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Scholes, Robert John

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

Robert John Scholes

A thesis submitted to the
Faculty of Science
University of the Witwatersrand, Johannesburg
for the
Degree of Doctor of Philosophy

October 1987

ABSTRACT

Scholes, R.J., 1987 **Response of three semi-arid savannas on contrasting soils to the removal of the woody component** Ph.D. thesis, University of the Witwatersrand, Johannesburg.

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 clea ing 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

This study was initiated and sponsored by Dr. H. F. Oppenheimer, to whom I am deeply indebted. The ongoing interest of Tony Lea and Hank Slack is much appreciated. I am grateful for the supervision provided by Dr. Brian Walker and Dr. Mike Mentis.

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.

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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

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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.

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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 .

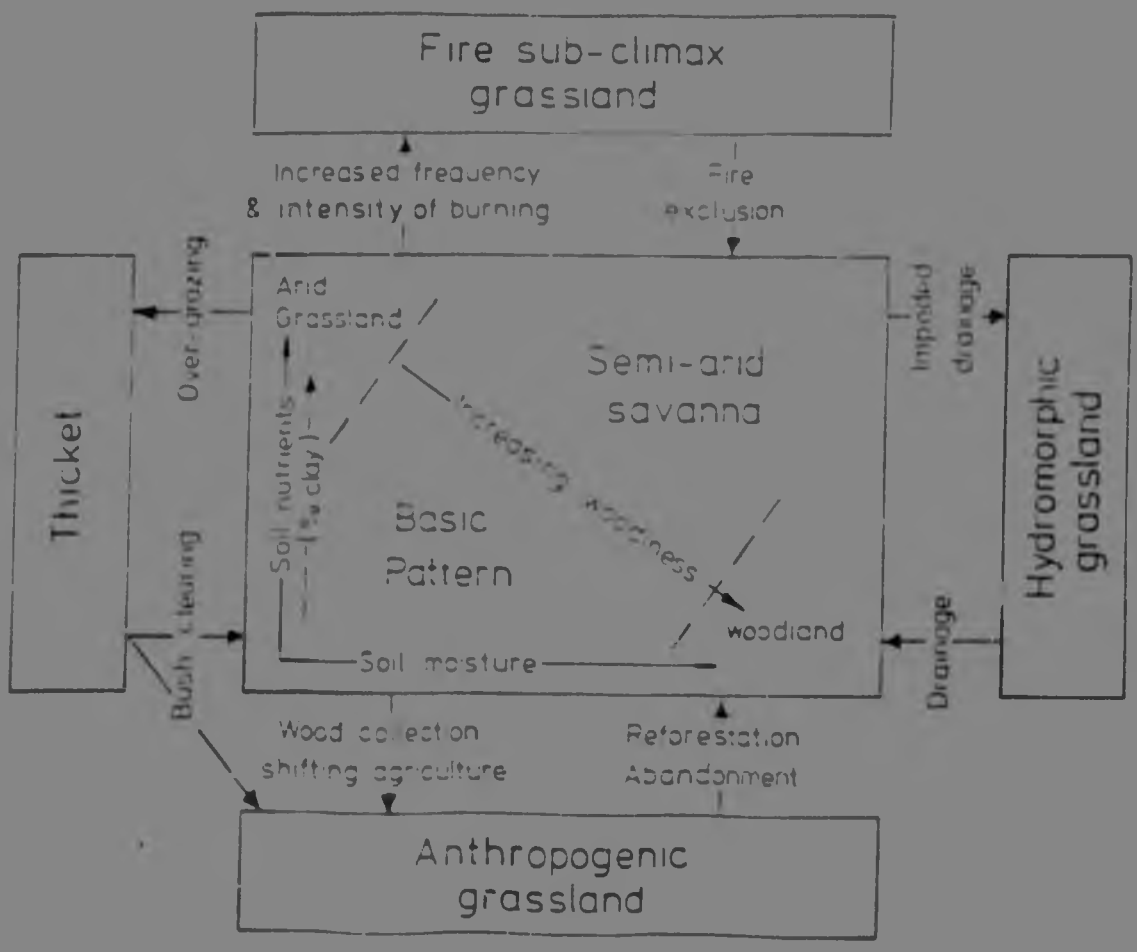

Figure 1. Structural trends in semi-arid savannas: basic pattern follows Walker (1985).

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 soil. 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 [illegible]its 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.

1.3 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

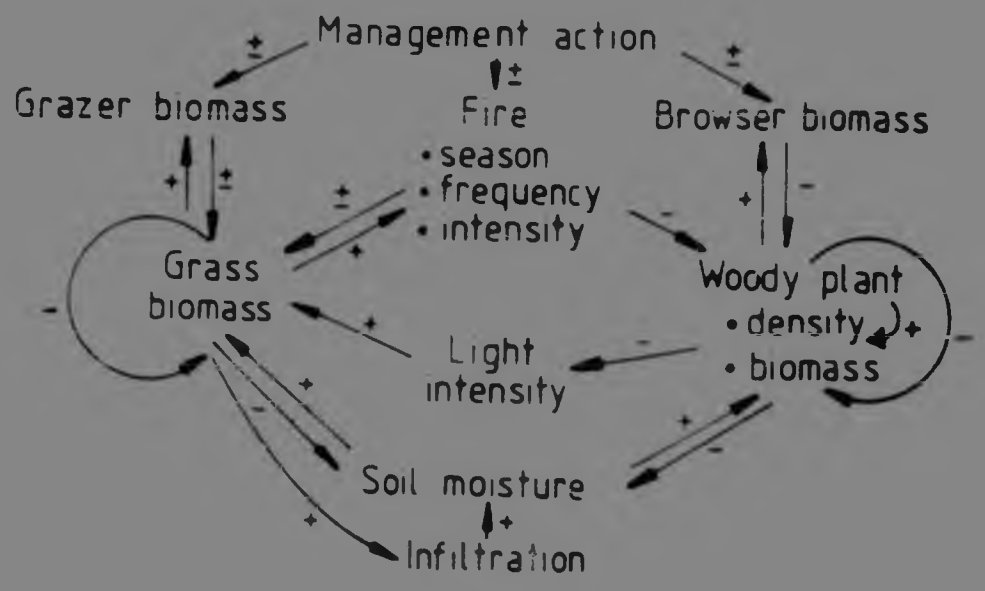

Figure 2. Causes of bush encroachment: positive arrows represent an amplifying interaction, negative arrows a diminishing interaction. For details, see the text.

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

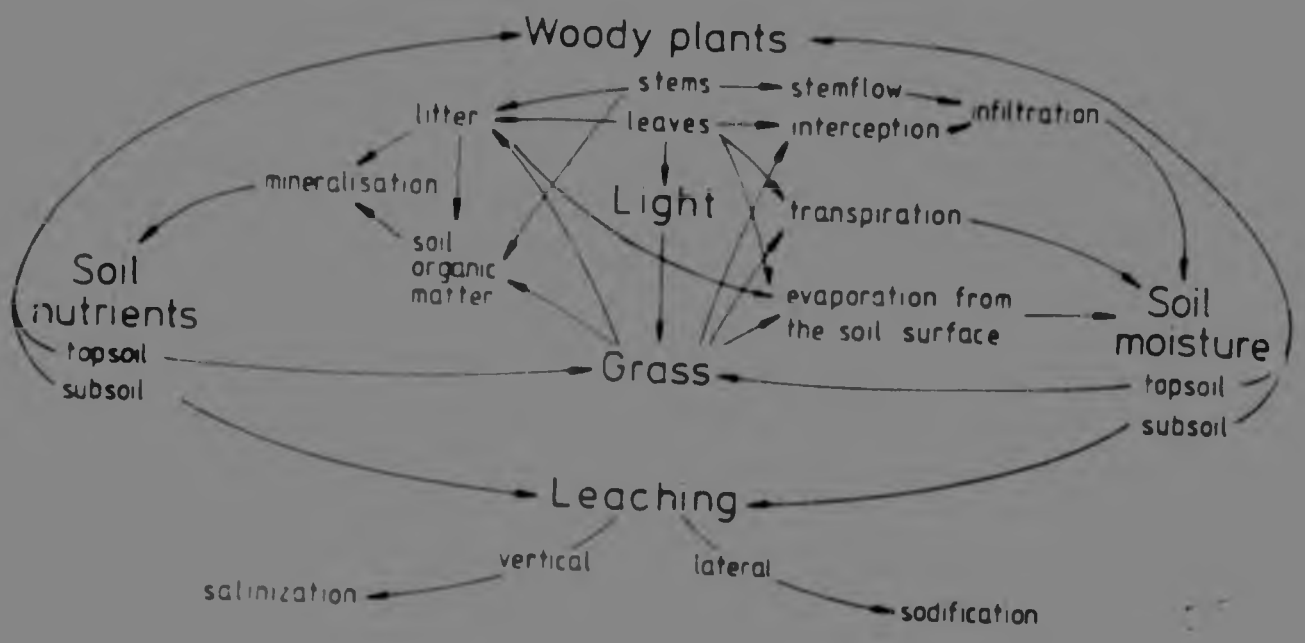

Figure 3. Interactions of woody plants with soil moisture and nutrients

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

moisture regime relative to the inter-canopy habitat, depending on the net result of all these interactions.

Transpiration. Transpiration by woody plants is a major component of the water balance in semi-arid savannas (Bate, Furniss & Pendle 1982). The immediate consequence of tree removal is therefore an increase in soil moisture, which stimulates an increase in grass production. In the longer term, transpiration by the increased grass biomass reduces the soil moisture content again except in the deepest soil levels where they have few roots. Soil moisture contents under an induced grassland may in the long term be lower than under the savanna from which it was derived (Strang 1969a). Deep drainage losses may increase where the grasses are shallow-rooted. Losses due to evaporation from the soil surface will decrease provided that a complete grass cover is maintained, but will increase if the soil is exposed.

1.3.2 PRIMARY PRODUCTION

Photosynthetic pathway. Woody plants have a C3 photosynthetic pathway and therefore under the warm, high light-intensity savanna conditions would be expected to have lower instantaneous photosynthetic rates than C4 grasses.

Transpiration pattern. Woody plants, due to their larger tissue water capacity, more sclerophyllous leaves and access to moisture in deep soil layers are likely to have a more conservative water use strategy than grasses do. In other words, their maximum transpiration rates are expected to be lower but sustained for longer into the drying cycle.

The differences in photosynthetic pathway and transpiration pattern will lead to differences in water use efficiency (WUE, $gH_2O.gCO_2^{-1}$) between trees and grasses. Which growth form will have the higher WUE depends on the specific environment in which they are grown; under savanna conditions C4 plants would be expected to have the advantage.

Total primary productivity could therefore decline or increase following tree removal, depending on environmental circumstances, species involved and clearing practices. Grass production increases unless the process of tree removal has also disturbed the herbaceous layer or altered its composition in favour of less productive (i.e. less efficient) species (Dye & Spear 1982).

Above-ground primary production in semi-arid savannas is in the region of 3000 kg.ha^{-1}yr^{-1}, with woody plants contributing about two-thirds of this (Rutherford 1978). Over half of the woody-plant production is leaf and current stem material, while the rest is woody tissue increment. These estimates are based on a very small data set, and the actual range is likely to be high. Considerably more data are available for the herbaceous layer alone, where annual aboveground production is in the range of 100-3000 kg.ha^{-1}. The range of primary production in savannas is largely a function of the available moisture and nutrients rather than mean annual rainfall *per se*, since the efficiency of conversion of rainfall into production is influenced by soil type (Rutherford 1980) as well as the seasonal distribution of rainfall. The proportion contributed by woody plants is a function of the savanna structure.

1.3.3 SECONDARY PRODUCTION

Forage availability and quality Woody plant tissues differ in availability and quality from grass tissues, and are consumed by a different spectrum of herbivores. The crude protein content of tree leaves is higher than that of grass and is fairly constant throughout the season, but may be rendered unavailable by the presence of digestion-inhibiting compounds. The total fibre is lower, but the proportion of indigestible fractions (lignin and cellulose) to digestible fractions (hemicellulose) is higher. Overall digestibility is consequently lower (Owen-Smith 1982).

Fodder availability is a function of its distribution in space and time. Browse is less available than grass since it is sparsely distributed over a range of height classes. The rate of energy acquisition by browsers may become critically low during the late dry season in deciduous savannas. Grazers are more likely to be faced with a protein scarcity during this period due to the decline in grass protein content with age (Barnes 1979). Even when woody plant biomass is high, the proportion of browsers to grazers in savannas tends to be low, and the proportion of browse to grass in the diet of mixed feeders is similarly low (Cooper 1984).

Food reserves Despite the high intraseasonal fluctuations in browse availability, it is more stable interseasonally than grass, since tree leaf production is less directly linked to rainfall in the current season than is grass production (Knoop 1982; unpublished litterfall data from Nylsvley). The tree leaf flush frequently precedes the first rains of the season. During periods of stress browse provides a reserve food source for grazers. Fallen flowers, fruits and leaves form an important dietary component of many non-browsing species.

1.3.4 NUTRIENT CYCLING

Nutrient pools Trees tend to have at least a few deep roots, and therefore have access to nutrients beyond the rooting range of grasses (Walter 1971). Complete tree removal would therefore reduce the nutrient pool available to the ecosystem, and nutrient losses would be increased because more leachate would pass below the rooting depth.

Nutrient concentrations The horizontal root extent of trees is usually several times the crown radius (Rutherford 1982). Nutrients are gathered over a large area, but are recycled by leaching and leaf fall mainly in the vicinity of the crown. The resultant mosaic of nutrient depleted sites between canopies and nutrient enriched sites below canopies is

particularly pronounced on dystrophic soils. In combination with hydrological and microclimatic changes in the canopy vicinity it creates a distinct sub-canopy habitat, which typically supports a different suite of herbaceous species to those growing between canopies. In particular, the productive and preferred species *Panicum maximum* is almost exclusively found in this habitat, despite its ability to grow elsewhere (Bosch & van Wyk 1970, Kennard and Walker 1973).

The sub-canopy habitat is gradually lost after tree removal (Brock, Haas & Shaver 1978, Barnes 1979, Dye & Spear 1982), resulting in a loss of spatial heterogeneity (patchiness) in the sward. The sward nutritional quality declines as a consequence of the disappearance of the palatable sub-canopy species. This quality decline counteracts the increase in forage quantity, and may be responsible for the disappointing increases in secondary production despite large increases in primary production (Louw & van der Merwe 1973, Harrington 1973b, Teague 1973, Pratchett 1978).

Nutrient turnover Leaf turnover in grasses occurs several times per season (Dankwerts *et al* 1984) but in savannas woody plants usually drop their leaves only once a year. Input into the litter layer by grasses is therefore fairly continuous but is concentrated into an annual peak for deciduous trees

Grass leaves and roots are more rapidly decomposed than tree leaves, and much more rapidly than lignified tissues (Bezuidenhout 1980). This has largely unknown implications for the dynamics of soil micro-organisms and organic matter

The nutrient pool bound in living and dead woody tissues may represent a significant portion of the total system nutrients on highly leached soils, and is protected from leaching itself The combination of high turnover low reserves and rapid decomposition makes nutrient cycling through grasses much faster than through trees, but also more labile (Frost 1985b). Clearing could result in an overall decline in system nutrient status if the woody tissues are harvested.

1.3.5 MICROCLIMATE

The microclimatic consequences of tree removal are an increase in radiant energy at the level of the herbaceous layer, an increase in wind run and a widening of temperature extremes. These have direct consequences on plant productivity and mammal thermoregulation (Gifford 1973, Pratchett 1978). Macroclimatic changes are unlikely provided the scale of clearing remains small.

1.3.6 HABITAT

Woody plants provide cover and breeding requirements for a wide range of animal species. The abundance of these species can be expected to decrease following bush clearing, whil the abundance of species with a preference for open areas will increase. For example, many antelope species (including impala, kudu and giraffe) leave their newly-born offspring concealed under bushes for long periods during the day, while in others (such as wildebeest) the young are born sufficiently mobile to escape predation by flight. The former group would suffer increased calf mortality following bush clearing, but not the latter. Similarly tree-nesting and fruit-eating birds would be disadvantaged relative to ground-nesting seed-eating species.

1.4 COMPETITION AND COEXISTENCE IN SAVANNAS

1.4.1 THE DETERMINANTS OF COMMUNITY STRUCTURE

Coexistence is often implicitly regarded as the absence of competition, much as health is regarded as the absence of disease (Aarsen 1983). This is not necessarily true, since competitition is an instantaneous interaction between two organisms, while coexistence is the long-term resultant of a large number of interactions (including competition) operating with varying strengths on the different life stages of the great number of organisms comprising two populations. Much of the controversy regarding the role of competition in determining community structure has arisen due to a failure to differentiate between its long-term evolutionary consequences (measured by fitness at a population level) and its shorter-term ecological consequences (measured by the density, biomass and productivity of the competitors). Although the two are linked, they operate at different time scales. This study is concerned only with the ecological time scale, that is, of the same order as the lifespans of the organisms involved.

The role of competition in structuring communities has been the focus of intense debate for several decades, as is illustrated by the extensive literature on the subject. The evidence is reviewed by Schoener (1983) and Connell (1983). There are two opposed schools of thought and a spectrum of intermediate positions.

The **equilibrium** school has its origins in the succession and climax concepts developed early in the century, and the mathematical models of competition developed by Lotka (1925) and Volterra (1926). Community structure is considered to be determined by internal biotic interactions, primarily competition and predation. Since Gause (1934) showed that complete competitors could not coexist, coexistence in nature was explained in terms of a competitive balance. Many factors have been suggested as mediators of this balance, including an unstable environment,

predation, bal- ed competitive abilities, resource partitioning (niche differentiation) and a balance of intra- and interspecific competition. If the system is moved a small distance from its equilibrium state, it will tend back to that state This view is exemplified for savannas by the hypothesis presented by Walter (1971).

His proposal (Figure 4 on page 25) was that trees required a relatively continuous water supply, which was obtainable only from deep soil layers. They also have roots in the topsoil, but are outcompeted there by grasses, whose roots are restricted to the topsoil. The competitive balance is therefore determined by the frequency with which water penetrates to the subsoil, thus explaining the greater woodiness under wetter climates and on sandy soils. The "Walter hypothesis" was the first explicit statement of the determinants of savanna structure and has formed the basis of most models of savanna dynamics (Walker *et al* 1981, McMurtrie & Wolf 1983) Walker & Noy-Meir (1982) point out that partial rooting depth separation and superior competitiveness by the grass are sufficient conditions for coexistence.

The opposing viewpoint, the **stochastic school**, holds that abiotic perturbations originating outside the system are more important than internal dynamics in structuring communities, which are therefore non-equilibrium, indeterministic assemblages (Grossman, Moyle & Whittaker 1982).

An example of an intermediate viewpoint is that of Wiens (1977) who considers competition to be an effective force, but only during sporadic periods of resource limitation

Even if resources were constantly limited, the various phases in the life history of an organism would be differently affected by this limitation. Competition may be important during one phase, but ineffe tual during another. The importance of the regenerative phases in particular in determining plant community structure has been pointed out by Grubb (1977).

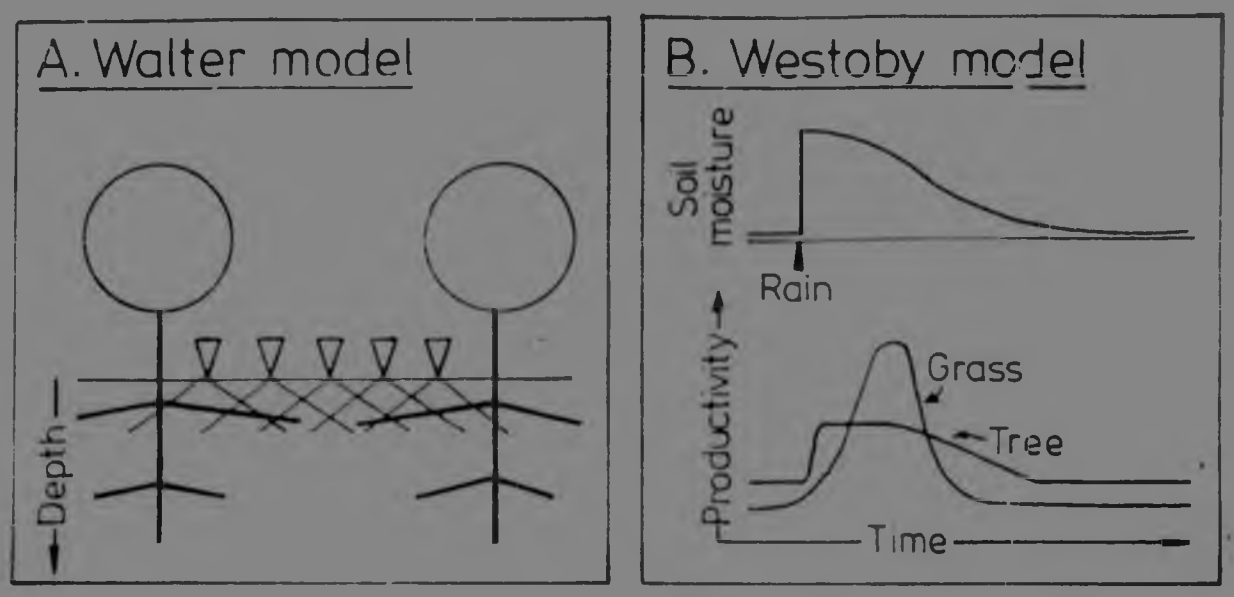

Figure 4. Two models of savanna structure and function: A. The Walter (1971) model is based on niche separation on a spatial axis (rooting depth). B. The Westoby (1980) model depends on separation in time between the different growth forms

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The attributes of the complete life cycle, viewed in the context of the environment in which it is conducted, are termed a strategy (Grime 1979). Westoby (1980) has built on this concept to develop a model of arid rangeland dynamics which depends on the interaction of plant strategies with an unpredictable environment. This approach includes elements of both the stochastic and equilibrium schools and is particularly relevant to semi-arid savannas. There are four main elements to his model:

1. Competition may be strongly asymmetrical, and favours established plants over regenerative phases;

2. The biotic and abiotic components of the system are interdependent;

3. Grazing operates differently on different life-forms;

4. Unpredictable rainfall offers a series of growth opportunities of variable lengths, which the different growth forms are variously equipped to exploit.

The Westoby model therefore relies on the interaction of a variety of plant strategies with an episodic and unpredictable water supply to explain the dynamics of the dominant growth forms found in arid regions. Interpreted in the context of semi-arid savannas (Figure 4 on page 25), this model suggests that trees have an advantage during the initial and final phases of a wetting cycle, at the price of slow growth rates, while grasses can achieve rapid growth, but only during the middle phase of the wet period. Established individuals of either group have an advantage over regenerative stages of the other group which means that changes following a disturbance such as a drought or heavy herbivory may persist after the disturbance has been removed. Irreversible changes can occur as a result of modifications to the soil. The model is as yet untested by field data. Since it is a probabilistic rather than deterministic model, it does not lend itself easily to simulation studies.

In the context of this study, competition is between two broad growth forms, woody plants and grasses, and not between genetically defined individuals. Thus this study is concerned with the coexistence and structure of a functional rather than taxonomic community. The higher genetic diversity within a group of species than within a single species should permit a greater plasticity in the response to competition and altered environments and thus permit coexistence more easily.

1.4.2 CONDITIONS FOR COEXISTENCE

The mechanism most commonly advanced for semi-arid savannas in Africa is niche separation along a rooting-depth axis (Walter 1971). Sarmiento, Goldstein & Meinzer (1985) emphasise a temporal separation of plant

production by phenological adaptations. These two options have also been advanced for explaining coexistence in grasslands (Parrish & Bazzaz 1976, Berendse 1979, Fowler & Antonovics 1981). Both fire and herbivory have been suggested as mediators of a competitive outcome in savannas, and can be viewed as differential predators (Cresswell 1978). Seasonality and fluctuations in resource levels are obvious in savannas and could potentially contribute to the avoidance of competitive exclusion (Ayala 1971).

1.4.3 DETECTION AND MEASUREMENT OF COMPETITION

Connell (1983) regards a change in abundance or resource use by a species following an opposite change in the abundance of a potential competitor to be sufficient field evidence for interspecific competition. The marked increase in grass production which has been universally observed following the removal of woody vegetation from savannas meets this requirement (see Table 1.3 for African experiments; Walker *et al* (1972) and Beale (1973) in Australia, Clary & Jameson (1981) and Hebel *et al* (1983) in North America) The reverse influence, that of grass removal on tree performance was demonstrated by Knoop & Walker (1984) in one case but not in another.

Regularity of distribution of individuals in a population (Pielou 1977), as well as an inverse correlation between plant separation and some measure of individual performance (usually crown diameter or volume) has been regarded as evidence for competition in desert shrubs (Yeaton and Cody 1976) and has been demonstrated for some savanna trees (Smith and Walker, 1983).

1.4.3.1 Limiting factors

The classical theory of plant limitation predicts that plant production should be linearly related to the availability of the single necessary factor in shortest supply and should be insensitive to small changes in the levels of other factors. Biologists have long realised that this is a gross over-simplification, since the availability of one factor commonly influences the assimilation efficiency of other factors. Thus while annual herbaceous production in semi arid savannas is linearly related to annual rainfall (see review in Rutherford 1980), the slope of the relationship varies according to soil nutrient status (Bell 1982). Fertilisation of savannas also leads to increases in herbaceous production. Nitrogen and phosphorus act synergistically to increase production more when applied together than when applied separately (Donaldson, Rootman & Grossman 1984).

Savannas receive very high levels of radiant energy relative to other biomes (Nix 1983), but the position of the tree layer between the herbaceous layer and the light source makes competition for light a potential factor in tree-grass interactions (McMurtrie & Wolf 1982). The canopy of most savannas (unlike woodlands or thickets) is however insufficiently dense to reduce light levels in the herbaceous layer below the light compensation point of C4 grasses. Harrison (in prep) indicates a reduction in irradiance of about 50% in the sub-canopy habitat. Most studies (Grossman 1978, Barnes 1979) show a slightly lower grass production beneath the canopy, but observation of semi-arid savannas, particularly in drought years, will frequently show the reverse. The exclusion of tree roots results in a large increase in grass production (Knoop & Walker 1984), suggesting that competition in savannas mostly occurs below-ground. It is possible that the grass canopy is sufficiently dense to deprive tree seedlings of light and thus prevent their establishment. Light levels and water use efficiency may also interact.

