour of grass growth is reduced by the shading of new growth by the accumulation of moribund material. At high levels of herbivory, the plant cannot replace the lost tissue as fast as it is removed, plant reserves are depleted, and mortality may result. More frequently, the vigour of the palatable grasses is reduced, allowing less palatable grasses to dominate the sward and woody plant seedlings to become established. This phenomenon is known as bush encroachment, and has been held responsible for the declining productivity of much grazing land (West 1947, Walter 1964, Scott 1966, Pienaar 1980). The encroached land may not return to its original state once grazing is removed. An episode of heavy grazing can therefore trigger an increase in woody plant density and biomass. A history of light grazing may be associated with a low woody biomass and density because the accumulation of grass allows frequent and intense fires. The factors involved in bush encroachment are discussed in detail later in this chapter.

Browsers are seldom responsible for the outright death of woody plants, with the exception of elephants uprooting non-coppicing trees. They act to distort the physiognomy and retard the growth rate, thereby keeping the tree within the height range of susceptibility to fires and future browsing (Pellew 1983). Fires similarly cause little mortality amongst mature savanna trees (Frost 1985a), but can kill saplings and keep small trees in an acceptable form for browsers. Woody plants have evolved an array of defences against burning and herbivory, which bespeaks a long history of exposure to both. Acting in concert however, fire and browsing can exert a significant influence on woody plant demography (Ward & Cleghorn 1970, Trollope 1982b) by controlling the rate of recruitment and growth of saplings. A reduction in browser biomass may therefore be a contributory factor to an increase in woody density. An increase in browsing is unlikely to result in a change in woody density in the short term, unless it could be sustained for long enough to influence recruitment rates. The biomass of pure browsers is however usually low relative to grazers due to the seasonally low biomass of woody plant leaf tissue in strongly deciduous savannas.

Elephants may temporarily achieve very high browsing rates, since when the browse resource is exhausted, they can switch to eating grass, or migrate to a new area. The effect of elephant feeding on savanna structure can be dramatic, but in many cases results in an increased woody density rather than a decrease. This is because many savanna trees have the ability to coppice from the base when the above-ground organs are damaged. This feature makes bush clearing by the mechanical means popular elsewhere in the world (bulldozers, chaining and bush-breaking) generally unsatisfactory in Africa (Pratt 1966a). The result of both is commonly a dense, low-growing, multi-stemmed thicket. Caughley(1976) has suggested that the elephant-woodland system may constitute a stable limit cycle with a period of about two hundred years. Unless the elephant population densities are locally very high, however, the impact of their feeding on savanna structure is small.

1.2.2.4 Fire

Fires may be initiated by lightning or by the activities of man. The evidence of plant adaptation suggests that the history of fire in Africa is ancient. The biggest changes in the burning regime probably occurred following the colonial period, when fire control became part of land-management policy. During the last half century official attitudes towards deliberate burning of savannas has swung from encouragement to complete prohibition and back to planned burning. The fire regime has three main components: frequency, intensity and season. The type of fire (with or against the wind, crown or ground fire) also has some bearing on the effects of the burn.

Fires cause little immediate grass mortality. The repeated reduction in grass biomass can result in a loss of grass vigour and ultimately mortality if it occurs at a frequency or season which does not allow the plant reserves to be fully replaced.

Fires generally act less by reducing tree density than by preventing recruitment and reducing tree biomass. Although the mortality of mature, undamaged savanna trees is low, a hot fire will kill young trees which have not yet elevated their buds above the flame zone (Frost 1985). The action of successive burns on scars caused by porcupine feeding is a major cause of mortality in large trees in the savanna at Nylsvley (Yeaton & Frost, in press).

The principal determinant of fire intensity is the fuel load available in the herbaceous layer, which is in turn controlled by rainfall, soil fertility, the degree of herbivory and competition by woody plants. Under high rainfall and high fertility conditions the exclusion of fire due to high herbivory or fire protection can result in succession to a woodier state. The influence of fire as a structural determinant declines with increasing aridity. Frequent burning at an intensity too low to retard tree growth, or at an inappropriate season, could lead to increased tree density due to the weakening of the grass sward.

1.2.3 FACTORS CONTROLLING BUSH ENCROACHMENT

Declining range productivity in savannas is often attributed to an increase in woody plant density or biomass (Staples 1945a&b, West 1947, Walter 1964, van der Schijff 1964, Scott 1966), based on photographic, plant demographic and (most frequently) anecdotal evidence. Millions of hectares of African savannas have been reported to be seriously encroached by woody plants, and millions more are susceptible to encroachment (Pienaar 1980). The causal factors are thought to be those illustrated in Figure 2 on page 14. An increase in grazing intensity beyond the point where it can be sustained by increased grass production leads to a decrease in the grass standing crop. The spaces created in the sward allow the establishment of woody plant seedlings which otherwise would have been excluded by competition for light, water and nutrients. The reduced fuel load reduces the frequency and intensity of fires, often abetted by deliberate fire exclusion, permitting the saplings to survive and grow to a stage where they are no longer fire-susceptible. The increased woody biomass further suppresses grass growth, and unless the stocking rate is radically reduced, this feedback effect will accelerate further encroachment. Eventually the productive capacity of the sward is reduced to a level where grazing becomes uneconomical, or the density of the thicket inhibits stock management.