It is therefore difficult to isolate a single limiting factor in semi-arid savannas, despite the clear evidence of competition. In the view of de Wit (1960) it is seldom possible to isolate a single limiting factor, but this does not prevent the analysis of competitive effects. Since moisture is a

prerequisite of nutrient mineralisation, transport, uptake and assimilation, it seems logical to examine water availability as a first approximation to resource limitation in savannas

1.4.3.2 Niche overlap

The degree of niche overlap has frequently been used as an index of interspecific competition, as frequently criticised (Abrams 1980). The criticisms have three main bases.

1. Degree of niche overlap is only equivalent to the competition coefficient (*sensu* Levins 1968) if the resource is limited and if the efficiency with which a unit of the resource is converted to biomass by each of the competitors is taken into account.

2. Presence of an organism in a resource category is not necessarily related to the amount of resource taken. Availability of the resource in the category must also be considered

3. Several different formulae are used to calculate niche overlap, some of which are not appropriate to all circumstances.

Properly applied, it is an index of the relative strengths of inter- and intraspecific competition, and not an absolute measure of the strength of competition *per se*. The degree of niche overlap between trees and grasses in savannas has never been measured except for casual observations regarding the relative depth of rooting and differences in phenology.

1.5 BUSH CLEARING AS A MANAGEMENT TOOL

Although frequently advocated as a technique of savanna management (Donaldson 1969, Ward & Cleghorn 1970, Barnes 1979, 1982), the high cost of extensive bush clearing has restricted its application in Africa. The problem of bush encroachment and the need to increase savanna productivity , coupled with the increasing value of the land and the decreasing relative cost of clearing are likely to make it a more attractive option in the future Many semi arid regions of Africa with a high rural population density are effectively undergoing bush clearing due to the huge demand for fuel wood.

1.5.1 REASONS FOR BUSH CLEARING

The motivations for bush clearing are conveniently treated under three headings, although they are not mutually exclusive.

1.5.1.1 Ecological

Bush encroachment. If it is assumed that a long-term equilibrium value for woody plant density is associated with every combination of climatic and soil conditions and there is evidence that recent disturbance has increased the woody density above this level, then clearing could be used to return the system to equilibrium Equilibrium theory predicts that the woody density should return to its "normal" value of its own accord if the disturbances causing the encroachment are removed; however, the process may have progressed to such a degree that the system is functionally altered, and will not return to the equilibrium mix (Walker & Noy-Meir 1982). In a less extreme case recovery may be possible under

fire and grazing management alone, but may proceed at an unacceptably slow rate due to the longevity of woody plants. Under these circumstances intervention by bush clearing may be justified.

Habitat modification. Selective bush clearing in a homogeneously wooded area will result in a mosaic of cleared and uncleared areas. There are theoretical reasons to expect a diverse habitat to be more resilient in the presence of disturbance and stress than a homogeneous one (Walker *et al* 1981). For this theory to apply to bush clearing, the cleared area must be functionally (and not just visually) different to the uncleared area.

A more diverse landscape should be able to support a more diverse animal community. Certain animal species (eg wildebeest) have a preference for open rather than in densely bushy habitats. This may relate to their feeding requirements or to predator evasion. Since grassland areas are relatively rare in savanna regions, and the tendency is towards increasing woodiness, these plains game may present conservation problems. It may thus be justifiable to create habitats which will enhance their viability

1.5.1.2 Economic

Cattle ranching. The principle economic activity in savanna regions is beef production Cattle make very limited use of browse, so any treatment which increases the production of grass has an economic benefit, which must be balanced against the cost of the treatment. Large increases in herbage production following bush clearing have been reported in numerous studies (see Table 1.3). Those studies which have measured the consequent boost to beef production report a more modest increase (Louw & van der Merwe 1973, Harrington 1973, Teague 1973, Pratchett 1978). No detailed cost benefit analyses of bush clearing have been made for African conditions. The cost analyses alone suggest at best a

marginal economic viability (Donaldson 1978, Scholes 1986) under current economic conditions. The wood yielded by bush clearing may, have economic value in an increasingly fuel and timber starved rural economy.

Recreational use. Where the land use is tourism or hunting it is conceivable that profits may be positively linked to the numbers and visibility of animals, both of which can be increased by bush clearing. The extremely high value placed on recreational land may make bush clearing a more economical method of increasing wildlife numbers and diversity than the acquisition of additional land

1.5.1.3 Aesthetic

A grassland with scattered trees is widely perceived to be aesthetically more desirable than denser, more shrubby vegetation types. Selective bush clearing can achieve such a park-like landscape.

1.5.2 METHODS OF BUSH CLEARING

This study is concerned with the general consequences of removing trees from savannas rather than with the specific disturbances caused by the application of a particular method of clearing. It therefore does not address the question of which methods should be used, except where the method has in itself major ecological consequences. Provided proper precautions are observed against the known hazards, the choice of clearing method is essentially determined by practical and economic rather than ecological factors. Table 1.2 lists a number of trials of bush clearing methods which have been undertaken within the area of reference of this study. Most clearing operations use a combination of methods drawn from the following broad groups.

Table 1.2 Some bush clearing methodological trials conducted in semi-arid savannas of Southern and East Africa.

Reference	Method	Species
Chemical methods		
Ivens (1958)	2,4,5-T	*Acacia* spp.
Philip (1962)	2,4,5-T	*Acacia* spp., *Lannea Commiphora*
Harrington (1968, 1973a)	Picloram	*A. hockii*
Lloyd, Bromwich & McNeill (1978)	Picloram/2-4D	*Brachystegia boehmii Colophospermum mopane*
Du Toit (1973)		*A. karoo*
Lamprechts (1974)	Various	Various
Sousa de Almeida (1974)	2,4-D/2,4,5-T	*Acacia* spp, *Dichrostachys*
Mechanical methods		
Glover (1959)	Chaining Buldozing	Various
Glascow & Duffy (1959)	Hand felling & burning	*Euclea divinorum Acacia pennata*
Evans Jones (1962)	Chaining	*A. mellifera*
Ward & Cleghorn (1964)	Ring-barking	*Brachystegia spiciformis*
Pratt (1966a,b)	Bush-breaker Mower Mattocking	*Disperma* sp. *Tarchonanthus camphoratus* *Acacia* spp.
Noel (1967)	Ring-barking	Various
Clatworthy (1969)	Slashing	*Brachystegia spiciformis*
Thomas (1970)	Mattocking	*Brachystegia spiciformis*
Rees (1974)	Mattocking	*Brachystegia spiciformis*
Denny (1968)	Ring-barking	Various
Natural methods		
Barnes (1965)	Fire & mattocking	*Brachystegia spiciformis*
Pratt & Knight (1971) Thomas & Pratt (1971)	Fire	*Tarchonanthus camphoratus* and *Acacia* spp.
Donaldson (1966,1967)	Fire	*Acacia mellifera*
Ward & Cleghorn (1970)	Grazing	*Brachystegia spiciformis*
Harrington (1974)	Chaining & fire	*Acacia hockii*
Trollope (1982b)	Fire & goats	*Acacia karroo*

The **natural** methods use browsers or fire to retard tree growth. Neither is consistently effective on its own against established woody plants (Barnes 1965, Ward & Cleghorn 1970, Aucamp 1980 and Trollope 1982b), but they can retard re-invasion of woody plants into a grassland created by other methods. In combination they may be considerably more effective in reducing the woody biomass (Trollope 1982b)

Burning can only be successfully used where sufficient fuel accumulates between burns to provide a hot fire. This is incompatible with heavy grazing in an area of low grass productivity. Apart from the loss of the standing crop once every three to four seasons, the major detrimental effect of burning is the alteration of species composition in favour of fire resistant plants (Trapnell 1959).

The **mechanical** methods physically sever the woody plants from their root stock, and include felling, root ploughing, chaining, bulldozing and ring-barking. The main ecological hazards relate to the soil disturbance by heavy machinery. Compaction and increased erosion may result (Buckhouse & Gifford 1976), especially if the debris is windrowed. A common drawback of these methods when applied in Africa is the widespread ability of woody plants to coppice from surviving root material. This growth form is especially common on sandy soils, where woody plants have a high root to shoot ratio. Mortality due to clearing is frequently low (Pratt, 1966a) and the coppice usually results in a denser vegetation than the original.

Chemical methods involve the application of arboricides as granules, foliar sprays, basal injections or cut-stump treatments. The compounds are generally toxic to both plants and animals, and rely on precision of application and dosage for specificity to woody plants. They result in standing dead material which may have to be removed to allow access by grazers.

1.6 REVIEW OF RELATED STUDIES

1.6.1 COMPETITION EXPERIMENTS IN SEMI-ARID SAVANNAS

1.6.1.1 Bush clearing trials

Numerous bush clearing experiments have been carried out in Australia (Walker *et al* 1972, Beale 1973), North America (Scifres, Mutz & Durham 1976, Clary & Jameson 1981) and Africa. Reviews are provided by Teague (1976) for Zimbabwe and O'Connor (1985) for Southern Africa. A summary of the details and findings of those performed in Southern and East Africa is presented in Table 1.3 and a map of their locations is given in Figure 5 on page 37.

The following general conclusions can be drawn from the studies reviewed

1. Grass production increases on the cleared site.

2. Herbaceous species composition changes, usually in the direction of lower quality. This change can involve the loss of sub-canopy species (eg. *Panicum maximum*), the gain of more mesic species (eg. *Urochloa mossambicensis*) or the proliferation of pioneer species (eg. *Aristida* spp) (Dye & Spear 1982)

3. Herbaceous production and composition on both cleared and uncleared sites is strongly influenced by rainfall. The effects of the treatment may be less than the effects of climatic variation (O'Connor 1985).

4. Trees regrow in the grassland unless they are prevented from doing so.

Table 1.3 Bush clearing experiments conducted in Southern and East Africa.

Region	Site	Woody species	Soil Texture	Rain (mm)	Duration (yr)	Summary of results	Reference
1 Tanzania	Mpwapwa	Acacia, Albizzia, Grewia, Commiphora	SaLo	c 600	7	Grazing days inc. from 64 to 300 /ha. Many forbs. Less erosion no clearing	Staples (1945a,b)
2 Kenya	Kisokon	A. senegal, Terchonanthus	SaLo	c 600	7	Tested grazing, fire, mowing & browsing. Trees regrow unless burned and mowed.	Bogdan (1954)
3 Zimbabwe	Matabeli	Brachystegia, Julbernardia	Sa	600	4	Hay yield inc. from 225 to 1350 kg/ha/yr. Goats could not control regrowth	Ward & Cleghorn (1964)
4 Zimbabwe	(11 sites)	Various		c 600	1	Mean hay yield inc. from 505 to 499 kg/ha/yr. (Range: wooded 83-1600, cleared 330-1940)	Ivy (1969)
5 Namibia	Camaraland	Acacia mellifera	Lo	430	5	Grass basal area inc., especially in desireable perennial species	Joubert (1968)
6 E Cape	Cathcart	Acacia karroo		435	2	Hay yield inc. from 159 to 514 and from 423 to 973 kg/ha/yr. No species change	Du Toit (1968)
7 N Cape (Malopo)	Bathhurst	A. mellifera	Sa	345	8	Hay yield inc. from 145 to 250 kg/ha/yr	Donaldson & Kelk (1970, 1974a,1974b,1974c)
	De Rust		Sa	300	6	from 320 to 1100	
	Arizona		Sa	300	7	from 250 to 750	
	Buttermere		Sa	305	6	Animal carrying capacity inc. 14%	
8 W Transvaal	Tsumeb	Acacia spp., Dichrostachys cinerea, Grewia spp.	Cl	588	20	Animal mass gain inc. from 7 to 14 kg/steer/yr. Selective clearing ineffective.	Louw & vd Merwe (1973)
9 SE Zimbabwe	Nuanetsi	Combretum apiculatum/ Sclerocarya birrea	LoSa	800	6	Selective clearing trial. Hay yield inc. from 1534 to 2409 kg/ha/yr.	Kelly et al (1978)
10 Namibia	Tsumeb (2 sites)	1 Acacia mellifera/ Commiphora angolensis	?	c 600	2	1 Hay yield inc. from 1309 to 2822 kg/ha/yr	van Niekerk & Kotze (19
	1 Thornveld	2 Termina is prunioides/	Dolo-			2 Hay yield inc. from 350 to 847 kg/ha/yr	
	2 Karst	Combretum apiculatum	mite				
11 N Transvaal	Mara	Combretum apiculatum	SaLo	416	3	Grazing days inc. from 200 to 300 /ha/yr	Donaldson (1978)
		& A. tortilis	SaLo	c 450	2	Hay yield inc. from 1600 to 2500 kg/ha/yr	Pieterse & Grunow (1985)
12 Botswana	Morale	A. nigrescens/Sclerocarya	SaLo	c 450	12	Stocking rate inc. 33%. No significant herb species shift.	McKe, (1968)
13 Botswana	(5 sites)	1 Central Kalahari bush		c 450	4	Mean hay yield inc. from 1950 to 2246 kg/ha/yr. Grass species composition improved, especially under partial clearing. Light level inc. from 60 to 190 MJ/m²/s x 10³. Duration of plant-available water increased	Pratchett (1978)
		2 Arid sweet bushveld					
		3 Southern Kalahari bush					
		4 A. nigrescens/C. apiculatum					
		5 Semi sweet mixed veld					
14 W Transvaal		Acacia erubescens	SaLo	473	10	0, 33, 66 & 100 % clearing. 33% had best grass species composition. P maximum & D eriantha inc.	Morris (1980)
15 SW Zimbabwe	Matopos	"Thornveld"	SaClLo	615	19	Hay yield inc. by 850 kg/ha/yr	Dye & Spear (1982)
	Matopos	"Sandveld"	Sa	615	19	525	
	Nyamandlovu	"Sandveld"	Sa	569	15	780	
	Tuli	"Sandveld"	Sa	450	15	100-1500	
						Species shift. Lost P maximum & D eriantha	
16 E Cape	Adelaide	Acacia karroo	Lo	290		Optimum grass prodn. with 100 trees/ha	Aucamp et al (1983)



Figure 5. The location of bush clearing studies listed in Table 1.3

These studies can be criticised on one or more of the following grounds.

The mechanism by which grass production is increased is at best only inferred. Most studies attribute the increase to a reduction in competition, but few monitor changes in the resource levels.

2. The initial standing crop and productivity of woody plants is seldom measured. Where quoted, it is usually given in terms of tree density or basal area, which bear a site-specific relationship to woody plant biomass

3. The above factors prevent the development of a general model of the bush clearing response and render the individual studies non-comparable and site-specific.

4. Usually only annual grass production and species composition are monitored. Other parameters, such as changes in runoff and erosion, are not measured.

The study reported by Dye and Spear (1982) is outstanding because it ran over a fifteen year period and was replicated on four different soil types. Their results are presented in Figure 6 on page 39. They came to the following conclusions.

1. Water use by trees was fairly constant between years on the same site. Thus over a wide range of annual rainfalls, absolute increases in grass production of 600-1000 $kg.ha^{-1}$ could be expected. The exception was the site at Tuli, where water use by trees appeared to increase with increasing rainfall. The authors offer no explanation for this result, which is possibly due to a greater degree of niche overlap on this arid site with shallow soil, or possibly to a water-nutrient interaction. On this site the grass production on the cleared treatment appeared to become nutrient rather than water limited at annual rainfalls above 600mm.

2. The slopes of the regressions between grass production and annual rainfall are higher on clayey than sandy soils but have a lower intercept. This means that grass production on clayey soils is lower at low rainfalls but higher at high rainfalls, and is therefore more variable overall.

3. The correlation coefficient for the regressions is higher on clays, implying a stronger water limitation and less carry-over of moisture between seasons. Similarly, the correlation coefficients were higher on uncleared sites relative to cleared sites.

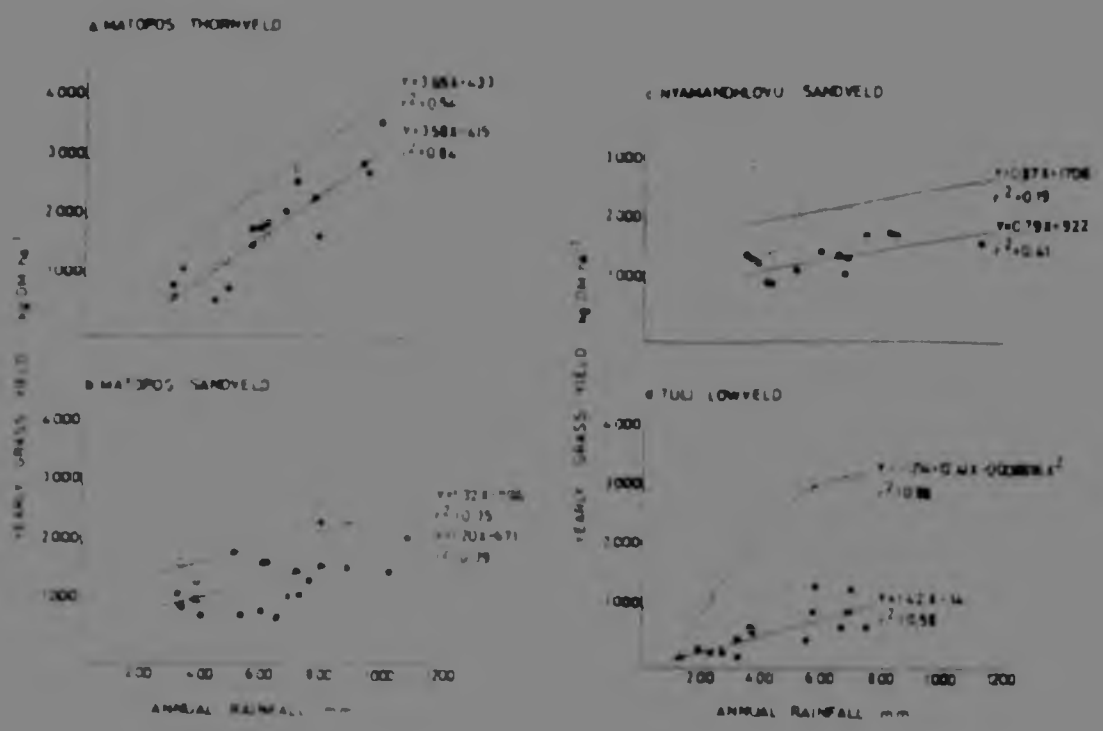


Figure 6. The relation between annual rainfall and grass production cleared (O) and uncleared (●) plots in four veld types (Dye & Spear 1982).

1.6.1.2 Partial clearing experiments

Donaldson and Kelk (1970) cleared *Acacia mellifera* to varying degrees in the Molopo district of the Western Transvaal Walker *et al* (1972) and Beale (1973) conducted similar trials in Australia, in *Eucalyptus populnea* and *Acacia aneura* woodlands respectively These authors showed an inversely concave dependency of grass production on tree standing crop, as illustrated in Figure 7 on page 40, and quoted ten other studies reporting a comparable relationship. Aucamp *et al* (1980), on the other hand, found an inversely convex relationship when they measured herbaceous production after increasing degrees of *Acacia karoo* removal

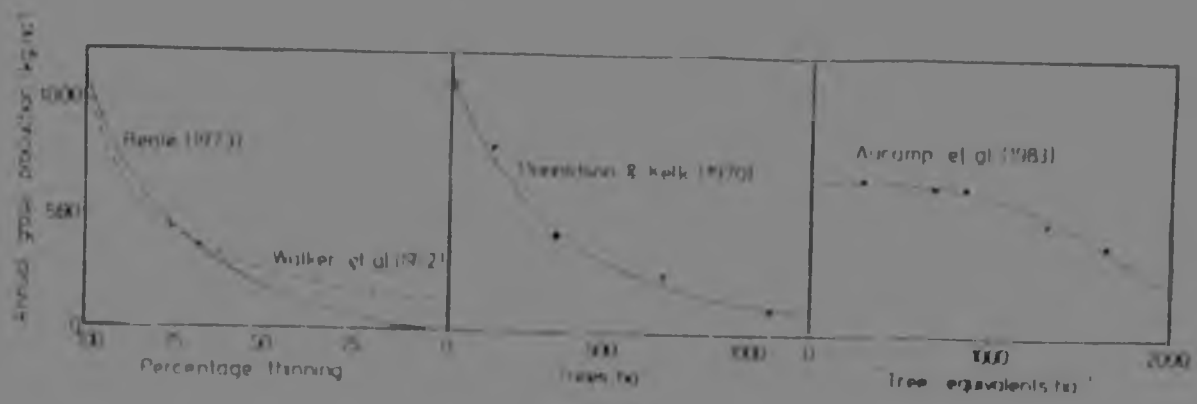


Figure 7 Form of the relationship beween tree biomass and grass yield

in the Eastern Cape, with a maximum grass production recorded at 300 tree equivalents ha^{-1}. The evaluation of these conflicting findings is difficult, since the degree of woodiness is quoted in non-comparable units. It is possible that the Aucamp *et al* curve represents the lower threshold of the other curves, but seems unlikely. The implications for bush clearing policy are large, since the concave curve predicts maximum cost-efficiency with total clearing, while the convex curve implies a non-zero optimum woody density.

Kelly, Schwim & Barnes (1978) investigated the removal of shrubs independently of trees. The results from the first two years following clearing show a large increase in grass production when the large trees were removed and when all woody plants were cleared but a small increase when only the small trees were removed. No data are provided as to the relative biomass of the large and small tree categories.

Knoop (1982) found no qualitative difference between the effect of trees and shrubs on grass production or soil moisture status.

1.6.1.3 Clearing with soil moisture monitoring

Strang (1969a) found an increase in soil moisture duration under grassland derived from *Brachystegia spiciformis / Julbernardia globiflora* woodland in Rhodesia, but that the grassland could dry the soil more completely than the woodland. Increases in soil moisture immediately following bush clearing have also been reported by Pratchett (1978) in Botswana, Knoop & Walker (1984) in the Northern Transvaal, Pieterse & Grunow (1985) in the Northern Transvaal and Gifford & Shaw (1973) in Arizona

1.6.1.4 Reciprocal manipulation experiments

Knoop & Walker (1984) measured the effect of the removal of grass on the growth of woody plants, and *vice versa*. In a community dominated by *Burkea africana* on sandy, dystrophic soils, the removal of grasses did not significantly increase terminal twig elongation of the woody plants. In an adjacent community on slightly heavier-textured soils with a higher nutrient status, grass removal increased terminal twig growth of *Acacia tortilis*. The exclusion of woody-plant roots significantly increased grass growth on both sites. The conclusions drawn from this study are that competition between trees and grasses is asymmetrical in the favour of trees, and varies in strength between sites and/or species. They further attempted to test the hypothesis that competition between trees and grass was mediated by a separation in the depth of rooting activity, and found that trees did have a larger proportion of their roots at greater depths in the soil, but that grasses nevertheless had access to deep soil layers

1.6.1.5 Regrowth of woody plants

Despite the general observation that coppice regrowth is a common consequence of bush clearing in Africa, very little work is published on the rate at which the woody biomass recovers. Strang (1969b) found that the dominant process of re-invasion in *Brachystegia spiciformis / Julbernardia globiflora* woodland was vegetative suckering rather than the establishment of new seedlings. He also measured the regrowth on clearings of known age (Strang 1974) and found that in the absence of fire full recovery required about fifty years. Recovery was rapid during the first twenty years after which it slowed down. The number of stems per hectare reached a peak at twenty years, after which it declined. This may be in accordance with the "3/2 thinning law" (Yoda *et al* 1963, White & Harper 1970). Frequent burning did not affect the number of stems, but did reduce the basal area and height of the regrowth. Where the plots had been cleared and cultivated, and therefore regrowth was entirely from seed, the recovery was much slower. Taush & Teuller (1977) simulated the recovery of Pinyon-Juniper woodlands in Eastern Nevada on the basis of a study of tree growth rings from clearings of different ages. They predicted an almost complete recovery after fifteen years.

1.6.2 HYDROLOGY OF SEMI-ARID SAVANNAS

The basic procedure for studying the hydrology of semi-arid regions was established by Slatyer (1961). Portions of the hydrological cycle have been well studied, such as rainfall interception and partitioning (Pressland 1973, De Villiers & de Jager 1981), transpiration (Pendle 1982) and runoff (Dye 1984). However, few integrated water-balance studies have been published for semi-arid savannas. A catchment-scale study was initiated in Uganda but was abandoned before any meaningful results were obtained (Edwards & Blackie 1979). The estimates presented by Bate, Furniss and Pendle (1982) for the Nylsvley study site are estimates

derived from the sub-continental water budget proposed by Whitmore (1971).

Complete water budgets for sites with and without woody vegetation have been calculated for a Pinyon-Juniper vegetation in Arizona by Gifford (1975). Runoff was higher on cleared sites, but the other components of the cycle were little changed.

1.6.3 MODELS OF SAVANNA DYNAMICS

The dynamics of the Walter hypothesis model of savanna function (Walter 1971) were quantitatively explored by Walker *et al* 1981, who found three stable equilibria: a grassland, a woodland and a savanna. An increase in grazing pressure could move the system out of the savanna domain of attraction and into that of the woodland. This was offered as an explanation for the tendency of savannas to become thickets under heavy grazing. Walker & Noy-Meir (1982) showed that exclusive access to subsoil water was not a necessary condition for the stability of the tree-grass mixture, but that given superior water uptake rates by grasses, preferential access to subsoil water was necessary to prevent the competitive exclusion of trees.

McMurtrie & Wolf (1983) included competition for light, water and nutrients in their model and come to similar conclusions. The model of Mankin & Risser (1983) also has rooting depth separation between trees and grass as the basis of coexistence. None of these models has been tested with parmeters derived from a real savanna.

1.7 STUDY OBJECTIVES

The overall aim of this study was to develop process based models of the tree grass interaction in semi-arid savannas. Such models can then be used to predict the effect of tree removal on grass production at any site for which the model parameters are known. The success of the models in predicting observed patterns of production acts as a test of current hypotheses regarding structure and function in semi-arid savannas. The detailed objectives were as follows

1. Conduct an experiment on three different soil types, monitoring selected ecological parameters on two treatments: a semi-arid savanna and the grassland derived from it by removal of all the woody plants. The soils were chosen to represent a range of fertility and hydrological properties, and the selected parameters were runoff, soil moisture availability, transpiration rates by the dominant woody plants and grasses, evaporation from the soil surface, herbaceous production and species composition.

2. Develop a simulation model for semi-arid savannas linking primary production to plant water use, calibrate it with data from the above experiment and test it against independently collected data.

3. Use the model to generate long term (40 year) simulations of the hydrology and primary production of plant communities on different soil types under increasing degrees of woody plant removal.

4. Use the model and independently collected data to test the following hypotheses

   a. H1 Grass production in semi-arid savannas is water-limited.
   Ho: Variations in water supply have no effect on grass production.
   Test: Failure of a water use based model of primary production in a savanna to account for qualitative and quantitative trends in harvest data will lead to rejection of the hypothesis.

b. H2: There are at least two axes (temporal and spatial) to the water-use niches of trees and grasses in semi-arid savannas, and both contribute to niche separation.
Ho: Water-use niche separation occurs on one or no axes.
Test: Determine the rooting-depth of trees and grasses in the field. Measure their transpiration and photosynthetic rates through a drying cycle in the field. Substitute both into the water balance model and validate it against field soil-water data. Run the model using historical rainfall records as input data, and test for niche separation using standard indices.

c. H3: In a two-species model of primary production in which the competition is asymmetric, the production of the species with the lower competition coefficient ("grass") will be an inversely concave function of the biomass of the other species ("trees").
Ho: The function has a linear or inverse convex form.
Test: Simulate grass production under a range of soil and rainfall conditions at several levels of tree biomass. Test the dependence of grass production on tree biomass for positive or negative curvature.

5. Estimate, from measurements of coppice regrowth, the rate at which woody plant biomass recovers following clearing.

6. Predict the combinations of annual grass production, woody biomass and herbivore stocking rate which permit the curtailment of woody plant recruitment by repeated burning.

2.0 THE STUDY AREA

2.1 GENERAL ECOLOGY OF THE KLASERIE PRIVATE NATURE RESERVE

2.1.1 LOCATION

The study area is a semi-arid savanna in the Klaserie Private Nature Reserve, adjacent to the western boundary of the Kruger National Park, 20 km south of the town of Phalaborwa, centered on 24° 15 S 31° 10 E. The reserve is a collectively-owned area of 650 km² managed for recreational game viewing and limited hunting. It is surrounded by properties under similar conservation orientated management. Although most of the boundaries are fenced a significant amount of game movement occurs between the Klaserie and adjacent areas. It would therefore be inaccurate to consider the Klaserie as an isolated ecosystem. It is part of a larger functional system which includes all portions of the Eastern Transvaal Lowveld that support wild ungulates as the dominant herbivores.

Prior to proclamation as a nature reserve in 1972, the main form of land use was hunting combined with some cattle ranching and crop farming. After 1972 factors such as fencing, water provision, reduction in hunting and control of poaching led to large increases in herbivore numbers. They reached levels unsupportable by plant production during the dry seasons of 1981/2 and 1982/3, when about 50% of the game population died (Schneebeli 1983, Scholes 1985). During the first two years of the study (July 1981-October 1983) the area was subjected to a severe drought and heavy grazing pressure. The last two years of the study (November 1983-June 1985) were characterised by good rains and light grazing.

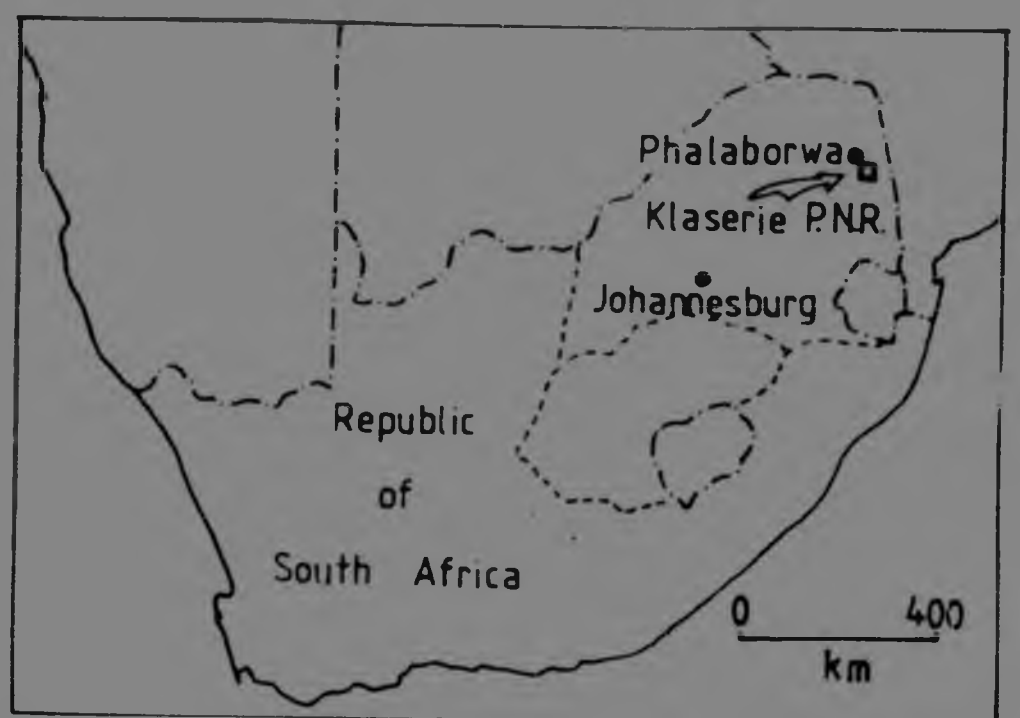


Figure 8. Location of Klaserie Private Nature Reserve

2.1.2 CLIMATE

A Walter climate diagram for Phalaborwa (Figure 9 on page 48) illustrates the characteristic features of a savanna climate: rainfall concentrated into a summer wet season of five to seven months, with a period of water stress for the remainder of the year and relatively high temperatures throughout the year with a virtual absence of frost. The mean annual class A pan evaporation at Phalaborwa is 2090 mm, which considerably exceeds the mean annual precipitation of 480mm. The classification under the Koppen (1931) system is BShw (Hot Savanna with summer rainfall). Under the system of bioclimatic units (Phillips 1983), the study site is transitional between sub-arid wooded savanna and arid wooded savanna.

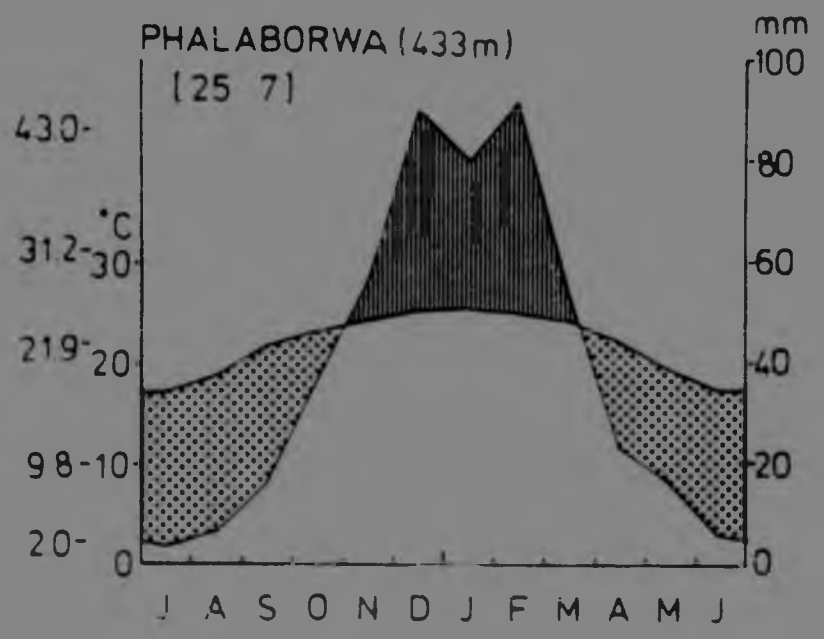


Figure 9 Climate diagram for Phalaborwa. Follows the conventions of Walter (1975). The stippled areas represent periods of water deficiency and the striped areas water sufficiency.

The regional rainfall isohyets reveal a trend towards lower rainfall in the north-east. In the context of the Klaserie Private Nature Reserve, this translates into a mean annual precipitation in the south-west of 500 to 550 mm, and 450 to 500 mm in the north-east. As is characteristic of semi-arid savanna regions, the annual precipitation is highly variable in both time and space. There is some evidence to suggest that the temporal variation is periodic (Tyson & Dyer 1975, Gertenbach 1980). The mid- and late-1970s were characterised by above average rainfalls in the region, while the project coincided with a period of exceptionally low rainfall. A diagram showing monthly rainfall and mean monthly temperature over the course of the project appears as Figure 10 on page 49.

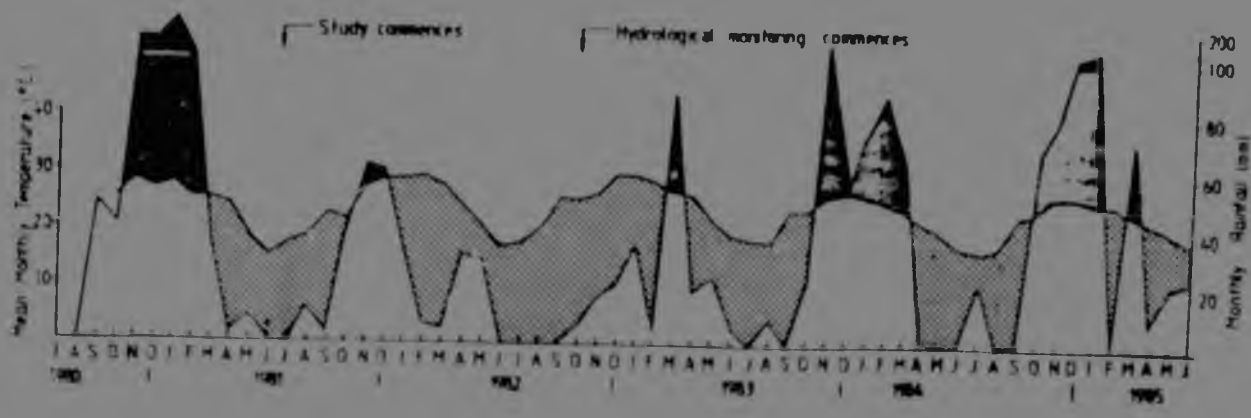


Figure 10. Monthly rainfall and mean monthly temperature recorded at Klaserie P.N.R.: Diagram follows the conventions of Walter (1975)

2.1.3 GEOLOGY, GEOMORPHOLOGY AND SOILS

The parent materials throughout the reserve are predominantly Archaean granites and gneisses (Cleverley & Bristow 1979). Considerable local variation of the mineral composition occurs, which influences the topography and soils, and therefore the vegetation. The southern area is gently undulating to flat, with frequent narrow doleritic intrusions. The characteristic catenary sequence that develops on granite-derived soils in the Lowveld, as described by Coetzee (1983) and Gertenbach (1983) is conspicuous here (Figure 12 on page 51), but the conditions for the formation of hydromorphic grasslands within the catena (known as seeplines) are seldom met (Olbrich 1984) Marginally hydromorphic soils are widespread, but of limited extent A tendency towards sodicity and duplex soils in the bottomlands (for a description of this phenomenon see Dye & Walker (1980)) is also widespread. The soils of the uplands tend to be coarse sand and stony with orthic A horizons and yellow-brown

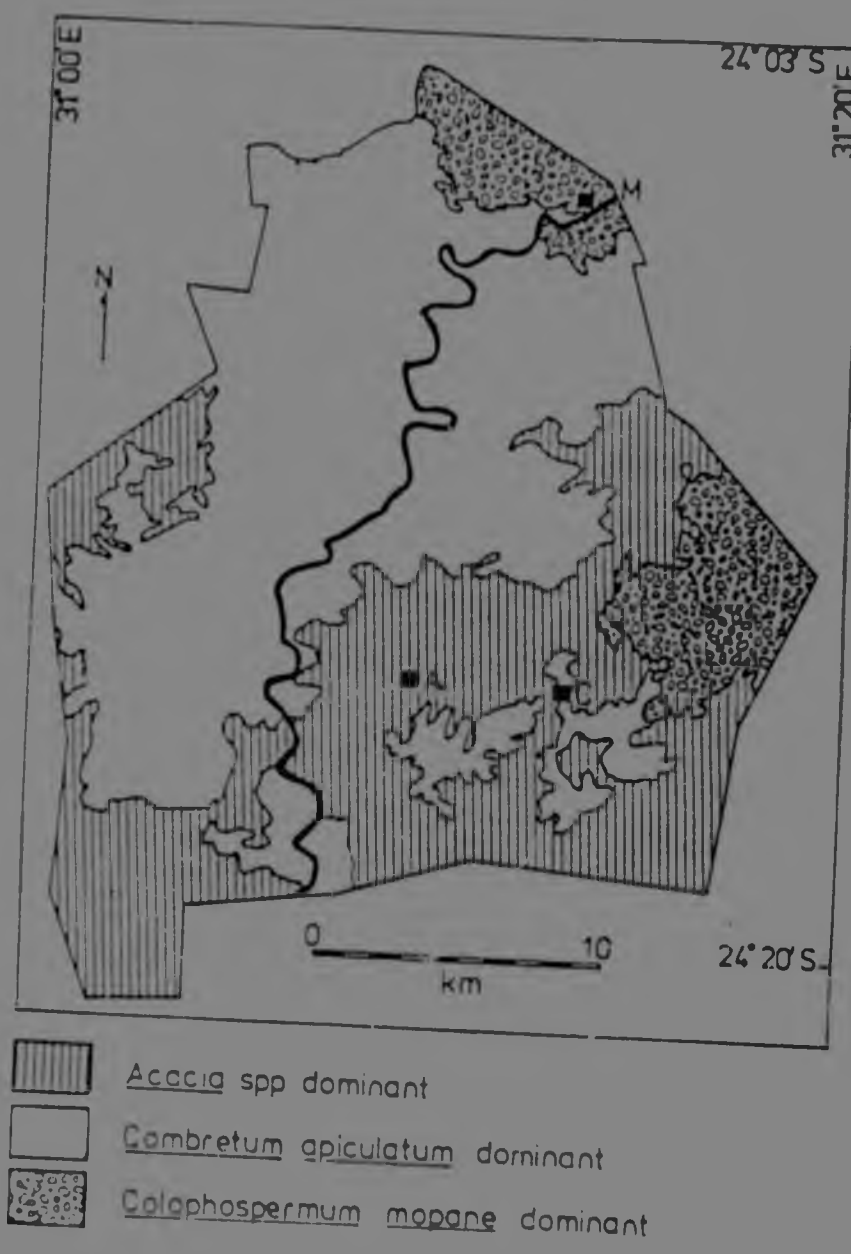


Figure 11 Simplified map of the vegetation of Klaserie P N R location of the study plots is indicated.

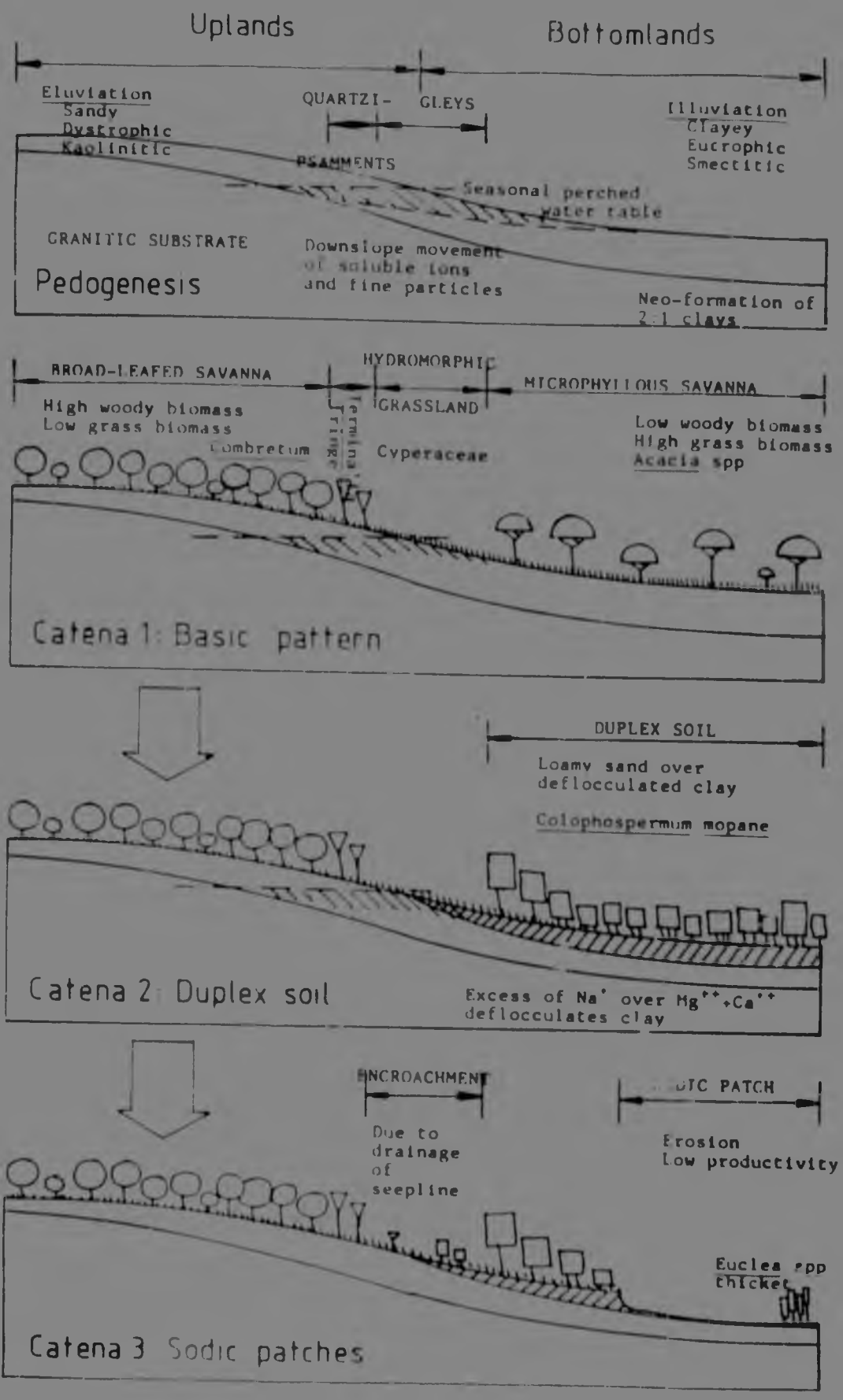


Figure 12. Catena development on granites in the lowveld

apedal B horizons, i.e. Clovelly or Hutton forms or, where shallower, Glenrosa (MacVicar *et al* 1977). The footslopes and bottomlands have more clayey soils, and thus more structure. Valsrivier form is typical, but on or near doleritic intrusions a melanic A horizon (such as Mayo form) is common.

The northern portion is steeply hilly with amphibolite, quartzite and quartz-schist predominating. The soils tend to be very shallow and therefore less differentiated than in the south. Glenrosa form is typical. On level areas Valsrivier form (Zuiderzee series) can be found. These soils do not fit into the catenary sequence outlined above, and the presence of water-rounded pebbles within the profile further suggests an independent ontogeny. Alluvial soils of the Dundee and Oakleaf forms occur near the major rivers

2.1.4 CATENAS ON GRANITE IN SEMI-ARID REGIONS

The soil and vegetation associations in Klaserie mostly follow a distinctive topographical sequence which is widespread in the Eastern Transvaal lowveld and other areas of semi-arid Africa. The pattern can be explained in terms of the catena concept of Milne (1935), and is illustrated in Figure 12 on page 51.

The eluviation of fine particles and soluble salts from the soil profile not only results in the increasing clay content and base saturation with depth that is characteristic of many soils, but is also responsible for a similar pattern at a landscape level. Ridgetop soils tend to be shallow, sandy and dystrophic, while bottomland soils tend to be deeper, clayey and eutrophic. The dominant clay mineralogy of the uplands is kaolinitic, with a Silicon : Aluminium ratio of 1:1. The Si : Al ratio in the soil solution of the bottomlands is higher due to the Si which leaches down from the uplands, and 2:1 clays (smectites and illites) develop by neoformation. Where doleritic dykes are present, smectites can also be the primary clay

minerals formed. The 2:1 clays have a much higher surface charge density than the 1:1 clays, and their high capacity to retain cations contributes to the high nutrient status of the bottomlands relative to the uplands.

The soils of the uplands and bottomlands are both alfisols (soils with a marked increase in clay content with depth in the profile). In a particularly well developed catena the bottomlands may contain sufficient 2:1 clays to qualify as vertisols Following sodification the bottomland soils are natrustalfs (alfisols, strongly duplex and dominated by sodium).

The water holding capacity of the coarse uplands soils is much lower than that of the finer bottomland soils, and their hydraulic conductivity is much higher. The granite which underlies the soil at a depth of 500-1500 mm is poorly permeable to water. Thus when the profile water content exceeds the water holding capacity in the upland soils, the excess water drains downhill along the soil granite interface. When it encounters the low permeability clays in the bottomland, a seasonal perched water table is formed. (The main water table is tens of meters deeper.) If sufficient water is present it appears at the soil surface as a seepline. The width of the seepline is a function of the available water, which is in turn determined by the length of the upslope catchment and the annual rainfall (Olbrich 1984).

This type of catena appears to form under a semi-arid seasonal climate on a gently undulating topography. Classically it is underlain by granites or gneisses, but a very similar sequence has been described on Karoo sediments by Purves & Bly . (1969) The Combretum and Acacia sites in the present study are representative f upland and bottomland catenal positions respectively (Table 2.1 & 2.2, Figure 14 on page 63). Comparable catenas have been described by Berry & Ruxton (1959), Calton (1963) in Tanzania and Watson (1964) in Zimbabwe.

The fidelity of the soil-vegetation complexes and the abruptness of the transitions between them makes the catenal pattern very obvious in the field. The uplands support a broad-leafed savanna dominated in Klaserie by *Combretum apiculatum*, while the bottomlands support a microphyllous

savanna dominated by *Acacia nigrescens*. This pattern parallels, at a local scale, the moist/dystrophic (upland) *versus* arid/eutrophic (bottomland) categories of Huntley (1982).

The seepline, where present, supports a treeless hydromorphic grassland rich in sedges. Above its upslope edge is a fringe of *Terminalia sericea* and *Dalbergia melanoxylon*. *T. sericea* is a shallow-rooted tree apparently able to tolerate occassional waterlogging in the subsoil. *T. sericea* is widely distributed on sandy soils, and is not an infallible indicator of seeplines.

Ions leach down the catena in order of their solubility. The granite parent material is a good source of sodium, and in time the monovalent Na^{+} comes to predominate over the polyvalent ions such as Ca^{++} and Mg^{++} in the bottomland soil solution. When a certain critical threshold is exceeded (Bresler, McNeal & Carter 1982) the clay particles in the soil deflocculate, which causes the soil to become much less permeable to water and roots. The soil is said to be sodic and this process is probably responsible for the abruptness of the vegetation boundaries on the catena. The vegetation of sodic soils is described by Dye & Walker (1980). In Klaserie they characteristically support *Colophospermum mopane* or *Euclea* spp. thicket. The soil usually has a duplex structure, with loamy sands overlying the deflocculated clays. In this condition they are fairly productive, but highly prone to erosion. Game tends to concentrate on these soils, possibly attracted by the high sodium content of the vegetation or the frequent presence of wallows. Exposure of the soil by overgrazing or tracks leads to the rapid loss of the A horison by erosion. The exposed deflocculated clays form a hostile substrate for most grasses and grass production declines drastically. Once such sodic or "saline" patches have formed it is very difficult to return them to a productive state (Dye & Stead 1978).

2.1.5 VEGETATION

The vegetation of the Klaserie has been described by Witkowski (1983) and mapped by Zambatis (1983). It is included in Acocks's (1953) broad category of Arid Lowveld. Under the system of landscape units developed for the Kruger National Park by Coetzee (1983) and Gertenbach (1983), the vegetation/soil complexes found in the Klaserie are mixed *Combretum/Terminalia* Woodland in the south with Olifants River Rugged Veld in the north and *Combretum/Colophospermum* Woodland in the east. The classifications of Witkowski and Zambatis are based on the plant associations alone. Although they differ slightly from each other in detail, the broad classification and distribution of vegetation types is similar. A simplified version of the Zambatis map is given in Figure 11 on page 50.

Sandy upland soils in the south of the reserve are dominated in the woody layer by *Combretum apiculatum*, in association with *Sclerocarya birrea* and *Lannea schweinfurthii*. The dominant trees are deciduous, broadleafed and non-spinescent. The herbaceous layer is variable, but usually includes *Schmidtia pappophoroides*, *Pogonarthria squarrosa*, *Aristida congesta*, *Digitaria eriantha*
and a large proportion of forbs.

Bottomlands in the same region have *Acacia nigrescens* as the woody dominant, in association with *Sclerocarya birrea*, *Albizia harveyi* and *Ormocarpum trichocarpum*. The trees are generally deciduous with microphyllous compound leaves and thorns. The major grasses are *Panicum coloratum*, *Sporobolus nitens*, *Bothriochloa radicans* and *Urochloa mosambicensis*.

A narrow seepline (5 m) is occasionally present between the uplands and bottomlands, but usually it is represented only by a few scattered *Terminalia sericea* and an increased proportion of sedges in the herbaceous layer.

The vegetation pattern is less obvious on the rocky, shallow soils of the hills of the northern portions of Klaserie which support *Combretum apiculatum* with *Sclerocarya birrea, Commiphora mollis, Acacia nigrescens, Boscia albitrunca* and *Terminalia prunioides*. The herbaceous layer is sparse, but is otherwise similar to that of the southern *Combretum* types.

In the north-east of the reserve *Colophospermum mopane* is overwhelmingly dominant in the tree layer on red sandy clay loam soils. The herbaceous layer has *Digitaria eriantha* and *Panicum maximum* under the canopies and *Schmidtia pappophoroides* in the open. Where *C. mopane* is extensive within the reserve it has a stunted, multi-stemmed growth form, but only locally (in the south) is it associated with a hardpan layer in the soil as is common elsewhere in Southern Africa (Cole, 1982). On better watered sites such as river banks the growth form is single-stemmed and tall.

Grewia spp. and *Cissus cornifolia* are the most prevalent shrubs throughout the reserve.

Various other vegetation types such as Riverine Woodland, Alluvial Savanna, Reedbeds, Old Lands and Riparian Thicket make a small contribution to the vegetation of the reserve.

Combretum apiculatum Woodland, *Colophospermum mopane* Woodland and *Acacia nigrescens* Woodland were selected as being not only representative of the vegetation of the Klaserie, but also of the continuum which exists between dystrophic savannas on sandy soils and eutrophic savannas on clayey soils. An experimental site was established in each of these types and will be refered to as the Combretum Site, the Mopane Site and the Acacia Site.