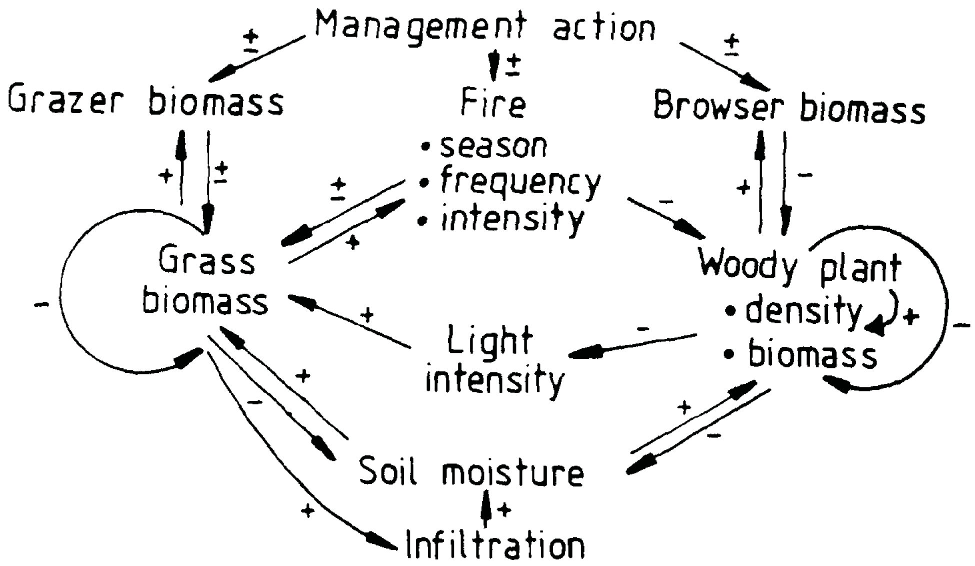

Figure 2. Causes of bush encroachment: positive arrows represent an amplifying interaction, negative arrows a diminishing interaction. For details, see the text.

Heavy grazing by domestic stock is frequently accompanied by a reduction in indigenous browsers (through hunting or veterinary control), which further encourages the growth of woody plants. The initial over-grazing episode may occur due to lack of timely stock reduction during a drought. An age class analysis of encroaching plants in Australia (Harrington & Hodgkinson 1986) indicates that encroachment is a sporadic rather than continuous process. Similarly, the opportunities for controlling bush encroachment by the manipulation of burning and grazing regimes may also be episodic.

Bush encroachment can alter the primary determinants of savanna structure as well. Replacement of the grass canopy by a tree canopy can result in capping of the soil, increased runoff and evaporation and therefore drier surface soil layers (Dyer 1983). Dyer suggests a downward shift in soil nutrients under encroached conditions, which would further favour trees.

In moist savannas a reduction in burning frequency alone is sufficient to cause bush encroachment (Trapnell 1959).

1.2.4 GRASSLANDS UNDER A SAVANNA CLIMATE

The result of total tree and shrub removal from a savanna is the creation of a grassland which usually tends back towards a partially wooded state if permitted to do so. It is therefore instructive to examine the conditions under which stable natural grasslands can be found within the bounds of the savanna region. As Whyte (1960) points out, grasslands in the tropics are confined to specific environments. Michelmore (1939) identified the following circumstances under which grasslands occur in Africa.

1. **Hydromorphic grasslands**. Situations which experience alternating extremes of saturation and drying (due to a combination of topographical position and the impedance of drainage) are inimical to the growth of trees, and are dominated by grasses and sedges (Cyperaceae) specifically adapted to this habitat. They are susceptible to invasion by woody plants if the waterlogging condition is altered by drainage or drought.

2. **Edaphic grasslands**. Soils with a high proportion of smectites (swelling clays) or toxic minerals are likewise deleterious to tree growth, which may be stunted or absent.

3. **Fire-subclimax grasslands**. Where the rainfall is high and grazing light enough to allow frequent intense fires, trees may be very sparse.

4. **Anthropogenic grasslands**. Where wood use by human inhabitants is consistently high an anthropogenic grassland may result.