2.1.6 BUSH ENCROACHMENT IN KLASERIE PRIVATE NATURE RESERVE

A comparison of aerial photographs taken of the whole of Klaserie in 1940 and 1974 revealed very few areas which could unequivocally be identified as having undergone bush encroachment during this period. A ground check of these areas revealed them to be marginally hydromorphic alluvia, and the main encroaching species to be *A. nigrescens*. No bottomland areas as typified by the Acacia site had become discernibly encroached, and the population age structure there is thought to reflect good seedling establishment by *A. nigrescens* but a strong selection for middle-sized (accessible) individuals by browsers. Given a reduction in browsing, the potential exists for encroachment by this species.

Stem diameter distributions per species were recorded at the three main experimental study sites. The stem diameter distributions are illustrated in Figure 13 on page 58. A species which is actively encroaching would be expected to have a size class distribution heavily weighted towards small individuals. This is the case for *Acacia nigrescens* at the Acacia site and *Sclerocarya birrea* at the Combretum site, but in both cases the rest of the population was fairly mature and the distribution probably reflects sporadic germination success and high seedling mortality.

The size structure for *Colophospermum mopane* is fairly even but this species also has a coppice growth form, so the diameter of the above-ground stems may bear little relationship to the age of the ligno-tuber. If encroachment by *Mopane* has occurred it is unlikely to have been a recent event, since there is no trace of pre-existing woody vegetation in the almost monodominant *C. mopane stands*. These stands appear identical on the 1940 and 1974 images.

The stem diameter structure of *Grewia bicolor* shows a weighting towards middle-sized individuals which may reveal encroachment during some period in the past. Interpretation of the stem size-distribution is complicated by the multi stemmed growth habit of this species. The *Grewia* bush is below the threshold of resolution of large-scale aerial photography and so encroachment by this species is unconfirmed.

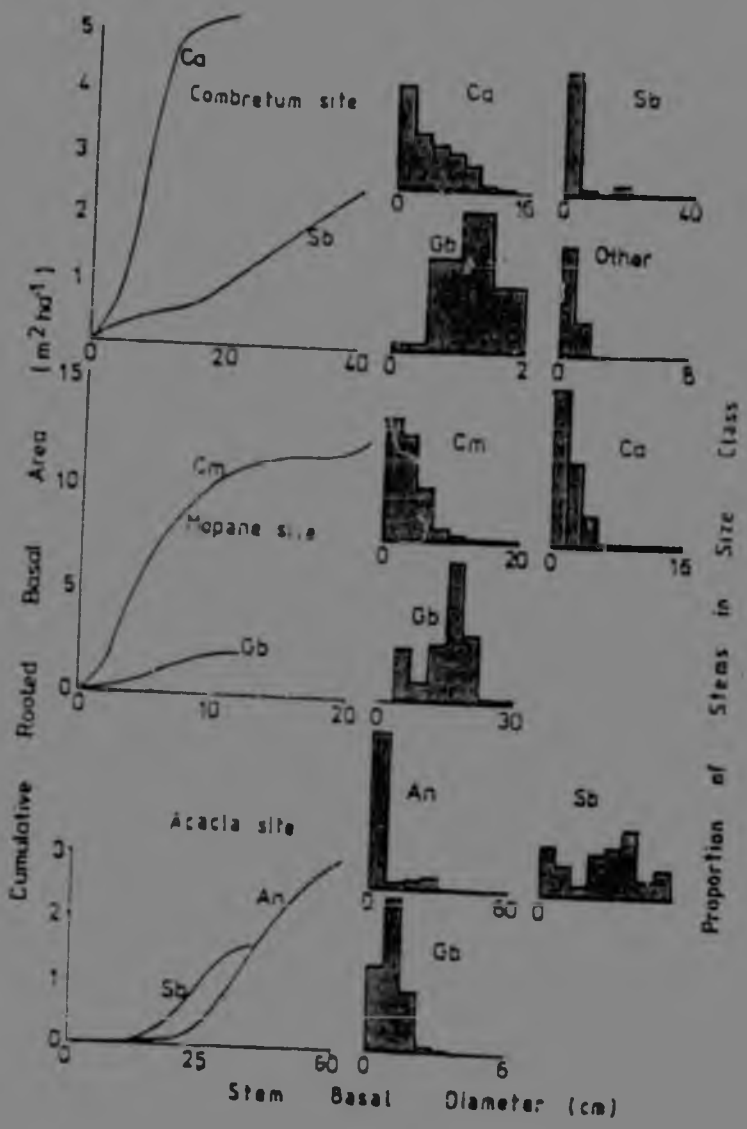


Figure 13 Stem diameter distributions for dominant woody plants: graphs on the left show the cumulative basal area of stems with a diameter smaller than the value on the x-axis. The approximate contribution to the total biomass by any size class can be read off them. Histograms on the right are the proportions of stems in each size class. These are an approximate indication of the age structure of the populations. *Ca-Combretum apiculatum, Sb-Sclerocarya birrea, Gb-Grewia bicolor, Cm-Colophospermum mopane and An-Acacia nigrescens.*

The presentation in Figure 13 of cumulative basal area of stems below a given diameter gives an indication of the contribution of each size class to the total woody basal area and, by implication, to the total woody biomass. The stem size threshold relating to a desired percentage of woody plant removal can be directly interpolated from these graphs.

2.2 THE EXPERIMENTAL SITES

2.2.1 SITE LAYOUT

The experiment was designed to determine the consequences of bush clearing on the hydrology, primary production and herbaceous species composition of the system. Each of the three study sites therefore consisted of a manipulation plot one hectare in extent in which all woody vegetation was removed, and an adjacent one hectare unmodified control plot. Replication of study sites within soil types was not feasible. The sites were selected with the aid of aerial photographs and ground surveys to satisfy the following criteria.

1. Representative of the species composition and density of one of the three major vegetation types identified above.

2. Soil hydrological characteristics distinct from the other two sites, so that in conjunction the sites should represent as broad a sample as possible of the range of savanna soil conditions.

3. Slope of 2 - 4%.

4. Relatively well developed soil without excessive stoniness.

5. Internally homogeneous as far as possible with respect to soil and vegetation.

6. Not excessively disturbed by proximity to water points.

The layout of the experimental plots at each site was identical in concept, although the positioning of the instruments varied slightly. The layout of the Acacia site was typical, and is illustrated in Figure 15 on page 64.

2.2.2 A COMMENT ON PSEUDOREPLICATION

Hurlbert (1984) criticises the design of many ecological studies on the basis that inferential statistical tests are applied to designs in which the replicates are not statistically independent, usually because they are clumped together in one plot rather than interspersed between the replicates of other treatments. The criticism is well founded, and applies to aspects of this study. The ecosystem-level researcher, however, is faced with a difficult choice. Should he concentrate his limited number of plots at one site, thereby strengthening the statistical inference but sacrificing generality, or should he spread the plots over the range of sites and abandon statistical tests?

This study has chosen to spread the plots; therefore all tests between the (unreplicated) treatment plots at a given site are, strictly speaking, invalid. However, it is still necessary to know the degree of error associated with sampling. Therefore replicate samples were taken in each plot. The magnitude of this error can only be assessed relative to the size of the treatment difference. The paired t-test (or similar) is a familiar and instructive vehicle for this comparison. The between-treatment tests should be interpreted in this light.

2.2.3 SOILS OF THE EXPERIMENTAL SITES

The soil hydrological characteristics were the dominant factor in the selection of the sites and are detailed in chapter 3. Table 2.1 and 2.2 describe the physical and chemical characteristics of the three soils prior to the experiment. The profiles are illustrated in Figure 14 on page 63. Although the Mopane site is intermediate between the Combretum and Acacia sites with regard to clay content, it is not necessarily intermediate on the eutrophy-dystrophy continuum. The first two sites represent elements of the same catenary sequence (but not the same catena), while the Mopane soils have a different pedogenic history.

Soil analyses were according to standard procedures (Black 1965, FSSA 1980). Cations were extracted in 1 N Ammonium bicarbonate at pH 7. Conductivity was determined in a saturated paste extract and texture by the hydrometer method. The values in Tables 2.1 & 2.2 are the means of two representative samples from separate pits (one located beneath a tree canopy and one in the open) in each treatment plot, thus four samples per horizon per site. Variation of the chemical properties within and between plots was high, which is a reflection of both the variability of nutrient availability typical of arid savannas and of the poor resolution of the analysis techniques.

2.2.4 VEGETATION OF THE EXPERIMENTAL SITES

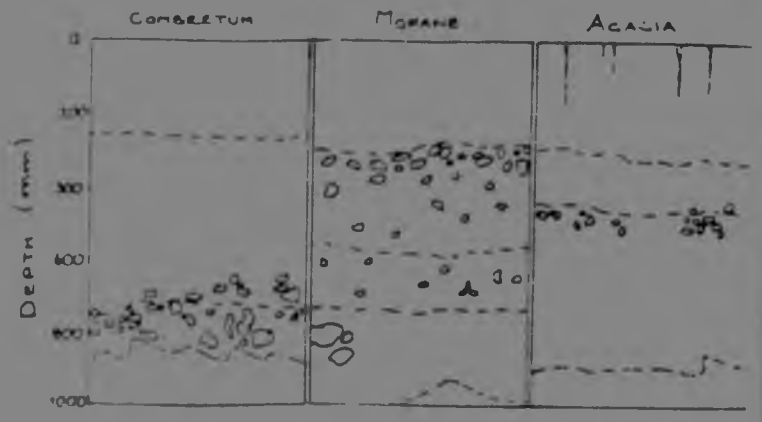
The rooted basal area of the herbaceous layer in each treatment was scored by the systematic placement of 2000 points per plot (10 lines of 200) using a Bruce-Levy bridge with 10 points of 1.5 mm diameter and point separation of 150 mm. The points were scored for contact with live plant material at ground level, plant litter and soil capping. The results are presented in Table 2.3. A significant pre treatment difference ($p<0.05$) between total grass basal area of the control and manipulation plot at the Acacia site was detected by a Wilcoxon rank-sum test and is

Table 2.1 Physical properties of the soil at each study site before clearing. Each value is the mean of four samples.

Site & Horizon		Depth	Bulk Density	Stoniness	Particle size distribution		
					Sand	Silt	Clay
		cm	kg m^{-3}	%	%		
Combretum	A	0-20	1.66	32	83	9	8
	B1	20-40		75	80	9	11
	B2	40-70		75	81	9	10
Mopane	A	0-25	1.79	12	79	4	17
	B1	25-40		62	74	3	23
	B2	40-80		56	68	6	26
Acacia	A	0-30	1.87	13	64	11	25
	B1	30-50		58	63	9	28
	B2	50-90		68	61	8	31

Table 2.2 Chemical properties of the soil at each study site before clearing. Each value is the mean of four samples.

Site & Horizon		Depth	pH 1M KCl	Nitrogen Total	Nitrogen Avail NO	Nitrogen Avail NH	P Bray 1	K	Major cations Na	Major cations Mg	Major cations Ca	EC
		cm		mg.kg^{-1}				cmol(+).kg^{-1}				mS
Combretum	A	0-20	[illegible]	532	4	15	13	0.49	0.60	1.40	3.34	686
	B1	20-40	[illegible]	350	8	11	9	0.45	0.85	1.85	3.41	585
	B2	40-80	[illegible]	387	0	9	6	0.47	0.83	2.14	3.90	629
Mopane	A	0-25	[illegible]	1070	0	12	15	0.78	0.09	2.12	9.09	326
	B1	25-40	[illegible]	730	0	18	5	0.36	0.07	2.91	12.58	298
	B2	40-80	[illegible]	730	25	22	15	0.35	0.14	3.35	23.34	300
Acacia	A	0-30	[illegible]	571	2	23	2	0.84	0.24	3.75	10.01	618
	B1	30-50	[illegible]	534	0	22	3	0.56	0.20	4.77	10.63	558
	B2	50-90	[illegible]	368	0	17	6	0.68	0.23	6.27	14.21	599



Combretum site

Series Glenrosa
Form Glenrosa

A_1 0-250 Orthic, brown 7 5YR 4/4 (moist) coarse loamy sand; loose, apedal; many medium and coarse angular quartz fragments; gradual transition.

B_{21} 250-700 Lithocutanic, bright brown 7 5YR (moist) coarse loamy sand, loose, many medium and coarse quartz fragments, gradual transition.

C 700-900 Bright brown 7 5YR 5/6 (moist) coarse sand, loose, apedal

R 900+ weathered gneiss

Mopane site

Series Zuiderzee
Form Valsrivier

A_1 0-280 Orthic, reddish brown 5YR 4/6 (moist) medium sandy loam; loose; apedal; many fine to coarse angular and half-round quartz fragments, few fine and medium roots; clear transition.

B_{21} 280-560 Pedocutanic, bright reddish brown 5YR 5/8 (moist) coarse sandy clay loam; hard; strong coarse blocky structure; few medium soft $CaCO_3$ concretions; many fine and medium angular quartz fragments, gradual transition.

B_{22} 560-720 Orange 5YR 6/8 (moist) medium sandy clay loam; slightly hard; strong medium blocky structure; common fine diffuse red mottles, many medium and coarse soft and hardened $CaCO_3$ concretions; common medium roots, gradual transition.

C 700+ Orange 5YR 6/8 (moist). Unconsolidated material.

Acacia site

Series Mayo
Form Mayo

A1 0-300 Melanic, very dark brown 10YR 2/2 (moist) medium sandy clay loam; hard; weak prismatic structure, many fine roots; clear transition.

B_{21} 300-500 Pedocutanic, dark brown 7 5YR 3/2 (moist) sandy clay loam, extremely hard; medium blocky structure, many fine and medium roots, gradual transition

B_{22} 500-900 Pedocutanic, dark brown 7 5YR 3/2 (moist) clay loam, extremely hard, medium blocky structure, many small half-rounded quartz inclusions, gradual transition

C 900+ Lithocutanic, bright brown 7 5YR 5/8 (moist)

Figure 14. Soil profiles at the three study sites

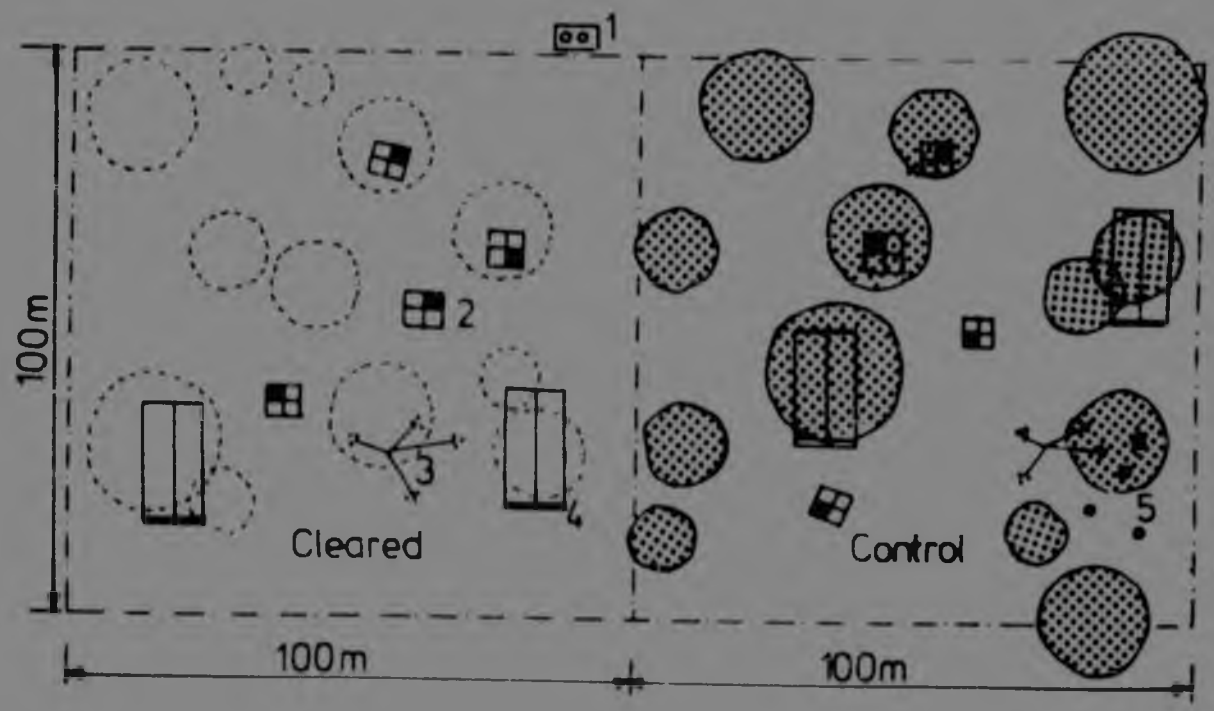


Figure 15. Layout of a study site: Based on the Acacia site, not to scale 1) Recording raingauges 2) Marked tillers and herbivore exclusion frames 3) Array of soil moisture sensors 4) Paired runoff plot 5) Lysimeters.

attributed to a patch of *Bothriochloa radicans* in one corner of the cleared plot.

The percentage bulk contribution by species was estimated by ranking the contributions in 100 0 5x0 5 m quadrats per plot according to the method of t'Mannetje and Heydock (1963), as modified by Barnes, Odendaal & Beukes (1982) The results appear in Table 4.1. The herbaceous layer composition was markedly different between the sites, but was not markedly different between the control and treatment plots within the sites prior to the experiment. The dry-weight-ranking method does not lend itself to statistical comparisons. The composition subse-

Table 2.3 Percentage rooted basal cover by grasses, November 1981.

Site	Acacia		Combretum		Mopane	
Species	Cleared	Control	Cleared	Control	Cleared	Control
Digitaria eriantha	0.36	0.69	0.24	0.36	2.80	2.20
Panicum maximum	0.27	0.21	0.12	0.33	0.50	0.50
Schmidtia pappophoroides	0.06	-	-	-	0.75	0.30
Aristida congesta	0.15	0.15	0.06	0.12	0.20	0.30
Bothriochloa radicans	1.47	0.27	-	0.06	-	-
Panicum coloratum	0.81	0.84	0.30	0.09	-	-
Other grasses	-	-	-	-	0.35	0.30
Cyperaceae	-	-	0.21	0.09	0.30	0.15
Forbs	0.06	0.06	0.09	0.27	-	-
Total	1.34	2.22	1.00	1.42	4.90	3.75
Standard error	0.95	0.78	0.67	0.62	1.06	0.15

quently changed as a combined consequence of the treatment and the drought.

Woody vegetation was characterised by recording the species, height, diameter above the basal swelling of each stem and the long and short canopy diameters of every woody plant occurring within eight 5x50 m systematically located belt transects per treatment. A woody plant was defined as having secondary lignification and the potential to grow above the herbaceous layer (i.e. exceed 1 m in height). Stems growing further than 0.5 m away from their nearest neighbour of the same species were considered to be individual plants. Plants with more than 50% of their rooted basal area within the transect were considered to be totally included, otherwise totally excluded. The plant density, basal area and canopy cover per species and site is presented in Table 2.4. The application of t tests to the data revealed no significant differences at the 95% confidence level between control and manipulation plots at each site.

Table 2.4 Density, basal area and canopy cover of woody plants at each study site prior to the experiment. Each value is the mean of eight replicate 5x50 m belt transects.

Species	*Density* (*plants.ha*$^{-1}$)		*Basal area* ($m^2.ha^{-1}$)		*Canopy cover* (%)	
	Clear	*Control*	*Clear*	*Control*	*Clear*	*Control*
1. Combretum site						
Combretum apiculatum	312	336	2.87	3.54	29.0	31.0
Sclerocarya birrea	84	164	0.97	2.20	4.1	10.2
Grewia bicolor	124	140	0.25	0.45	5.8	7.6
Cissus cornifolia	124	136	0.23	0.11	4.1	2.2
Others combined	164	116	0.18	0.58	2.6	7.6
Totals	808	892	4.50	6.88	45.6	58.6
Standard error	269	183	2.79	2.65	13.9	20.5
2. Mopane site						
Colophospermum mopane	872	731	6.40	9.50	35.7	36.3
Combretum apiculatum	72	200	0.40	1.10	4.4	8.3
Grewia bicolor	40	72	0.10	0.10	2.4	2.8
Others combined	-	77	-	0.24	-	2.6
Totals	984	1080	6.90	10.94	41.6	50.0
Standard error	420	127	3.00	2.74	11.3	9.1
3. Acacia site						
Acacia nigrescens	36	148	1.50	3.67	4.6	19.9
Sclerocarya birrea	24	16	0.70	1.20	3.8	3.5
Grewia bicolor	240	72	0.67	0.12	11.8	3.0
Cissus cornifolia	76	20	0.08	0.02	1.8	0.2
Others combined	148	432	0.27	0.42	7.1	4.3
Totals	524	688	3.22	5.43	39.1	30.9
Standard error	266	345	3.29	5.91	17.9	34.4

3.0 HYDROLOGY

The soil moisture regime, an expression of the integrated effect of all the hydrological processes operating at a site, is one of the primary determinants of savanna structure and function (Frost *et al* 1986). It is therefore logical to focus a study of structural/functional change in savannas on alterations in hydrological processes. Furthermore, soil moisture controls the soil nutrient status (the other primary determinant of savanna structure), both in the long term (through the rates of pedogenic processes) and the short term (by limiting nutrient availability).

There is much circumstantial evidence to suggest that primary production is directly linked to soil moisture availability in semi-arid savannas (Rutherford 1980). Several workers have sought to relate the bush clearing response to changes in soil moisture content (Strang 1969a, Pratchett 1978). Aspects of the water relations of savanna plants have been studied in detail, but the overall knowledge of the hydrology of semi-arid savannas is fragmentary. Bate, Furniss and Pendle (1982) present that which is available for southern Africa.

Hydrological changes as a consequence of savanna clearing are of interest for their own sake as well. Small changes in the proportion of water providing runoff or recharging the ground water could have major consequences in a semi arid region. Runoff is also very closely linked to erosion (Morgan, 1979). Leaching influences the nutrient balance of the system and most pedogenic processes.

A schematic hydrological flow diagram for a generalised semi-arid savanna is given in Figure 16 on page 68. The conceptual model has only one spatial dimension (the vertical) and thus does not apply to situations which receive a significant proportion of their water input from sources other than precipitation, for example run-on from adjacent areas or lateral

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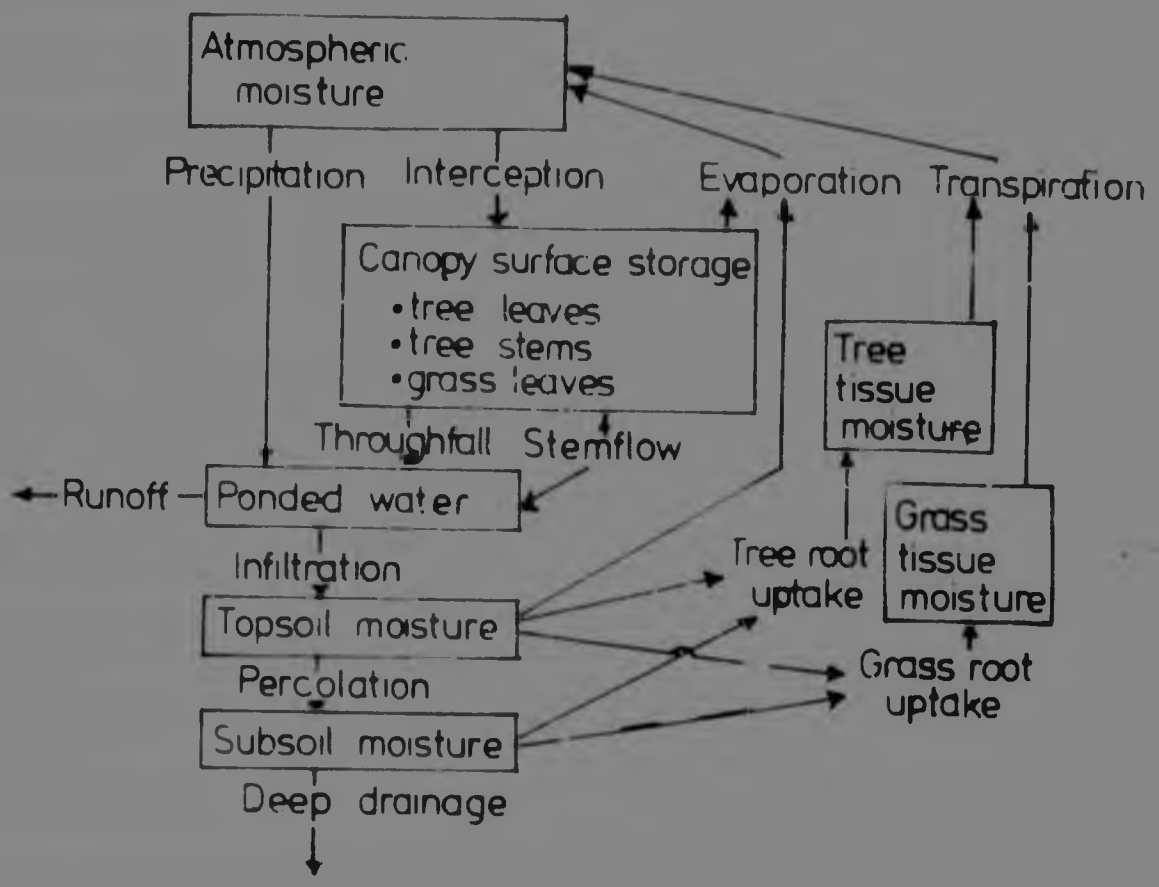

Figure 16 Generalised hydrological cycle for a savanna

subsurface flow. Thus riparian fringes and hydromorphic seeplines are excluded. These areas constitute a very small proportion of the Klaserie Private Nature Reserve, which is not to belittle their importance as wildlife habitats or areas of bush-clearing potential. The grass and woody dynamics of such areas differ qualitatively, however, from the generalised savanna scheme. Riparian fringes generally support dense thicket or tall gallery forest, permitted by the reliable supply of deep ground water. Seepline zones are generally treeless due to the alternating extremes of saturation and dehydration.

The simplifying assumptions that have been made in the general savanna hydrological model are as follows.

1. The atmospheric water pool is so large and mobile that it is independent of local terrestrial hydrological events. In other words, limited bush clearing does not alter the macroclimate.

2. Rainfall is the predominant form of precipitation and is the sole input of water into the system.

3. The savanna soil and vegetation are spatially homogeneous in a horizontal plane. The upper and lower scale limits of the model are defined by significant soil differences (at a scale of hundreds of meters) and the pattern imposed by tree canopies (ten meters) respectively. Some of the implications of these large and small scale variations are explored in the study

4. Trees and grasses are the only vegetation forms considered.

5. Hydrological cycling through higher trophic levels is insignificantly small. The internal plant water pool is relatively small.

3.1 PRECIPITATION

Rainfall at Klaserie is concentrated into the months of September to April, and occurs as convective storms of variable (but often high) intensity, usually in the late afternoon or evening, or as long-duration low-intensity drizzle associated with cyclonic systems. Rainfall statistics for the region are presented by Gertenbach (1980) and Green (1969a & b). Monthly rainfall recorded over the period of this study is given in Table 3.1., and daily rainfall in appendix 1

From a plant production viewpoint, the important parameters of rainfall are its depth (quantity) and temporal pattern The hydrologically important rainfall parameters are rainfall depth nd intensity. The data used to simulate long term rainfall patterns were those from the weatner station at Skukuza, 150 km southeast of Klaserie. Although Skukuza

Table 3.1 Rainfall by month and site during the study period. Daily rainfall data for each site is recorded in Appendix 1.

Month	1982/3			1983/4			1984/5		
	Combret	Mopane	Acacia	Combret	Mopane	Acacia	Combret	Mopane	Acacia
July			(2.5)						
August									
September									
October	8		(8)				150	105	149
November	13	20	27	164	87	162	99	145	87
December	12	13	10	85	60	116	44	104	90
January	63	68	56	120	56	83	195	228	188
February	4	6	3	38	73	58	100	91	101
March	102	83	127	127	96	74	102	114	92
April	13	15	15						
May		(22)	(12)				40	25	33
June		(6)	(6)						
Total	215	233	266	534	372	493	730	812	740

Values in parentheses are from the closest permanent raingauge.

(Combretum- Xanatseni gate; Mopane- Ntoma lodge; Acacia: Wardens HQ)

receives 10% more rainfall on average than Klaserie, the distribution of event probabilities is assumed to be similar, since both stations occur in the same climatic zone. A long record, such as is obtainable from Skukuza (since 1910), was held to be more important than an exactly equal mean annual rainfall. Where the Skukuza data were used for modelling purposes, the depths per storm were reduced to reflect the lower mean rainfall at Klaserie.

If the "Walter hypothesis" is correct in suggesting that the balance between trees and grasses is a reflection of topsoil to subsoil moisture distribution (Knoop & Walker 1984), then the storm depth distribution, along with a knowledge of the water holding capacity of the soil, should provide an indication of the frequency with which moisture penetrates to the subsoil. This analysis is presented in Figure 17 on page 72. It indicates that when individual storms are considered in isolation, only 10% of the annual rainfall moistens the soil to depths exceeding 300mm in the Acacia site, 20% in the Mopane site and 28% in the Combretum site. These are underestimates of the true moisture inputs into the subsoil, (especially on sandy soils) since rain frequently falls on soil already wet by previous storms, and the influence of unsaturated soil moisture movement is not included. The episodic nature of savanna rainfall, however, allows these distributions to be used as a crude index of the relative moisture status of the top- and subsoil.

Rainfall depths and intensities were recorded at each study site for the duration of the study by plastic rain gauges (100mm orifice) and tipping bucket recording rain gauges (200mm) respectively. The gauges were installed in a pit with their orifices at ground level. The minimum resolution was 0.5 mm in both cases. Bucket tips were recorded to the nearest second on paper tape by a printing calculator (Casio Fp-10). The times were then analysed to produce a storm hydrograph.

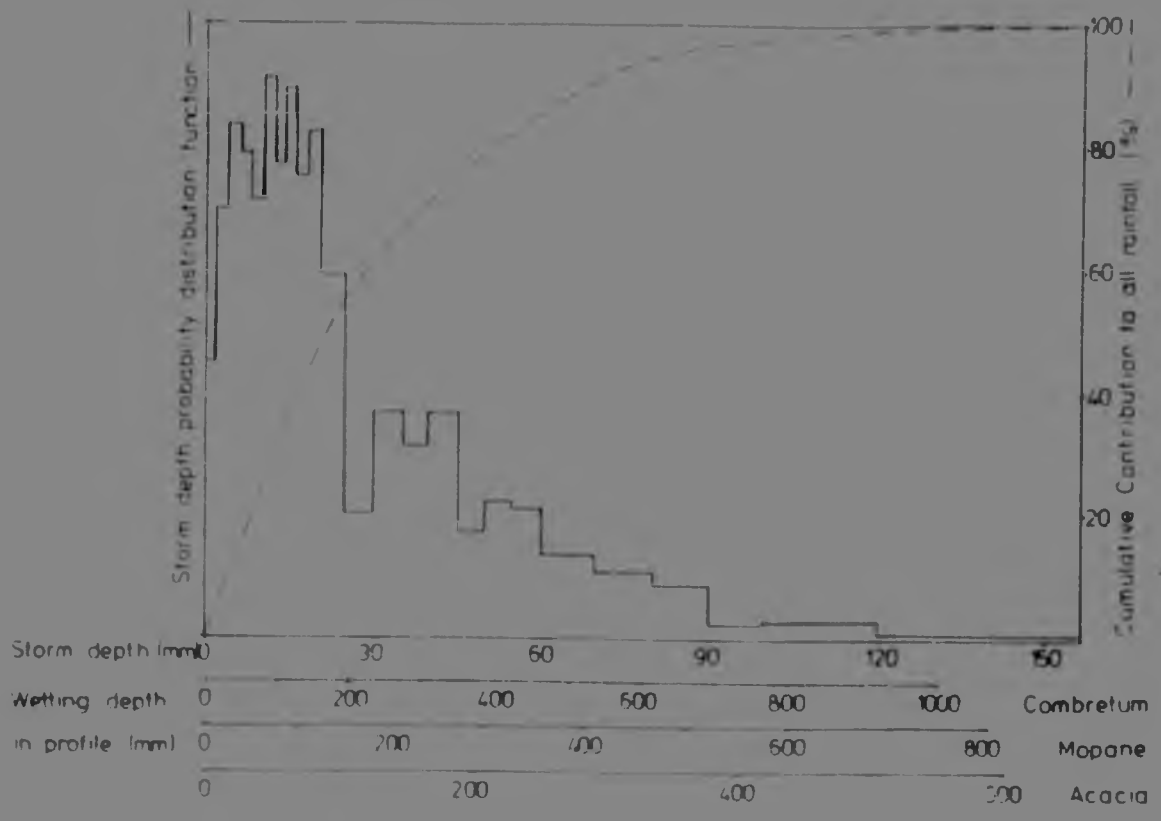

Figure 17. The distribution of storm depths: the histogram is the proportion of all storms in each depth class and the broken line is the cumulative contribution by each depth class to the total long-term rainfall. The wetting-depth equivalents to a storm of given depth are plotted for each study site, taking into account the water-holding capacity of the soil. The proportion of the rainfall penetrating beyond a given depth can be estimated by projecting a line vertically from the appropriate site axis to the broken line, and subtracting the corresponding value on the right-hand y-axis from 100%.

3.2 INTERCEPTION AND STEMFLOW

Interception is that portion of the incoming precipitation which initially strikes vegetation rather than the ground. Some of this intercepted rainfall drips off the canopy to the ground (throughfall). Provided the canopy is low (<6 m) these drops have a lower kinetic energy than incoming rainfall and thus result in higher infiltration, less splash erosion and less soil clay capping than direct rainfall. For modelling purposes, however, the throughfall was treated as direct precipitation, since the gain in precision is disproportionate to the increase in complexity (and uncertainty) which results from its inclusion as a separate variable.

A further portion of the intercepted rainfall runs down the plant stems to the ground (stemflow). While this constitutes a relatively minor portion of the total system water input, it has, like throughfall, an altered kinetic energy. Infiltration of this component of precipitation is further assisted by the presence of a crack between the bark and the soil, caused by the shrinkage and swelling of the stem and soil. Several workers have noted increased rainfall penetration beneath tree canopies (Pressland 1973), which is usually ascribed to stemflow. In its passage down the bark, the stemflow also picks up dust and plant exudates which result in it being nutrient enriched and dark brown in colour. For these reasons stemflow was regarded as an important contributor to the formation of the sub-canopy habitat and was recorded despite its small contribution to the overall water budget Since the focus was on the sub-canopy habitat, only stemflow of trees and shrubs was measured.

Various methods of gauging stemflow have been applied (Slatyer 1961, and de Villiers & de Jager 1981). All involve attaching a collar or gutter to the stem near ground level, which channels the flow into a container. In this study a spiral gutter made of 25mm diameter plastic hose was tacked to the tree stem and bonded to the bark with silicone sealant The spiral was kept shallow to prevent the flow from rushing out of the gutter, and consisted of at least one and a half turns around the stem (Figure 18 on page 74). The collecting containers were limited by practical considerations to twenty litres, and were sufficient for small



Figure 18. Stemflow collector

trees, but were frequently overtopped by large storms on large trees. The stemflow volume was measured by weighing the containers after each storm to the nearest 0 1 kg with a spring balance

Five specimens of each of the two species with the highest basal area in each site were fitted with stemflow gauges The five stems were selected to represent the range of diameters found in the site. In the Mopane site, all ten stems were allocated to *Colophospermum mopane*.

Regression analysis was used to relate stemflow yield to storm depth, duration and stem size Storm duration accounted for little variation in

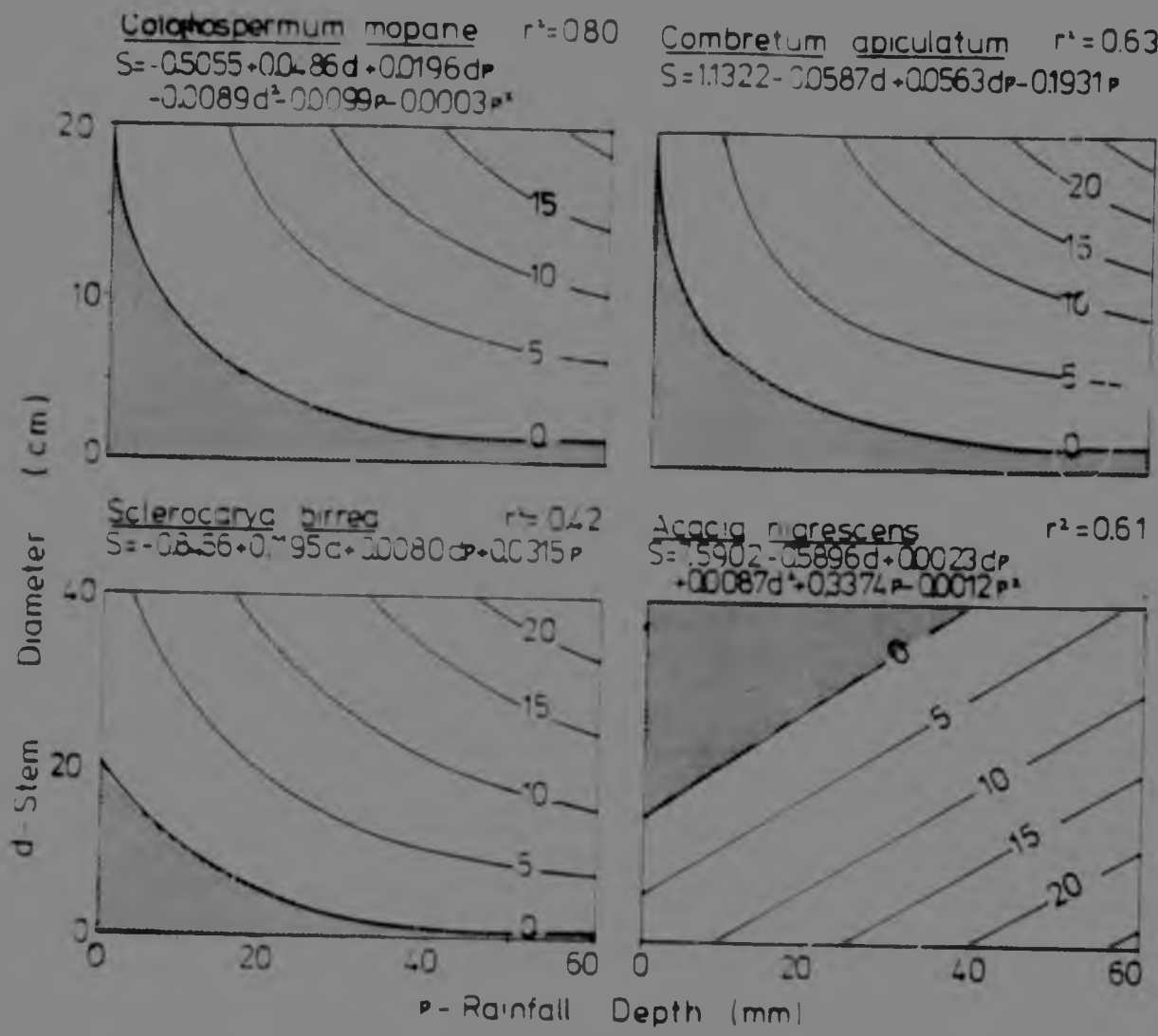

Figure 19. Stemflow per trunk as a function of stem size and storm depth.

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any of the models so it was excluded. Models including storm depth and stem basal diameter provided the best fits to the stemflow yield data, and are presented in Figure 19 on page 75. One third of the stemflow data were randomly excluded before the regressions were calculated, and were used for calculating the predictive power of the models, expressed as the r^2 values in the diagrams. The yields from *Grewia bicolor* were very variable and no plausible model could be fitted.

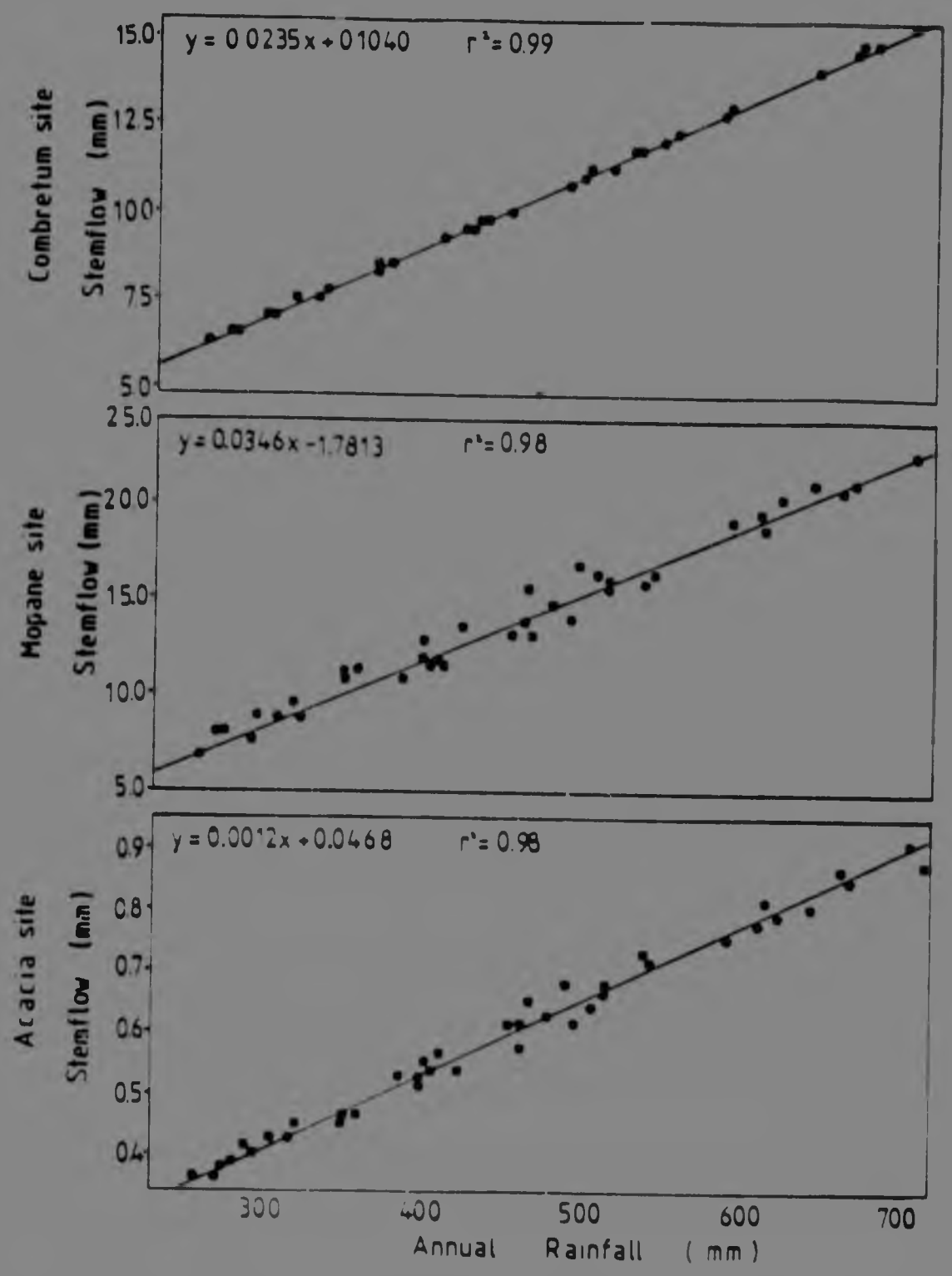

Figure 20. Stemflow per hectare per annum as a function of annual rainfall: n=40, some points are coincident

The atypical form of the stemflow-rainfall-stem diameter relation for *Acacia nigrescens* is thought to be due to the high trunk storage capacity and horizontal canopy architecture of this species. The spreading branches of large trees limit the stemflow reaching the trunk to an amount less than the storage capacity Therefore large trees yield less stemflow than small.

Stemflow per unit ground area per year cannot be estimated by simple multiplication of the estimates per stem per storm by the number of stems per hectare and the number of storms per year, due to the strong non-linearities in the prediction equations. The probability distributions of storm sizes and stem diameters must be taken into account. The former were obtained from forty years of rainfall records at Skukuza, and the latter from the initial site survey data. These distributions, when substituted into the equations for estimating stemflow per stem, yielded the long-term stemflow predictions presented in Figure 20 on page 76. While stemflow contributes a minor component to the annual water budget (3% Mopane site, 2% Combretum site and 0.2% Acacia site), if this supply is considered to be concentrated into an area of 0.25m radius around the stem, the local contribution can be considerable. Assuming an annual rainfall of 500mm, this area receives an additional 300, 250 and 500mm of moisture as stemflow (over and above the throughfall it receives) on each site respectively.

The third possible fate of intercepted precipitation is to be evaporated from the wet plant surfaces. Water leaving the system in this fashion is known as interception loss Whether it is a true loss, or whether by the cooling and humidifying effect of its evaporation it partially replaces transpiration losses (McNaughton 1981) is an unanswered question. Since it occurs at a time when transpirational demand on the plant is low (due to low temperatures and high humidities following a storm) it seems conservative to treat it as a loss

The magnitude of interception losses in semi-arid savannas is largely unknown, but has been estimated as up to 15% of the annual rainfall by de Villiers (1982). Estimates for grasslands, which have a much higher leaf area index than savannas, are considerably lower (Burgy & Pomeroy

1958, Beard 1962, Whitmore 1971), which suggests that the de Villiers (1982) figure is an overestimate. Sophisticated models of interception loss, such as those by Rutter *et al* (1971) and Gash (1979) allow for evaporation from wetted surfaces during and after the storm. For the short-duration high-intensity storms characteristic of semi-arid savannas, however, it is pragmatic to ignore evaporation which occurs during the storm. Assuming that the plant has a negligible ability to absorb moisture directly through its canopy surface, interception loss per storm can then be equated to the canopy storage volume for a fully saturated canopy, this being the amount of water available for evaporation after the storm. The canopy storage volume is that quantity of water held on the wetted exterior of a plant against gravity. It is composed of a leaf storage volume and a stem storage volume, and for the purposes of this study is treated as a constant per unit area of each substrate, regardless of storm intensity, wind direction and speed.

Leaf and stem storage volumes were determined for the dominant tree and grass species at each site by measuring the increase in mass of fresh leaf and bark sample after wetting with a fine mist spray. The surface volumes for the entire plant were calculated from regressions of leaf and stem surface area against stem diameter The values for the storage volume of tree leaves appear in Table 3.8, and the regressions in Table 4.1.

Simulation modelling revealed these estimates to result in net interception losses considerably lower than published estimates, which are in the range of 5-10% of the annual precipitation The method of estimating canopy storage volume may have underestimated the true storage volume, or the evaporation during the storm may be higher than expected.

3.3 RUNOFF AND INFILTRATION

The precipitation which reaches the ground surface either percolates into the soil (infiltration) or runs off the soil surface (runoff), initially as overland flow and ultimately as streamflow. Infiltration and runoff are thus complementary, and will be discussed as a single phenomenon.

Runoff is of paramount importance to engineering hydrologists and soil conservationists and there is a good empirical knowledge of the factors that influence it (Morgan 1979). There is however no definitive physical description of the process of infiltration, despite much interest in the field (Philip 1969). Equations of many forms can be fitted to steady-state cumulative infiltration data (Collis-George 1977), and the choice of which to use is dependent on convenience rather than rigour. Most follow Philip (1969) in describing cumulative infiltration as the sum of two terms. The first (sorbtivity) is proportional to the square root of elapsed time, while the second is directly proportional to elapsed time. The infiltration rate thus tends to the saturated infiltration rate as time tends to infinity.

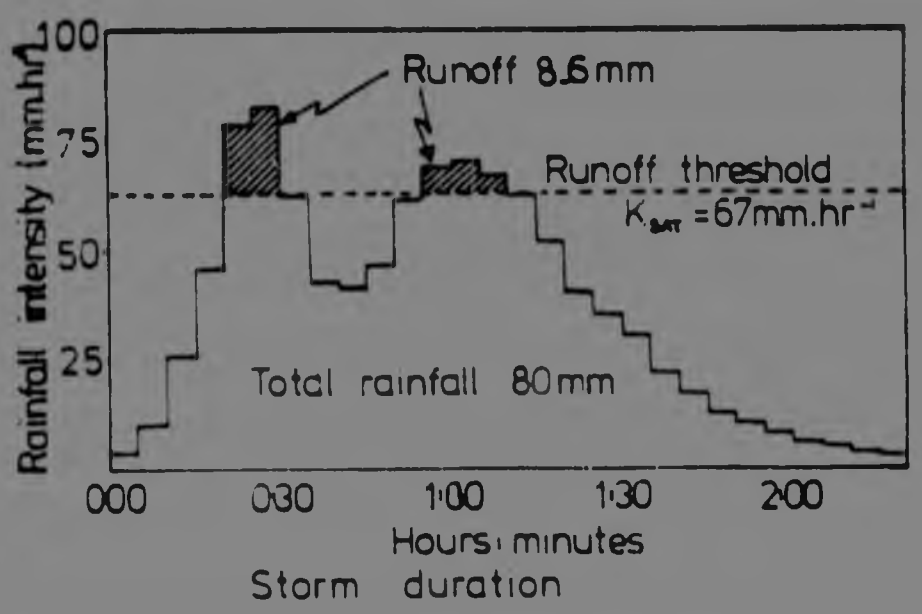

Figure 21. Calculation of infiltration rate from a storm hydrograph: a hypothetical example.

Table 3.2 Estimates of the critical infiltration rates at each site derived from runoff data and storm hydrographs.

Site Plot	Day	Rainfall (mm)	Infiltration rate ($mm.hr^{-1}$) Grassland 1	2	3	4	Woodland 5	6	7	8
Combretum	262	77	50					50		
	494	35	70	70				70	70	
	500	63	144			106	142	144	137	
	580	82					132	132	158	158
	634	75	96	112				89	100	106
Mopane	526	18	60	60	60	54	60	54	54	53
	630	48	151	133		151	151		133	133
	871	23	145	141	141	133	151	151		172
	883	75	175	175		152	189	175	189	175
	934	95	142	152	142	78	152	142	142	152
	956	49	84			81				
	989	39	226		226	174				
Acacia	500	57	142	152			141	132	118	
	517	24	79	79			61		79	
	526	60	152	164	164		152	152		
	527	12					73	70	73	73
	577	22	80							
	580	24	142				180	200		
	600	38	73		89		89			89
	923	30	190		190		193		193	
	932	67	61	61	61		61			
	992		112		112					

Further complexity is introduced when natural rainfall is considered rather than ponded infiltration or steady-state simulated rainfall, since natural rainfall fluctuates in intensity and energy.

Runoff was measured in each site by gauging the output of eight standard length (22 m) runoff plots with a tipping bucket flow-meter (Figure 22 on page 81). The width of the plots was 1.8 m in the Mopane site where the tree canopies were small and closely spaced, but 3.6 m in the other two sites to allow a more representative sample of the sub-canopy area.



Figure 22 Runoff plot equipped with a tipping-bucket flow-meter: number of tips is recorded by a mechanical counter.

The plot walls were constructed of galvanised steel sheet (0,3 mm x 350 mm) buried to a depth of 150 mm. The plots were paired to reduce variability and construction costs, with two pairs (four plots) in the wooded and two pairs in the bush cleared area. The plots were placed so as to include tree canopies, but avoid abnormal patches such as termitaria or gullies, and were oriented perpendicular to the slope contours. They were constructed a year before bush clearing began, to allow them to stabilise and to permit a pre-clearing control runoff level to be established. The latter objective was not satisfactorily achieved due to the paucity of rainfall events during the pre-clearing season.

Total runoff is the integral of the difference between the instantaneous rate of water supply to the soil surface and the infiltration rate. The runoff per storm for each plot was expressed as a depth in millimetres by dividing the runoff volume (corrected for the gutter area) by the plot

area. Storm duration, which bears little relation to the instantaneous rainfall intensity, accounted for very little of the variance in runoff yield and was ignored in further analysis. The procedure by which infiltration rate was estimated from cumulative runoff data and 5-minute rainfall rates is illustrated in Figure 21 on page 79. The assumption is that infiltration rate is constant over the period of the storm. While this is obviously incorrect (Collis-George 1977), a dynamic approach to infiltration rate would have been beyond the scope of this study.

The critical infiltration rates for storms at each site as calculated by this method are presented in Table 3.2. The variability is enormous, and is due to high spatial variability (between runoff plots) as well as high temporal variability due to variations in storm depth and intensity and ground cover conditions over the period of the study. The high variability masks any treatment effect which may have been present.