Tropical montane and desert grasslands are outside the climatic scope of the savanna definition applied in this study. It is therefore suggested that a single removal of woody vegetation can only result in a self-maintaining grassland if the necessary conditions for a hydromorphic or fire sub-climax grassland are met.

1.3 THE INFLUENCE OF WOODY PLANTS ON SAVANNA FUNCTION

It is appropriate to discuss the possible consequences of removal of woody plants in the context of their influence on savanna function. The pathways by which they influence the primary determinants of savanna structure and function are illustrated in Figure 3 on page 17. They are functionally different to grasses in the following broad respects.

1.3.1 HYDROLOGY

Interception, infiltration, runoff and erosion. Interception by tree canopies alters both the amount of rainfall reaching the ground (due to interception losses) and its kinetic energy. These factors interact with site and soil characteristics to determine the infiltration rate and therefore the amount of runoff. The raindrop energy, runoff and site characteristics in combination determine the soil erosion rate and the degree of clay cap formation, which in turn feeds back on the infiltration rate (Morgan 1979). Interception by the grass canopy has similar effects, but at a much smaller scale.

The complexity of the interactions involved means that tree removal could have opposite hydrological consequences on different sites or at different times. In general interception losses can be expected to increase slightly, while runoff, erosion and capping decrease provided a dense

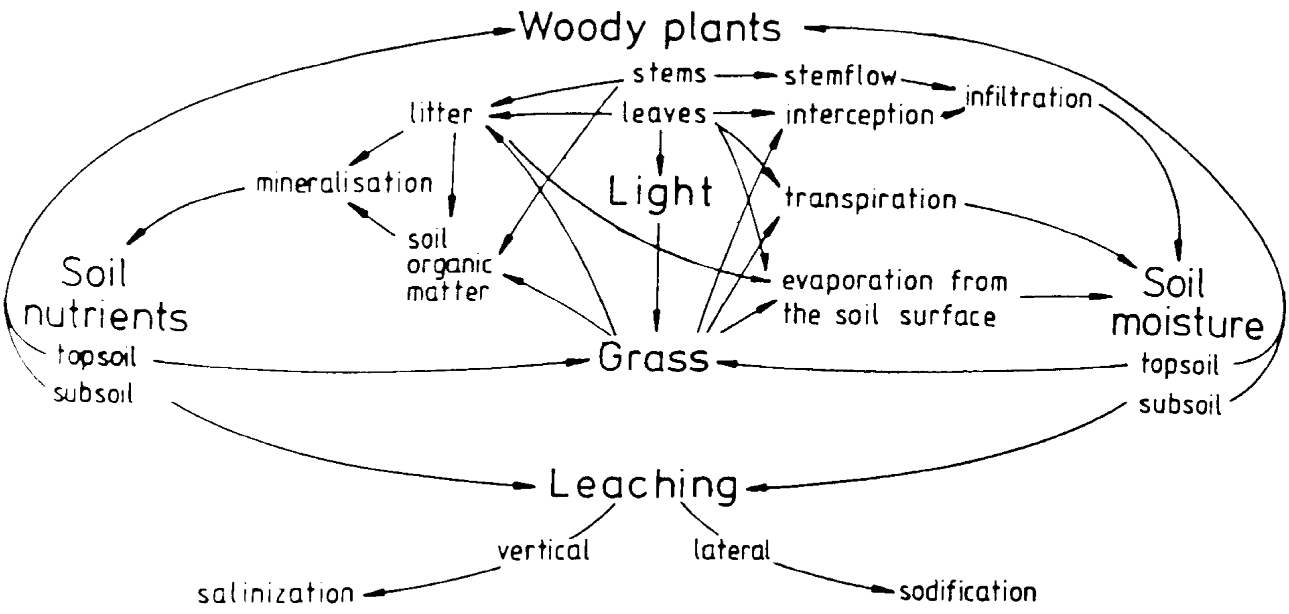

Figure 3. Interactions of woody plants with soil moisture and nutrients

grass cover is maintained. If the grass cover is reduced by heavy herbivory or clearing disturbance however, exactly the opposite trends can occur, especially on clayey soils (Gifford 1973, 1975).

Stemflow. Intercepted rainfall is partitioned into canopy stored water (which evaporates to cause interception losses), throughfall and stemflow. Throughfall and stemflow are nutrient enriched due to the dust and leachates which they collect on the canopy. The sub-canopy habitat receives less moisture overall than the inter-canopy habitat, due to tree interception losses, but in the immediate vicinity of the stem may be considerably moister due to the stemflow contribution (Pressland 1973, de Villiers 1982). Infiltration rates beneath the canopy may be higher than between canopies (Kennard & Walker 1973, Kelly & Walker 1976) and therefore runoff losses lower. Shading by the canopy alters both the grass transpiration rate and the evaporation rate from the soil. The sub-canopy habitat may therefore have a more, or less, favourable