The approach of Barnes (1974) of simply plotting infiltration against storm depth suffers from a high degree of self-correlation, leading to spuriously well-fitted models. Therefore runoff was directly plotted against storm depth. The plots (Figure 23 on page 83) show a wide scatter of points. The runoff yields from the different sites cannot be directly compared since they come from storms with different characteristics. Regression lines were calculated so that they formed a maximum and minimum envelope which included most of the points. The qualitative conclusions that can be drawn from them are that the regression slope for the maximum envelope, which is inversely related to the steady-state infiltration rate, was highest on the Mopane site. The regression intercept, which is directly related to the sorbtivity factor in the Philips equation, was highest on the Mopane site and lowest on the Acacia site. Overall the Mopane site lost 2-15% of its rainfall as runoff, the Acacia site 1-7% and the Combretum site 0.5-5%.

The experimental design is pseudoreplicated so inferential statistics tests cannot be applied to the results. Runoff per treatment, as a percentage of total precipitation, is presented for each site in Figure 24 on page 84.

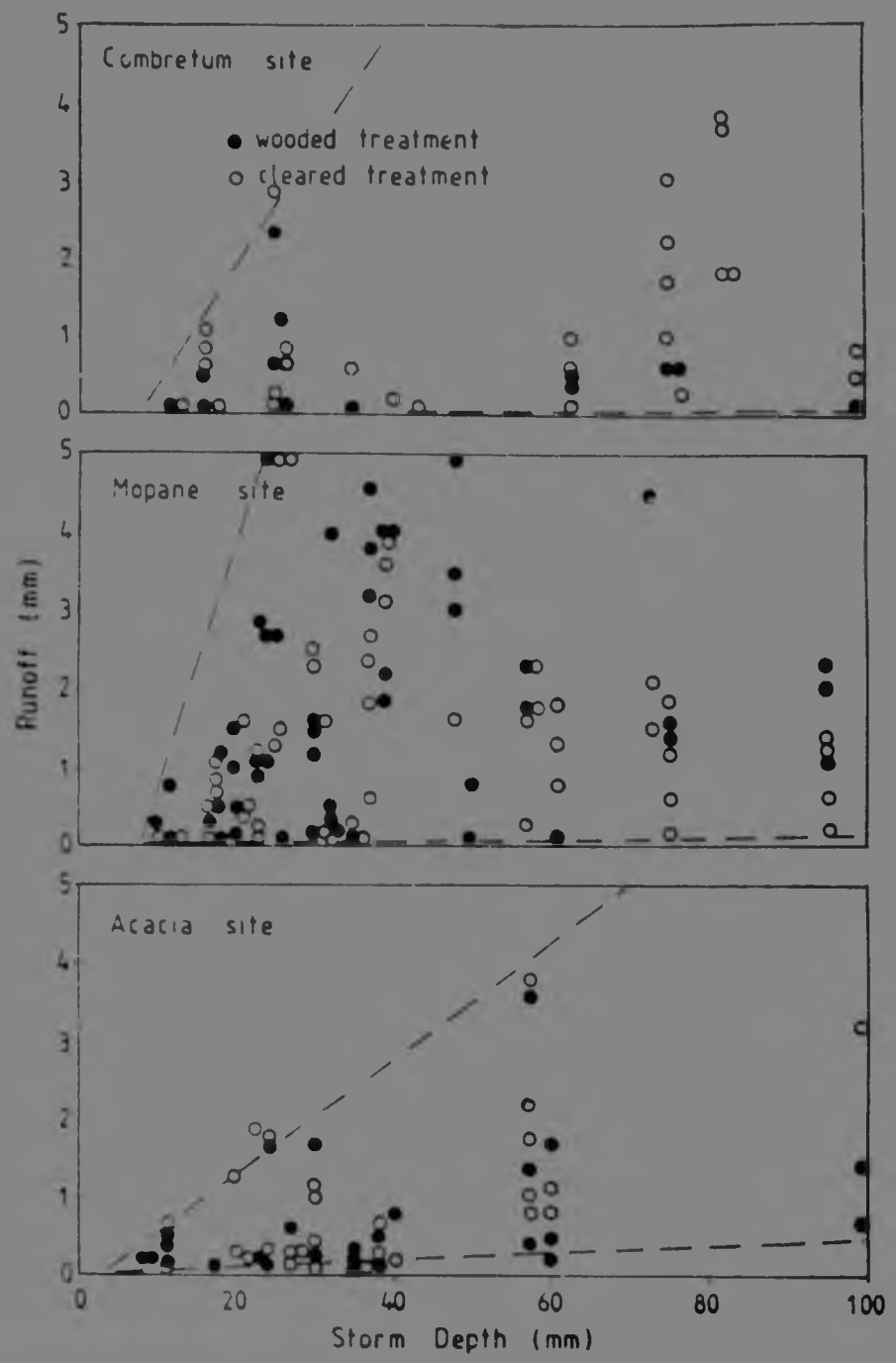

Figure 23. Plots of runoff depth versus rainfall depth: the lines represent the maximum and minimum envelopes which include most points.

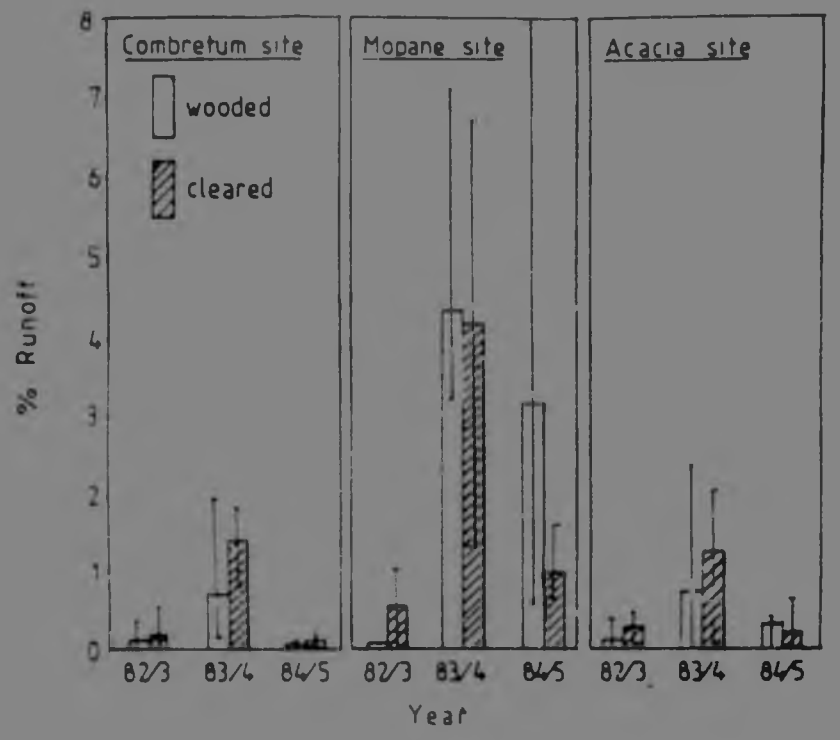

Figure 24 Percentage runoff per treatment and site: mean of four plots per treatment, bars represent the maximum and minimum range recorded. Clearing took place in the winter of 1983.

The figure shows an increase in runoff in all sites during the 1983/4 season, when the grass cover was extremely low due to the drought. The increase is greater on the cleared treatments than the control treatments at the Combretum and Acacia sites, but not at the Mopane site. There was a general trend towards lower runoff in grasslands than woodlands in the second post-clearing season, once a good grass cover was established. The variability between runoff plots is indicated by the range of values obtained. In each treatment there was at least one "rogue" plot which consistently yielded more runoff than the others, possibly due to crust formation on the surface.

The consistently greater runoff yield from the Mopane site illustrates the danger of assuming that the soil clay content continuum necessarily reflects a continuum in hydrological (or nutrient) properties. The silt

content and the distribution of sand grain sizes are also important, as well as the clay mineralogy. In this case the Mopane site, a sandy loam, has a clay content (17%) intermediate between the loamy sand Combretum site (8%) and the sandy clay loam Acacia site (25%), yet the runoff yield is higher. This can be attributed to the tendency of the Mopane site soils to form both raindrop impact crusts and microfloral crusts on the soil surface, which reduce the infiltration rate. There is a higher proportion of smectitic clays at the Acacia site (inferred from the cracking in the profile) which may prevent crust formation by their self-mulching action.

3.4 SOIL MOISTURE DYNAMICS

The theoretical dynamics of soil water storage and movement have been widely studied, and a large number of empirical predictive models have been developed (Haverkamp, Vauclin, Touma, Wierenga & Vachaud 1977 and de Jong & Cameron, 1979). It is usual to divide soil moisture movement into two types, although the transition between them is continuous and broad. When the soil is at or near saturation (more than approximately 80% of the pore space is occupied by water), flow is relatively rapid and is described by Darcy's law in terms of the hydraulic head gradient (with gravitation as the major component) multiplied by the soil saturated hydraulic conductivity (K_{sat}) which is a function of pore size and tortuosity. When this "gravitational water" has drained away the soil is said to be at field capacity. When the soil is drier than this, the hydraulic gradient is dominated by the matric potential (which is a function of soil moisture content) and flow is said to be unsaturated.

The theory of flow in unsaturated porous media is based on work by Childs & Collis George (1950) and Millington & Quirk (1961). The principal difference between saturated and unsaturated flow is that the hydraulic conductivity at soil moisture levels below saturation is strongly non-linearly related to soil moisture content (θ). Hydraulic conductivity

decreases nearly exponentially with a decrease in soil moisture content, causing unsaturated flow at say 50% of field capacity to be orders of magnitude slower than saturated flow. Thus most of the movement of water in soils is due to saturated flow, especially when the soils are coarse-textured. Thus for many purposes unsaturated flow can be ignored, as it has been in previous models of savanna dynamics (Walker *et al* 1981, Walker & Noy-Meir 1982, McMurtrie & Wolf 1983). However, when there are strong hydraulic gradients in the soil and long periods between successive wetting events, unsaturated flow could be a significant component. Since these conditions frequently occur in semi-arid savannas, and small moisture fluxes could make a critical difference to coexistence models based on the differential rooting depth hypothesis, the effects of unsaturated hydraulic conductivity were included in this study.

The relationship between the hydraulic conductivity at a given soil moisture content ($K(\theta)$) and the soil moisture content is usually assumed to be unique for a given soil type (although it is probably hysteretic to varying degrees). Since it is determined by the soil matric forces, which are in turn determined by the particle size distribution, it is related to the soil moisture characteristic curve, the function that describes the dependence of soil water potential (ψ) on soil moisture content. Since both functions are difficult to determine, such a relationship would be very useful, and several attempts have been made to define it (Jackson, Reginato & van Bavel 1965, Maulem 1976). No generally accepted or universally applicable form exists for either function however, and thus the equations chosen to express (and therefore link) them are based on considerations of computational ease rather than physical theory.

The system suggested by van Genuchten (1980) has been used in this study because it is consistent, mathematically tractable and has a minimum of parameters. The problem of unsaturated flow then resolves into one of determining the parameters.

Water flow in the soil can also occur in macropores (Beven & Germann 1982). The importance of this mode of flow is largely unknown and is probably highly variable both between soil types and spatially within one

soil type. Macropores are common in clays, and are probably most important there due to the low hydraulic conductivity of the bulk soil. Swelling clays present a special problem, since the vertical cracks which they develop when dry form ideal macropores, but soon close up due to the swelling of the clays once wetted; thus the $K(\theta)$ curve is not unique. The Acacia site in this study probably behaves in this manner to some degree. Once the moisture has penetrated the profile via a macropore its rate of absorption into the soil mass is limited by the rates of conventional soil water movement processes, which somewhat reduces the importance of macropore flow.

3.4.1 SOIL WATER POTENTIAL

The characteristic curves were determined on disturbed samples on a pressure plate apparatus. Two soil samples were run for each soil type and horizon at each pressure head (-30, -100, -200, -500, -1000, and -1500 kPa). The moisture content after equilibration was determined by mass loss after drying at 105 °C for 24 hours, and converted to a volumetric proportion by multiplying by the bulk density, determined by the clod immersion technique. A function of the form described by van Genuchten (1980)

$$\theta = [1/1+(a\psi)^n]^m \quad \ldots 3.1$$

where

$$\theta = (\theta - \theta_{res})/(\theta_{sat} - \theta_{res}) \quad \ldots 3.2$$

and θ is the relative volumetric soil moisture content, θ is the volumetric soil moisture content, θ_{res} is the residual soil moisture content after prolonged air drying, θ_{sat} is the soil moisture content at field capacity, ψ is the soil water potential (kPa) and a, m and n are constants, was fitted to the points using a statistical curve fitting routine (SAS NLIN, SAS Institute 1982) (Figure 25 on page 88). The values of θ_{sat} and θ_{res} were determined *in situ* by taking soil samples a few hours after a

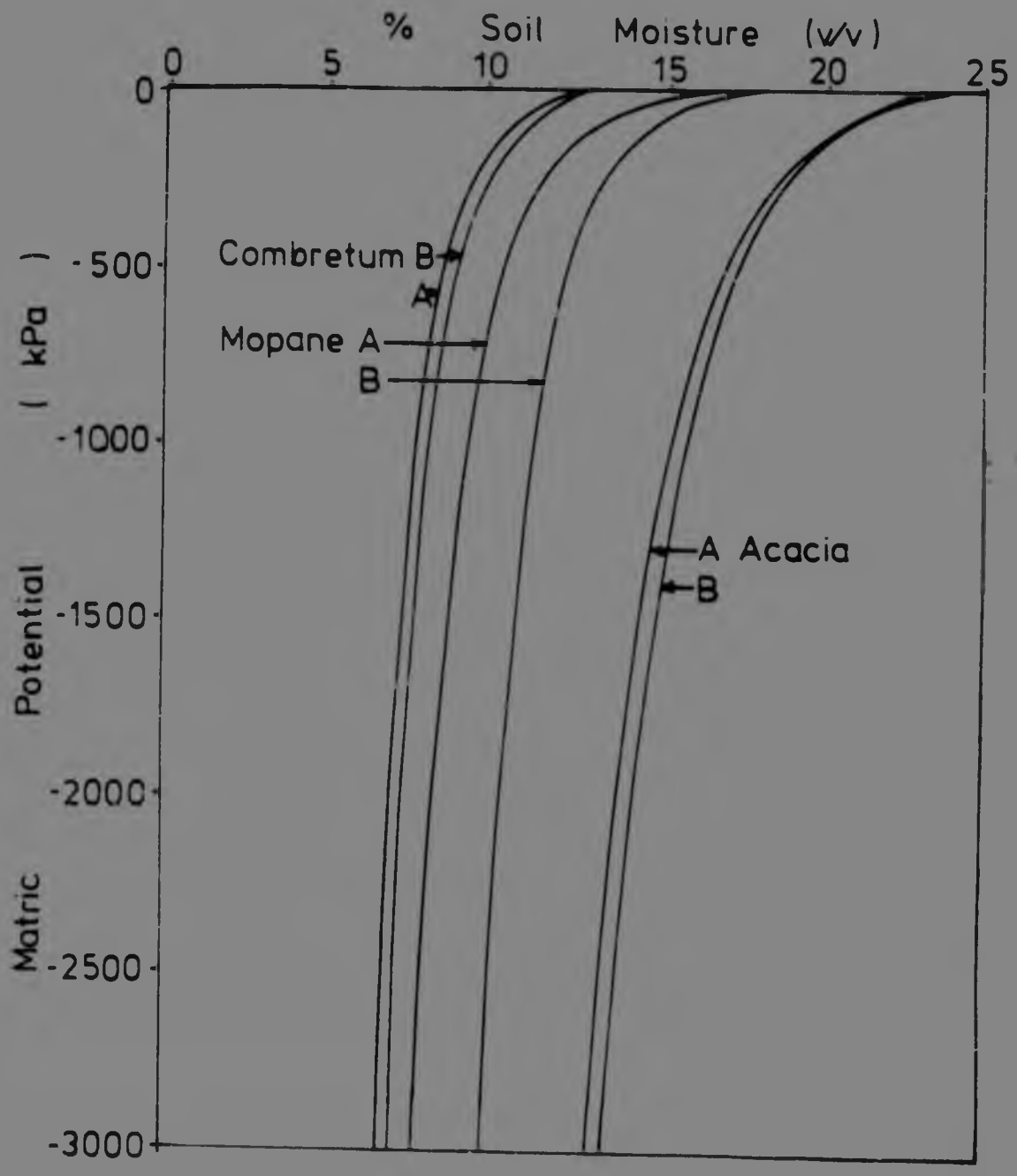

Figure 25. Soil moisture characteristic curves

large storm and after a prolonged period of drought respectively. The characteristic curve parameters for each site are given in Table 3.3.

Table 3.3 Soil characteristic curve constants.

Site	Horizon	θ_{sat}	θ_{res}	m	a
Combretum	A	0.127	0.012	0.2275	0.0231
Combretum	B	0.133	0.012	0.2306	0.0192
Mopane	A	0.165	0.017	0.2890	0.0200
Mopane	B	0.180	0.021	0.1925	0.0317
Acacia	A	0.237	0.052	0.4401	0.0048
Acacia	B	0.237	0.052	0.4011	0.0050

3.4.2 THE HYDRAULIC CONDUCTIVITY FUNCTION

The hydraulic conductivity function was derived by manipulating the characteristic curve, following van Genuchten(1980).

$$K_{rel}(\theta)=\theta^{\frac{1}{2}}[1-(1-\theta^{1/m})^{m}]^{2} \quad ..3.3$$

where

$$K_{rel}(\theta)=K(\theta)/K_{sat} \quad ..3.4$$

and $K_{rel}(\theta)$ is the relative hydraulic conductivity at θ, $K(\theta)$ is the true hydraulic conductivity and K_{sat} is the saturated hydraulic conductivity. The calculated $K_{rel}(\theta)$ functions are illustrated in Figure 26 on page 90

The value of K_{sat} was estimated by successive approximation in order to match simulated soil moisture profiles against those measured in root-free soil columns in the field

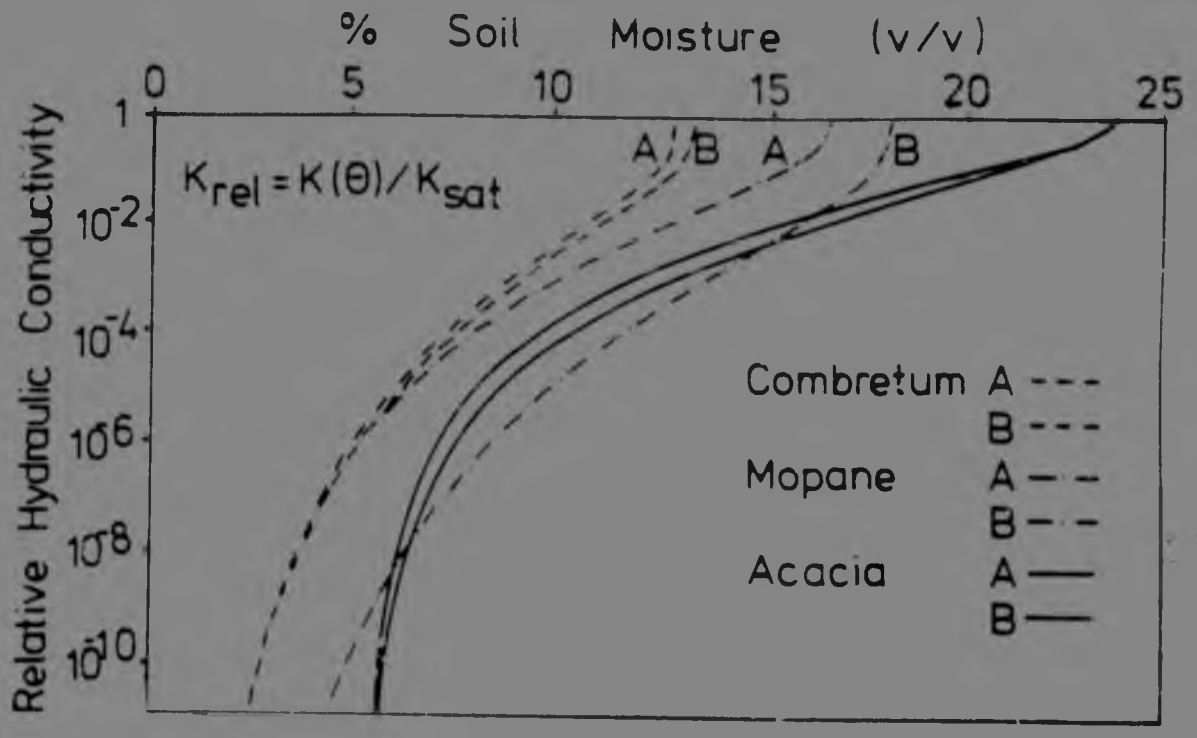

Figure 26. Calculated relative soil hydraulic conductivity

3.4.3 SOIL MOISTURE CONTENT

Soil moisture content was monitored routinely for each treatment at each site using an array of gypsum block sensors (Bourget, Elrick & Tanner 1958). Two types were used (for reasons of availability); Delmhorst blocks at the Mopane site and Beckman CEL-WFD blocks elsewhere. The arrays consisted of twelve blocks, equally divided between sub-canopy habitat and open areas, with two replications in each. Each replicate consisted of three blocks, buried at depths of 50 mm, 350 mm and 700 mm. These depths corresponded approximately with the soil surface layer, the transition from A to B horizons, and the B to C horizons.

A soil column approximately 1 m in diameter surrounding one of the sub-canopy replicates and one of the open replicates in the treatments destined to be bush-cleared were sterilised by the addition of 30 g of tebuthiuron ("Spike") to the soil surface. These columns functioned as controls, free of root water uptake. Soil water changes in these columns were therefore purely as a result of soil and atmospheric factors. Tebuthiuron has a soil half-life of about two years, and dosage was repeated annually at the beginning of the rainy season. No plants grew within the sterilised area and the moisture data from the columns suggest that no major recolonisation by roots from surrounding areas occurred. Tebuthiuron is inactivated by clays, and sterilisation of at least one of the Acacia site columns was incomplete.

Moisture could be lost from the root-free columns by evaporation or by vertical or lateral flow into the adjacent soil. The relative importance of lateral versus vertical flow was difficult to assess, but the persistence of moisture in the sterilised columns through the winter months (when the surrounding soil was dry) suggests that both were minor in comparison to evaporation.

Blocks were placed by augering separate holes for each, and tamping the block into position surrounded by sieved (<2 mm) soil of the same horizon. The lead wires were brought to a central metering point which was within 5 m of the placement. Blocks were placed at least three months before metering began to allow for equilibration.

Metering was via a circuit described by Goltz, Benoit & Schimmelpfenning (1981), modified by the addition of a selector switch to allow the entire array to be measured through a single connector. The accuracy of metering was greatly in excess of the accuracy of calibration of the blocks.

The blocks were individually calibrated against known soil water potentials in a pressure plate apparatus. Calibration was conducted at -30, -100, -200, -500, -1000 and -1500 kPa in sieved soil from the horizons in which the blocks were to be buried (Figure 27 on page 92), simultaneously with the determination of the soil characteristic curve. All soil moisture values were expressed on a volumetric basis. The calibrations

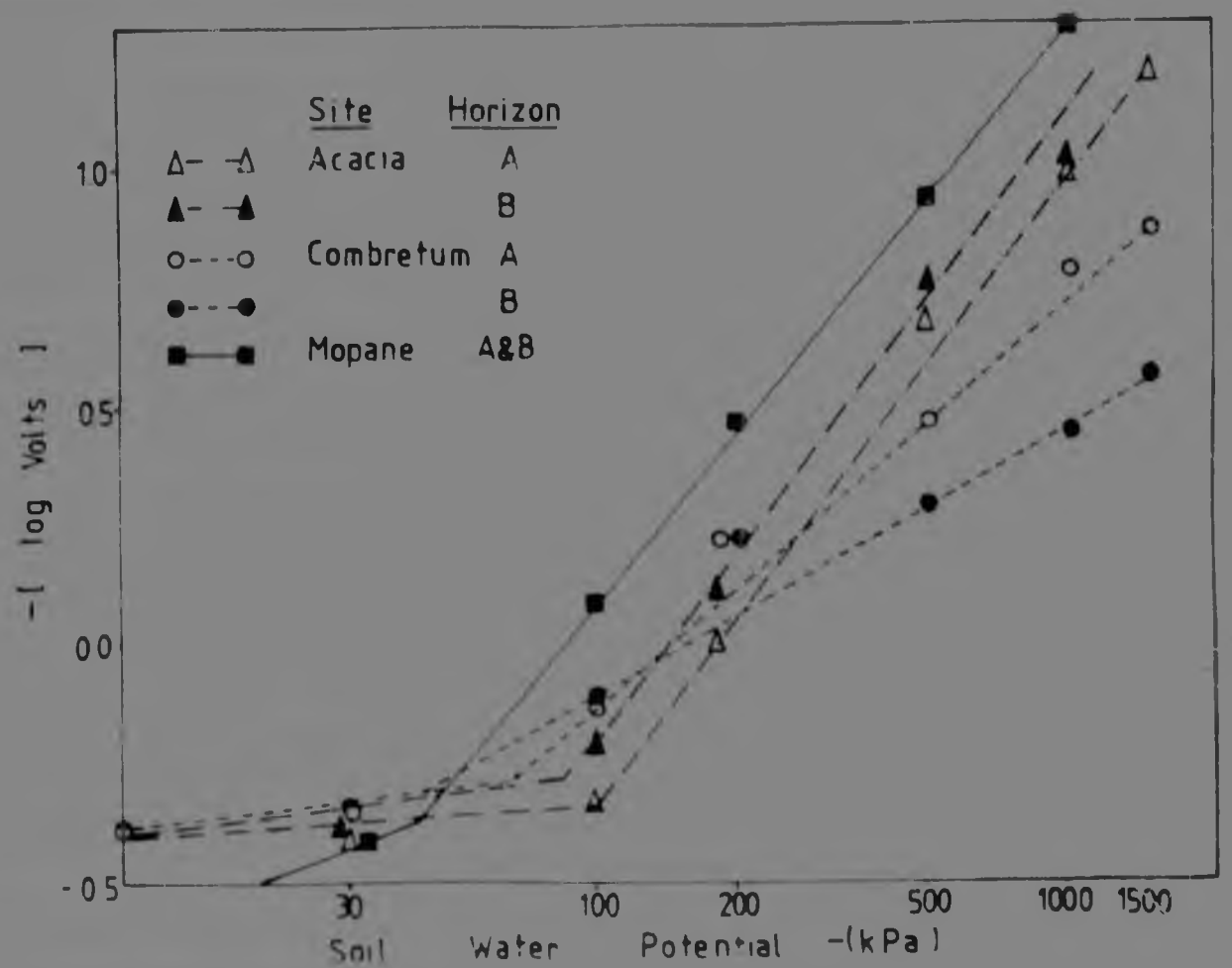

Figure 27. Mean calibration curves for gypsum moisture blocks on the pressure plate apparatus.

were checked *in situ* by taking gravimetric moisture samples at the high and low extremes of the moisture range as indicated by the buried blocks. The laboratory and *in situ* calibrations were highly correlated, (Combretum site F=56.41, n=11, p<0.0001, Mopane site: F=44.07, n=9, p<0.0002; Acacia site F=54.91 n=10 p<0.0001) but the laboratory calibration overestimated the field moisture levels. This is due to the use of disturbed soils in the laboratory, as well as inherent inaccuracies in the pressure plate method. The *in situ* calibration was used in further calculations.

Soil temperatures were taken at each depth for the first season in order to correct for the temperature dependence of the blocks, but was found to fluctuate little on a daily basis, except at the surface. In relation to the accuracy which can reasonably be expected with the use of gypsum blocks the increase in precision did not justify the increase in effort required to make this correction.

A computer program was written to convert the meter readings (in volts) to soil water potential, via the calibration curves and then to soil moisture content via the characteristic curve. The soil moisture status data for the experiment are graphically summarised in Figure 28 on page 94, Figure 29 on page 95 and Figure 30 on page 96. In the graphics, the thickest lines represent periods of near-saturation (>-100 KPa), the medium lines moisture adequacy (100-500 KPa) and the thinnest lines partial stress (500-1500 KPa). Blank spaces occur where the soil water potential was below -1500 KPa. Blank spaces within the "wet" areas represent days on which no data were available; the water status is inferred from neighbouring records.

Soil moisture readings were taken daily after rainfall (when conditions permitted) until the soil reached wilting point (as determined from the vegetation condition) and thereafter every three days, or in times of prolonged drought, weekly. The sampling scheme was therefore neither random nor fully systematic, and the frequency of days on which the soil profile was recorded as having plant-available moisture ("wet days"; $\psi <$ -1500 kPa; Table 3.4) is positively biased relative to the true frequency. However, all the blocks were always measured on the same day, and the data can therefore be tested for differences in the duration of plant-available water between blocks using the χ^2 test of association. The unequal sample sizes are due to the use of half of the soil moisture blocks in the cleared treatments to monitor the root-free columns and to occasional electronic failures (hyenas and elephants were both intrigued by the exposed connector sockets). Where the term "overall" is used in the following discussions, it means that the treatment was regarded as being "wet" if plant available water was present at any depth at any one of the sensors (excluding those in the root-free columns, which constitute a treatment on their own).



Figure 28. Soil moisture content during 1982/3 wet season periods of plant available moisture by site, treatment and depth. The thickness of the line indicates relative water availability.



Figure 29 Soil moisture content during 1983/4 wet season: periods of plant available moisture by site, treatment and depth. The thickness of the line indicates relative water availability

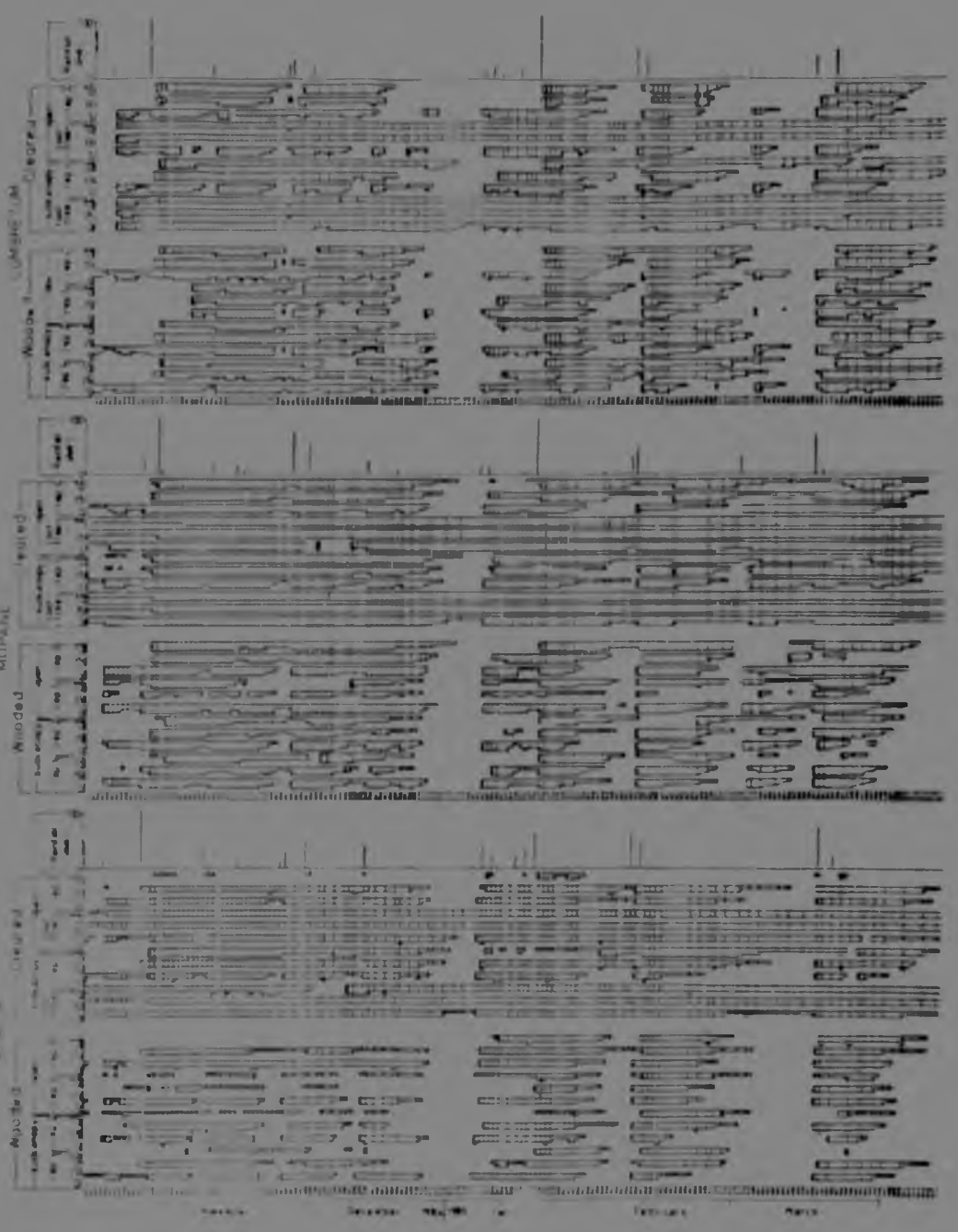

Figure 30. Soil moisture content during 1984/5 wet season: periods of plant available moisture by site, treatment and depth. The thickness of the line indicates relative water availability.

Table 3.4 The frequency of days without plant-available water in the soil profile ("dry") in treatments with and without woody plants.

Site & season	Depth (mm)	Wooded Dry	Wooded Wet	Cleared Dry	Cleared Wet	Frequency Dry Wooded	Frequency Dry Cleared	Chi square	Probability	
Combretum	50	101	195	67	75	0.34	0.48	7.776	0.005	**
82/3	350	199	97	85	59	0.67	0.59	2.848	0.092	*
	700	244	52	132	12	0.82	0.92	6.646	0.010	
	all	13	61	8	66	0.18	0.11	1.387	0.239	
83/4	50	97	231	53	109	0.30	0.33	0.504	0.478	
	350	131	197	74	88	0.40	0.46	1.468	0.226	
	700	145	183	70	92	0.44	0.43	0.044	0.834	
	all	18	64	0	82	0.22	0.00	20.220	0.000	***
84/5	50	116	320	63	153	0.27	0.29	0.476	0.515	
	350	129	307	79	137	0.30	0.37	3.246	0.072	*
	700	146	290	61	155	0.33	0.28	1.834	0.176	
	all	7	104	0	111	0.06	0.00	7.228	0.007	***
Mopane	50	143	133	57	81	0.52	0.41	4.067	0.044	**
82/3	350	241	35	130	8	0.87	0.94	4.684	0.030	**
	700	264	12	122	16	0.96	0.88	7.661	0.006	***
	all	17	55	11	61	0.24	0.15	1.596	0.206	
83/4	50	106	198	51	105	0.35	0.33	0.217	0.641	
	350	149	153	75	81	0.49	0.48	0.036	0.849	
	700	244	60	98	58	0.80	0.63	16.450	0.000	***
	all	13	65	1	77	0.17	0.01	11.300	0.001	***
85/6	50	77	339	22	184	0.19	0.11	6.312	0.012	**
	350	124	292	25	181	0.30	0.12	23.619	0.000	***
	700	136	280	23	183	0.33	0.11	33.554	0.000	***
	all	5	101	0	106	0.05	0.00	5.121	0.024	**
Acacia	50	157	135	85	63	0.54	0.57	0.533	0.465	
82/3	350	215	77	128	20	0.74	0.86	9.446	0.002	***
	700	284	8	148	0	0.97	1.00	4.130	0.042	**
	all	25	49	27	47	0.34	0.36	0.119	0.731	
83/4	50	116	[illegible]	38	128	0.35	0.23	7.994	0.005	***
	350	190	138	57	109	0.58	0.34	24.533	0.000	***
	750	290	38	131	35	0.88	0.79	7.897	0.005	***
	all	19	65	0	84	0.23	0.00	21.423	0.000	***
84/5	50	130	298	37	177	0.30	0.17	12 690	0.000	***
	350	143	285	29	185	0.33	0.14	25.689	0.000	***
	700	219	209	104	110	0.51	0.49	0.377	0.539	***
	all	11	99	0	110	0.10	0.00	11.579	0.001	***

*=90, **=95, ***=99 % level of confidence

3.4.3.1 Treatment effects

The problem of pseudoreplication must be borne in mind when interpreting the between-treatment statistical tests. In the Combretum and Mopane sites the cleared treatments tended to dry out more slowly than the wooded treatments in the early part of the season (when the grass biomass was low), but more rapidly late in the season. In the Acacia site drying was always fastest in the trees-and-grass treatment. Drying was to lower water potentials in the Combretum grassland than woodland site, but was comparable or inconsistent elsewhere.

There was no overall significant difference at the 90% confidence level between treatment plots in the frequency of wet days before the clearing treatment was imposed. This was true for all sites, although there were some significant differences at specific depths (Combretum: wooded>cleared at 50 & 700 mm; Mopane: cleared>wooded at 50 & 700mm but wooded>cleared at 350; Acacia wooded>cleared at 350 & 700mm). These differences are attributed to the chance effects of spatial variability in soil moisture distribution. Although the number of samples was high due to replication in time, the spatial replication was low (only two per depth in the cleared treatments, and four per depth in the wooded treatments).

In all sites the cleared treatment was wetter overall than the wooded treatment in both post clearing seasons. The strength of this effect, as indexed by the probability level, was in all cases greater in the first than the second post-clearing season, and was greatest in the Acacia site and least in the Mopane site.

In the Combretum site there were no statistically significant trends with depth, but the 700mm depth was wetter in the cleared treatment and the 50 and 350mm depths were drier in both post clearing seasons. In the Mopane site all depths were wetter in the cleared treatment, although only the 700mm depth was significantly so during the first season. In the second season all depths were significantly wetter in cleared treatment, with the effect being strongest at the 700mm depth. In the Acacia site

all depths were significantly wetter in the cleared site during both seasons except for the 700mm depth in the second season, where the difference was not statistically significant. The treatment effect was strongest at the 350mm depth.

It is therefore concluded that bush clearing results in an immediate increase in the duration of plant-available water in the soil profile. These results agree with those of Strang (1969a) and Pratchett (1978). This effect may gradually be lost as the grass biomass increases and therefore increases the moisture demand, but will probably persist if rain falls at times of the year when grasses are physiologically inactive, or in amounts large enough to penetrate beyond the zone where most grass roots are found. The depth at which the effect is most strongly expressed increases with decreasing water-holding capacity and the strength of the effect (in this study) is related to soil texture rather than to the tree leaf biomass before clearing.

3.4.3.2 Root-free columns

The persistence of moisture in the deeper horizons of the root-free columns once wetted is apparent for all sites, and especially so in the Combretum site where evaporation is low due to the sandiness of the soil. This shows that the permeability of the underlying strata (vertical flow) and the unsaturated hydraulic conductivity (lateral flow) are both small. The consequences of an excess of moisture in the profile are therefore likely to be lateral saturated flow above the lithic contact. Water penetration to the deeper horizons occurs most readily in the Combretum site and least frequently in the Acacia site, as would be expected from the water-holding capacity and hydraulic conductivity data. Evaporation was effective to greater depths in the Acacia and Mopane sites due to the increased depth of the capillary fringe with decreasing soil pore size.

Table 3.5 Frequency of days with no plant-available water in the soil profile ("dry") in sub-canopy and open habitats of wooded grasslands.

Site & season	Depth (mm)	Sub-canopy Dry	Sub-canopy Wet	Open Dry	Open Wet	Frequency Dry Sub	Frequency Dry Open	Chi square	Probability	
Combretum	50	47	101	54	94	0.32	0.36	0.736	0.391	
82/3	350	96	52	103	45	0.65	0.70	0.751	0.386	
	700	135	13	109	39	0.91	0.74	15.770	0.000	***
83/4	50	50	114	47	117	0.30	0.29	0 132	0.717	
	350	68	96	63	101	0.41	0.38	0.318	0.573	
	700	77	87	68	96	0.47	0.41	1.001	0.317	
84/5	50	68	150	48	170	0.31	0.22	4.698	0.030	**
	350	78	140	51	167	0.36	0.23	8.026	0.005	***
	700	84	134	62	156	0.39	0.28	4.984	0.026	**
Mopane	50	71	67	72	66	0.51	0.53	0.015	0.904	
82/3	350	135	3	106	32	0.98	0.77	25.518	0.000	***
	700	133	5	131	7	0.96	0.95	0.348	0.555	
83/4	50	50	102	56	96	0.33	0.37	0.521	0.470	
	350	67	85	82	70	0.44	0.54	2.962	0.085	
	700	106	46	138	14	0.70	0.91	21.263	0.000	***
84/5	50	32	176	45	163	0.15	0.22	2.693	0.101	
	350	64	144	60	148	0.31	0.29	0.184	0.668	
	700	58	150	78	130	0.28	0.38	4.370	0.037	**
Acacia	50	70	76	87	59	0.48	0.60	3.982	0.046	**
82/3	350	102	44	113	33	0.70	0.77	2.13	0.144	
	700	140	6	144	2	0.96	0.99	2.056	0.152	
83/4	50	59	105	57	107	0.36	0.35	0.053	0.817	
	350	103	61	87	77	0.63	0.53	3.202	0.074	*
	700	128	36	162	2	0.78	0.99	34.469	0.000	***
84/5	50	55	159	75	139	0.26	0.35	4.419	0.036	**
	350	75	139	68	146	0.35	0.32	0.515	0.473	
	700	113	101	106	108	0.53	0.50	0.458	0.498	

*=90, **=95, ***=99 % level of confidence

3.4.3.3 Tree canopy effects

The hydrology of the microhabitat immediately below the canopy of a large tree differs from that between tree canopies due to differences in both water supply and water demand. It is impossible to say *a priori* which habitat will be wetter since it is the resultant of several conflicting processes; increased stemflow, herbaceous biomass and infiltration but decreased precipitation and radiant energy.

Table 3.5 Frequency of days with no plant-available water in the soil profile ("dry") in sub-canopy and open habitats of wooded grasslands.

Site & season	Depth (mm)	Sub-canopy Dry	Sub-canopy Wet	Open Dry	Open Wet	Frequency Dry Sub	Frequency Dry Open	Chi square	Probability	
Combretum	50	47	101	54	94	0.32	0.36	0.736	0.391	
82/3	350	96	52	103	45	0.65	0.70	0.751	0.386	
	700	135	13	109	39	0.91	0.74	15.770	0.000	***
83/4	50	50	114	47	117	0.30	0.29	0.132	0.717	
	350	68	96	63	101	0.41	0.38	0.318	0.573	
	700	77	87	68	96	0.47	0.41	1.001	0.317	
84/5	50	68	150	48	170	0.31	0.22	4.698	0.030	**
	350	78	140	51	167	0.36	0.23	8.026	0.005	***
	700	84	134	62	156	0.39	0.28	4.984	0.026	**
Mopane	50	71	67	72	66	0.51	0.53	0.015	0.904	
82/3	350	135	3	106	32	0.98	0.77	25.518	0.000	***
	700	133	5	131	7	0.96	0.95	0.348	0.555	
83/4	50	50	102	56	96	0.33	0.37	0.521	0.470	
	350	67	85	82	70	0.44	0.54	2.962	0.085	*
	700	106	46	138	14	0.70	0.91	21.263	0.000	***
84/5	50	32	176	45	163	0.15	0.22	2.693	0.101	
	350	64	144	60	148	0.31	0.29	0.184	0.668	
	700	58	150	78	130	0.28	0.38	4.370	0.037	**
Acacia	50	70	76	87	59	0.48	0.60	3.982	0.046	**
82/3	350	102	44	113	33	0.70	0.77	2.134	0.144	
	700	140	6	144	2	0.96	0.99	2.056	0.152	
83/4	50	59	105	57	107	0.36	0.35	0.053	0.817	
	350	103	61	87	77	0.63	0.53	3.202	0.074	*
	700	128	36	162	2	0.78	0.99	34.469	0.000	***
84/5	50	55	159	75	139	0.26	0.35	4.419	0.036	**
	350	75	139	68	146	0.35	0.32	0.515	0.473	
	700	113	101	106	108	0.53	0.50	0.458	0.498	

*=90, **=95, ***=99 % level of confidence

3.4.3.3 Tree canopy effects

The hydrology of the microhabitat immediately below the canopy of a large tree differs from that between tree canopies due to differences in both water supply and water demand. It is impossible to say *a priori* which habitat will be wetter since it is the resultant of several conflicting processes; increased stemflow, herbaceous biomass and infiltration but decreased precipitation and radiant energy.

A comparison of the frequency of "dry" sample days between sub-canopy and between-canopy habitats is given in Table 3.5. In the Combretum site the whole profile tended to be wetter between than beneath canopies, although the difference was only significant in the wet 1984/5 season, and at 700mm in the dry 1982/3 season. This result could reflect the dominant effect of interception losses in this site where infiltration rates are always high.

In the Mopane site, where the difference between habitats was significant, the open sites were drier at the 700 mm depth (350 mm in the 1982/3 season) indicating deeper penetration of moisture beneath than between canopies. This is in agreement with the findings of Pressland (1973), and may reflect the relatively high contribution by stemflow in this site.

In the Acacia site the between-canopy habitat was also drier than the sub-canopy habitat whenever the difference was significant, although the depth at which the effect occurred varied between seasons. In both the wettest and driest seasons the biggest difference was in the surface soil layers, while in the 1983/4 season it occurred at 700 mm. Overall there was a non-significant trend for the between-canopy habitat to be drier in dry seasons and wetter in wet seasons than the sub-canopy habitat. These differences could be due to the marked changes in grass biomass and species composition that occurred at this site between dry and wet years. The difference was retained after clearing.

3.5 EVAPOTRANSPIRATION

3.5.1 PAN EVAPORATION

The annual course of Class A pan evaporation, an approximate index of atmospheric evaporative demand, is illustrated in Figure 31 on page 102. It is well fitted by a cosine function ($F=262.8$, $n=182$, $p<0.0001$),

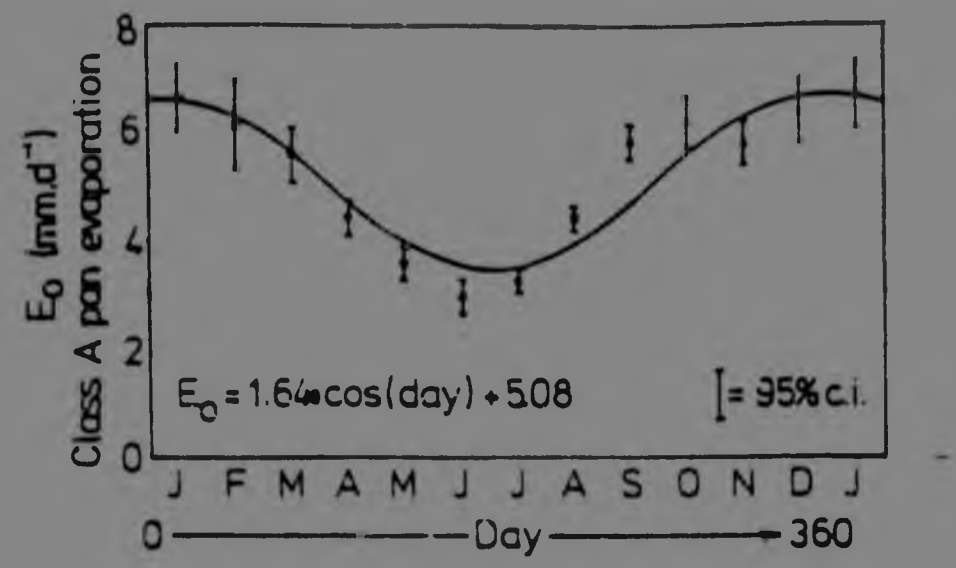

Figure 31 Annual course of Class A pan evaporation: based on 14 years data from Skukuza

suggesting that potential evapotranspiration is largely controlled in this region by radiant energy supply. The depression in November is probably due to the cloudiness and high humidity associated with that month.

3.5.2 EVAPORATION FROM THE SOIL SURFACE

The theory governing evaporation from a bare soil surface is detailed by Philip (1957) and Black, Gardner and Thurtell (1969). The general pattern is an initial phase of rapid, almost constant rate evaporation, followed by a phase of declining rates where the cumulative evaporation is proportional to the moisture content of the upper profile. The transition between the two phases can be quite sharp. In broad terms, the initial rates are limited by atmospheric factors (the evaporative potential

and energy flux) while soil factors (the thermal and hydraulic conductivity) are limiting during the falling rate phase.

Rates of evaporation from the soil were determined at each site by the repeated weighing of soil-filled lysimeters (Figure 32 on page 104). The lysimeters were packed with soil from the A horizon to a density approximating the *in situ* soil bulk density. The lysimeters were cylindrical with a perforated base draining into a container for collecting moisture percolating through the entire column. They were embedded in the soil inside closely fitting housings so that the top of the soil column was level with the soil surface. The housing projected 10 mm above the soil to prevent runoff from swamping the lysimeter.

During the 1982/3 season, the lysimeters were constructed of PVC pipe with an internal diameter of 103 mm enclosing a soil column 150 mm long. Weighing was on an Ohaus triple beam balance to a theoretical resolution of 0.1 g (equivalent to 0.01 mm of water). During the 1983/4 season the lysimeters were constructed of tin plate (modified 5 *l* double-container paint tins) with a soil column diameter of 170 mm and length of 240 mm. Weighing was on a Ktron electronic balance via a mass dividing beam to a theoretical resolution of 0.1 g (0.02 mm of water). The theoretical resolutions were not obtainable under windy field conditions, and readings were taken to the nearest 0.2 mm of water.

The lysimeters were weighed on the same occasions as soil moisture was metered. When water had collected in the bottom container, the lysimeters were weighed before and after emptying the accumulated liquid.

Four lysimeters were installed per study site, in the uncleared treatment. Two were placed under tree canopies and two away from tree canopies. The soil columns were kept free of plant growth. Examples of lysimeter drying curves are shown in Figure 33 on page 105 and evaporation values during the constant rate phase are given in Table 3.6. Homogeneity of slope tests show all the rates to be significantly different from one another at the 95% confidence level, indicating a high spatial variability. The difference between samples was in most cases greater than the difference between treatments, but evaporation

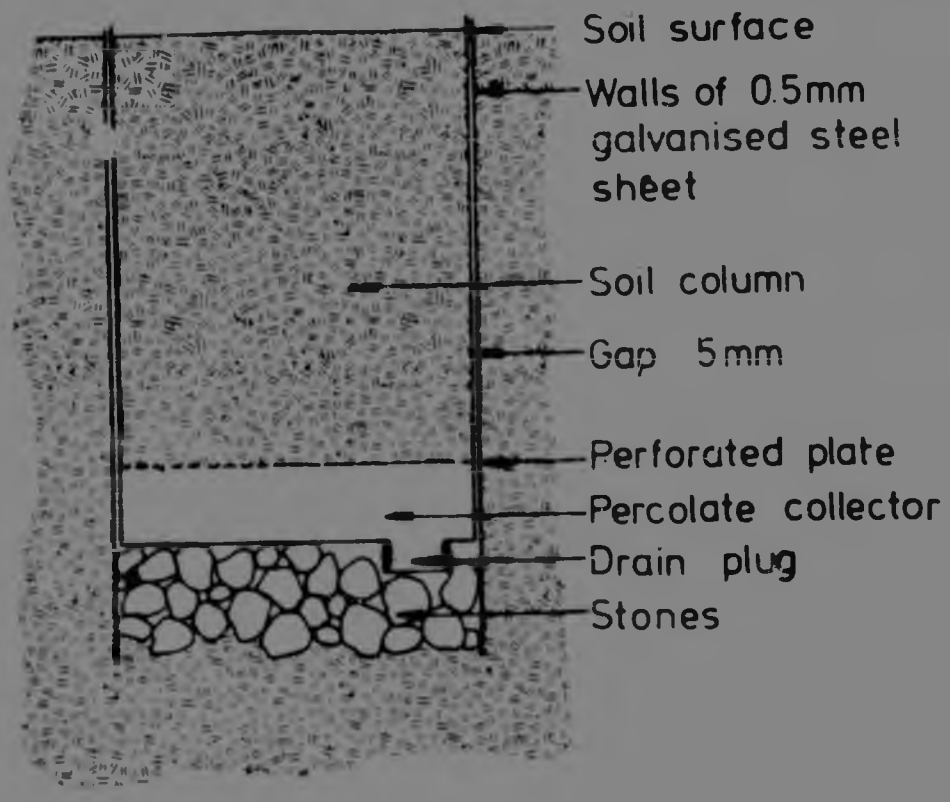

Figure 32. Lysimeter design

in the open was usually slower than in the sub-canopy habitat. Evaporation during the constant rate phase, which contributed about 75% of the water lost by evaporation, was highest at the Mopane site and lowest at the Combretum site, again illustrating the fallacy of assuming that all soil physical parameters mirror the clay-content continuum.

Evaporation from the soil surface is a major component of the hydrological cycle in semi-arid regions (Whitmore 1971), with a magnitude of a similar order to that of transpiration. The finding that it was inversely related to the level of radiant energy received at the soil surface, in apparent contradiction to theory (Nakano, Cho & Hillel 1983), was therefore investigated further

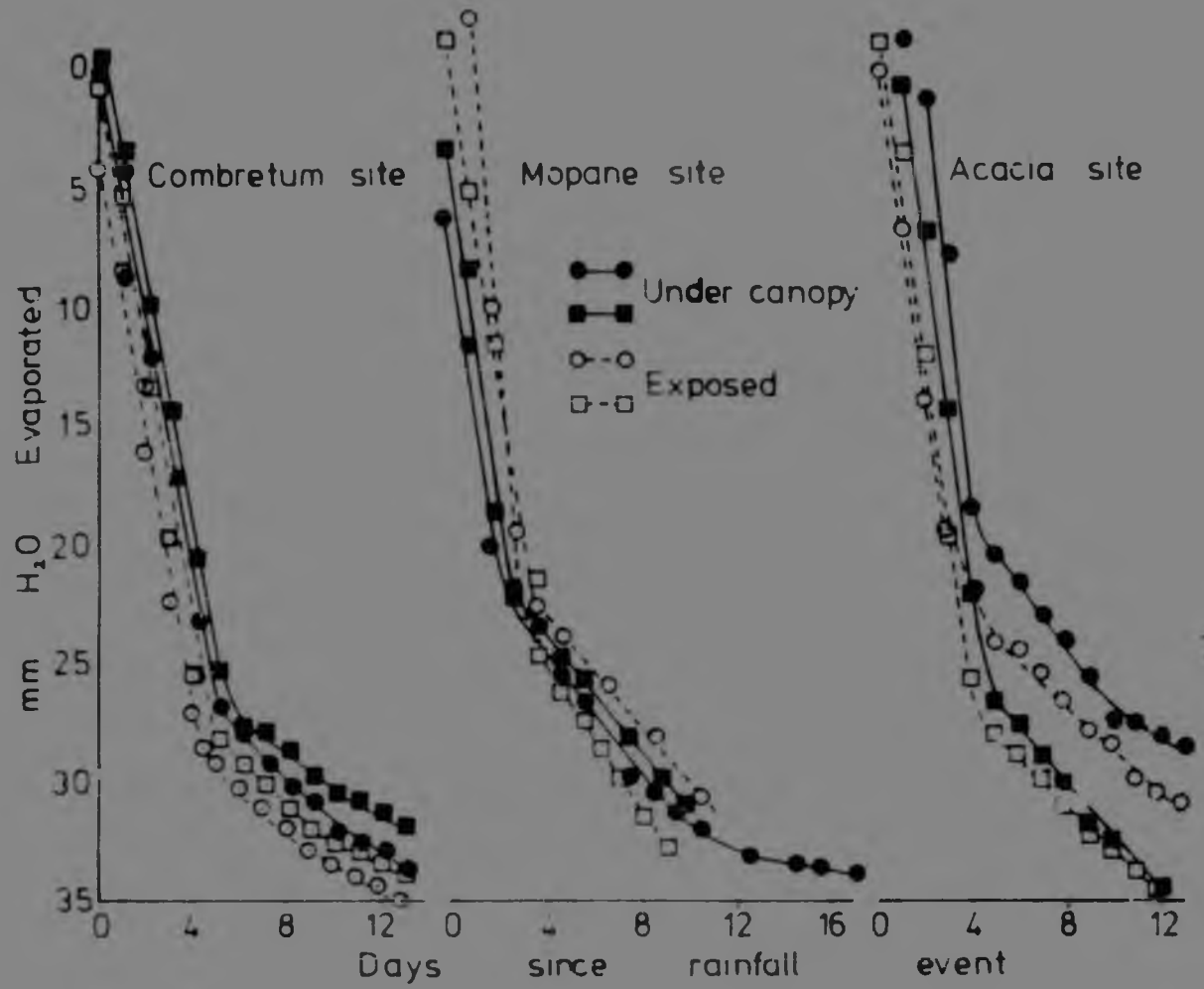

Figure 33. Lysimeter drying curves: O=Rep 1, II=Rep 2.

The lysimeters, still filled with soil from the three sites, were installed at a central location and shaded 100, 70, 50 and 0% with commercial shade cloth. The lysimeters were wetted with rainwater and the evaporation rates were monitored daily through four drying cycles, the shading level being rotated for each cycle.

The results of this experiment are illustrated in Figure 34 on page 107. Shading only slightly reduced the evaporation rate, and the relationship between irradiance and evaporation is complex. Since all the field lysimeters were shaded to some degree at different times of the day, and

were within the grass canopy boundary layer, it is not possible to make a direct comparison between the field data and the shading experiment. It is suggested that the evaporation rate under conditions of high atmospheric demand is limited mainly by the ability of the soil to transport moisture upwards to the soil surface, even during the initial drying phase. Under high irradiance, high evaporation conditions a barrier of dry soil with a consequently low hydraulic conductivity forms at the soil surface, which retards further evaporation. As a consequence, shading has only a slight effect on evaporation from the soil surface.

When the atmosphere is hot and dry, as it is most of the time in the semi-arid savannas, a large component of the energy required to drive evaporation from the soil (or plant) surface is provided by sensible heat, which can be advected from neighbouring unshaded patches. Harrison (in prep) found that sensible heat contributed a large proportion of the sub-canopy thermal balance in the savanna at Nylsvley. Therefore the

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Table 3.6 Evaporation rates from a bare soil surface during the constant-rate phase (rates > 1 mm.d^{-1}).

Site	Sub-habitat		mean	s.d.	n	Habitat mean	Pooled mean
			mm.d^{-1}				
Combretum	Open	1	2.4	2.0	21		
		2	2.8	2.0	22	2.60	
	Subcanopy	3	2.7	2.1	23		
		4	3.0	2.4	22	2.85	2.73
Mopane	Open	1	3.1	2.2	16		
		2	2.8	2.2	21	2.95	
	Subcanopy	3	4.3	3.5	19		
		4	4.0	3.6	18	4.15	3.55
Acacia	Open	1	2.5	2.2	33		
		2	3.5	3.1	35	3.00	
	Subcanopy	3	2.9	2.4	35		
		4	2.9	2.3	37	2.90	2.95

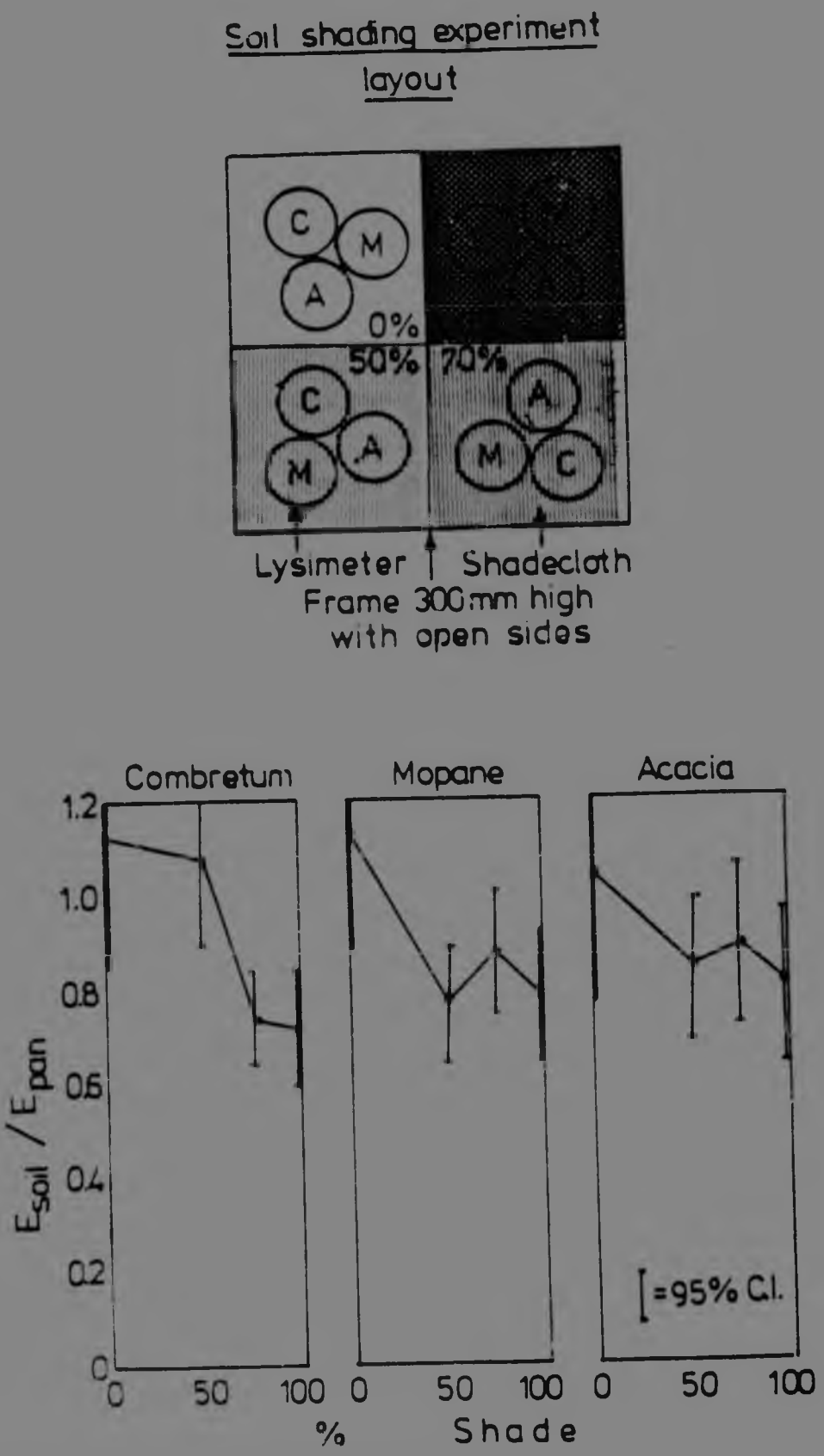

Figure 34. Influence of shade intensity on evaporation from the soil. bars indicate 95% confidence intervals.

major role of the grass and tree canopies in reducing evaporation from the soil surface is probably not through shading the soil surface, but through increasing the boundary layer resistance to the diffusion of moisture and heat. In this respect grasses, with a dense, low canopy are much more effective than trees, with a diffuse, high canopy. This hypothesis was not directly tested by the study. For modelling purposes the evaporation rate was assumed to be inversely proportional to the combined tree and grass canopy cover. Another factor which was not considered was the effect of surface litter on the evaporation rate, which is undoubtably important, but difficult to model.

In derived grasslands, shading, canopy diffusive resistance and surface litter are all increased above the levels in an uncleared savanna, provided that grazing and burning intensities are sufficiently low to allow a dense grass cover to develop. It is therefore anticipated that clearing of woodlands will decrease evaporation from the soil surface, thus increasing the water use efficiency (dry matter production per unit rainfall) of the system as a whole.

3.5.3 TRANSPIRATION

The measurement of transpiration for water balance purposes is technically difficult because most of the available techniques alter the plant environment and thus modify the transpiration rate (Slavik 1974). Furthermore, in order to obtain rates for an entire plant community, accurate measurements of the transpiration rate of each contributing species for all times of day and night and for all canopy aspects must be known. Since most measurements are made on a single leaf or portion thereof, the leaf area contribution of each species must also be known. Even with all this information, which is logistically almost impossible to obtain, the pitfalls of extrapolating from a small sample to an entire community are legion.

The approach of this study was twofold: estimate the transpiration rates by extrapolation from individual leaf rates; and compare these estimates with the results of a water-balance model based on the daily soil moisture readings. The partitioning of evapotranspiration into soil, tree and grass components could also be roughly estimated by comparison of soil moisture depletion in the root-free, grass only and trees plus grass profiles.

The leaf-based methods were used to determine the form of the dependence of transpiration rate on soil moisture conditions, as well as to reveal differences in the water use patterns of various species. Instantaneous transpiration rates were determined at two-hourly intervals throughout the day on eight occasions at each site. On several occasions measurements were taken throughout the night as well, to confirm that transpiration essentially ceased during the night. Sunlit leaves were used for all measurements. The total daily transpiration per gram of leaf tissue was calculated by integrating the area under the diurnal progression of transpiration rate. Examples of the daily course of transpiration rate under wet and dry soil conditions at each site are given in Figure 35 on page 110.

The cut-shoot weight loss technique (Slavik 1974) was selected for woody plants because of its simplicity and applicability to different leaf forms. Approximately 10 g of leaf and shoot material was cut from the parent plant and immediately weighed on a Ktron digital balance to the nearest 0.01 g. The sample was then replaced in its original position in the canopy and reweighed after five minutes. The mass difference was taken to be transpiration loss, and expressed per unit dry weight of leaf material per unit of time. The method was found to be unreliable for grasses.

Prior trials using time intervals between two and ten minutes showed a period of five minutes to be sufficient to show a measurable mass loss but insufficient to cause marked wilting of the sample. No sudden spurt of transpiration following severing of the shoot was noted (the "Ivanov effect"), but rates gradually declined over the ten minute period. The five minute standard was adopted for comparative purposes. Transpiration measurements were taken two- or three-hourly throughout

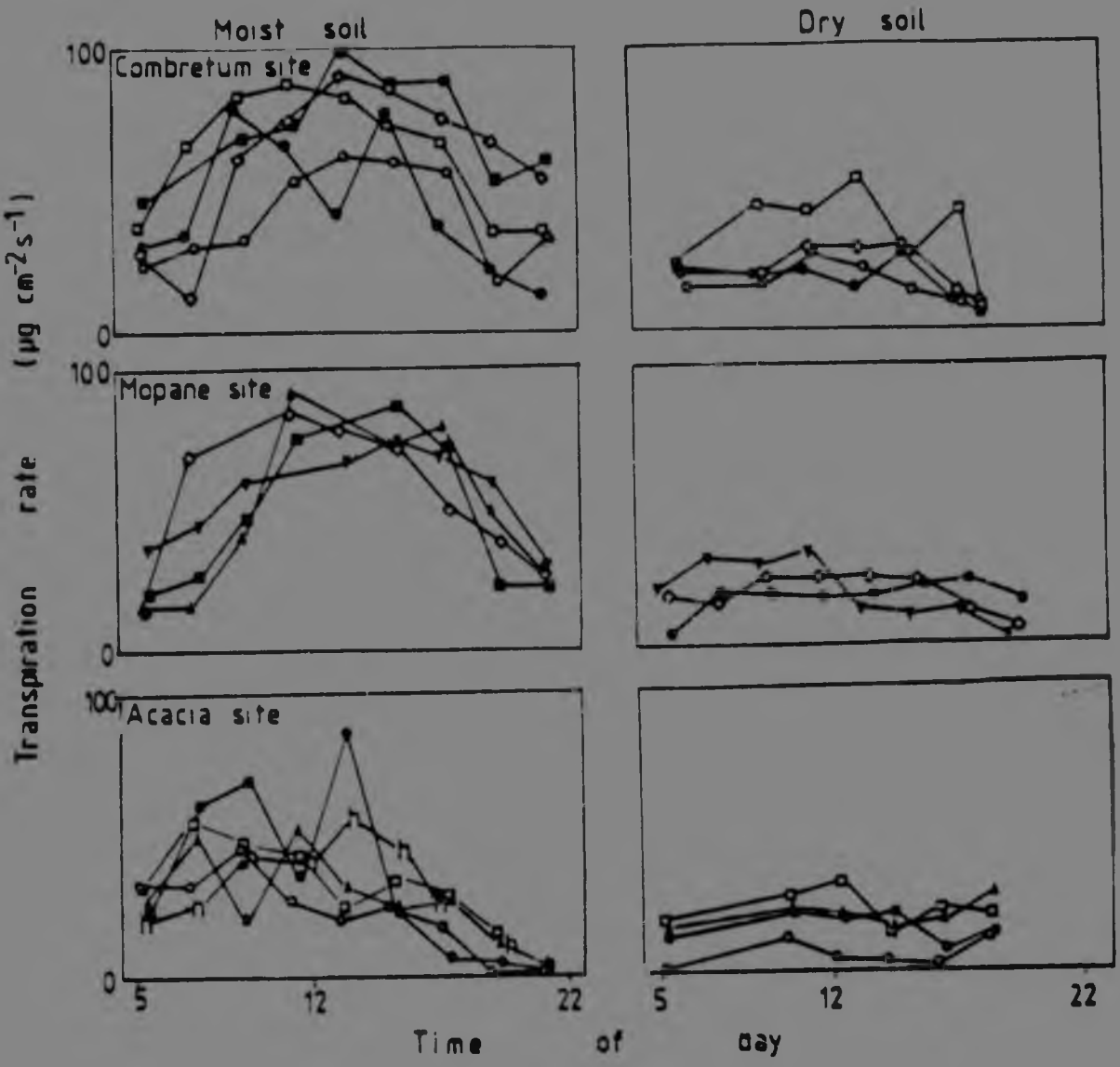

Figure 35. Daily course of transpiration rate: Combretum site ◇ =*Grewia bicolor*, □ =*Sclerocarya birrea*, ○ =*Combretum apiculatum*, ● =*Schmidtia pappophoroides*, ■ =*Panicum maximum*; Mopane site ■ =*Colophospermum mopane*, ● =*Combretum apiculatum*, ▼ =*Digitaria eriantha*, ▲ =*Acacia nigrescens*; Acacia site ▲ =*Acacia nigrescens*, □ =*Sclerocarya birrea*, ● =*Panicum maximum*, h=*Heliotropium sp.*, ○=*Combretum apiculatum*.

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the day and night on one sample each of the five dominant woody plants at each site. The measurements were taken on numerous occasions to provide a range of soil moisture conditions, as measured by the soil moisture sensors in each site.

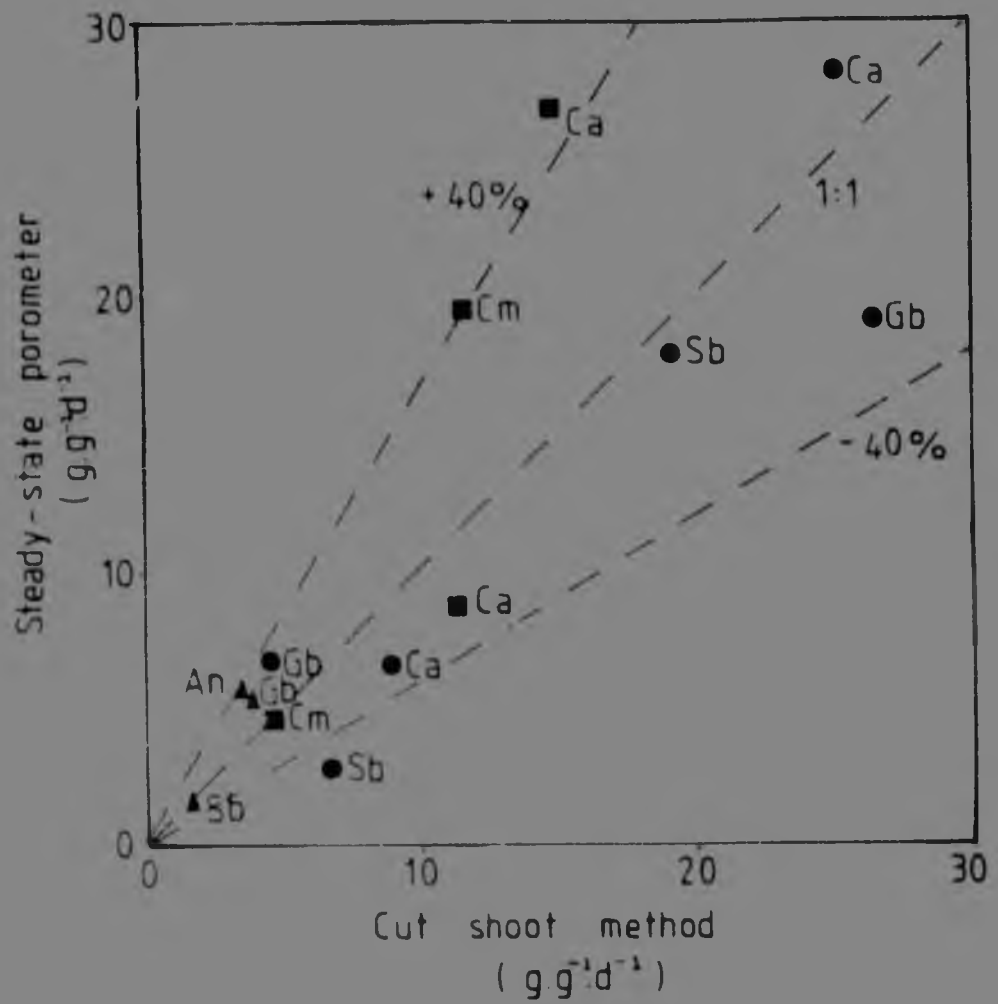

Figure 36. Correlation between porometry and the cut-shoot technique. Gb=Grewia bicolor, Sb=Sclerocarya birrea, Ca=Combretum apiculatum, Cm=Colophospermum mopane, An=Acacia nilotica

Transpiration rate measurements were taken on several occasions on dominant tree and grass species using a LICOR LI-1600 steady-state porometer. A comparison between the daily transpiration calculated by the dry weight based cut-shoot method and the leaf area-based porometer method was made using the specific leaf areas for each species involved

Table 3.7 Specific leaf areas (one side only) and canopy storage volume for the major species used in the study. Means and standard errors for 15 samples.

Species	Specific leaf area $dm^2.gDM^{-1}$	Canopy storage volume $ml H_2O\ gDM^{-1}$
Acacia nigrescens	*1.11 (0.10)*	*0.49 (0.16)*
Grewia bicolor	*0.87 (0.09)*	*0.61 (0.12)*
Colophospermum mopane	*0.81 (0.08)*	*0.59 (0.16)*
Combretum apiculatum	*1.47 (0.12)*	*0.77 (0.40)*
Sclerocarya birrea	*0.43 (0.03)*	*1.09 (0.80)*
Bothriochloa radicans	*0.20 (0.11)*	
Digitaria eriantha	*0.71 (0.26)*	
Panicum coloratum	*0.53 (0.34)*	
Panicum maximum	*0.92 (0.44)*	
Sporobolus nitens	*0.41 (0.14)*	
Schmidtia pappophoroides	*0.33 (0.20)*	
Urochloa mosambicensis	*0.80 (0.27)*	

(Table 3.7). Porometry was performed on adaxial surfaces only. The porometer could not be used on narrow leafed species. The comparison is presented in Figure 36. The estimates were in broad agreement for most species.

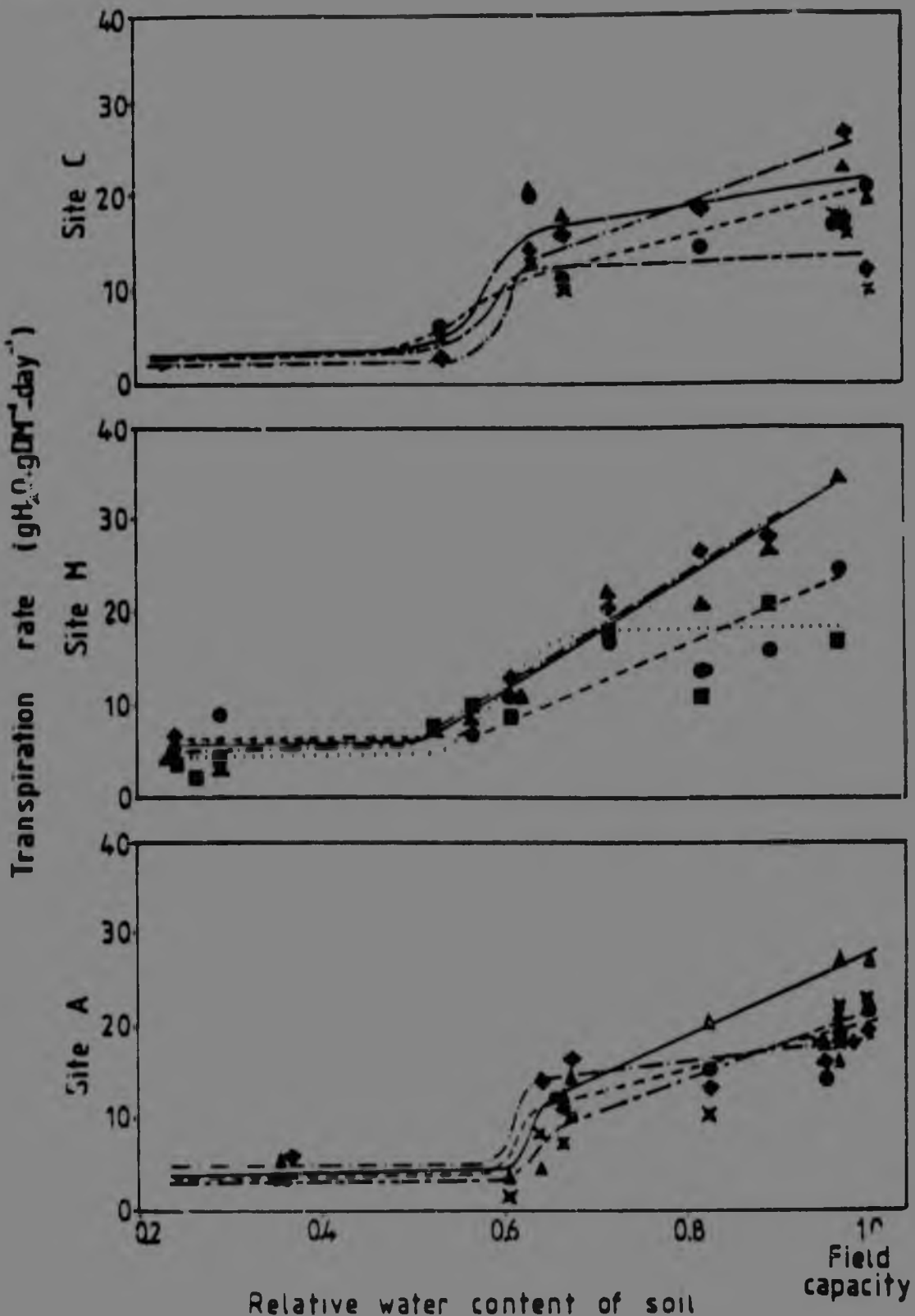

Figure 37 Relationship between daily transpiration and soil water potential: Soil moisture is weighted by root density in each layer ▲=Acacia nigrescens, ◆=Grewia bicolor, ■=Colophospermum mopane, ●=Combretum apiculatum, x-Sclerocarya birrea.

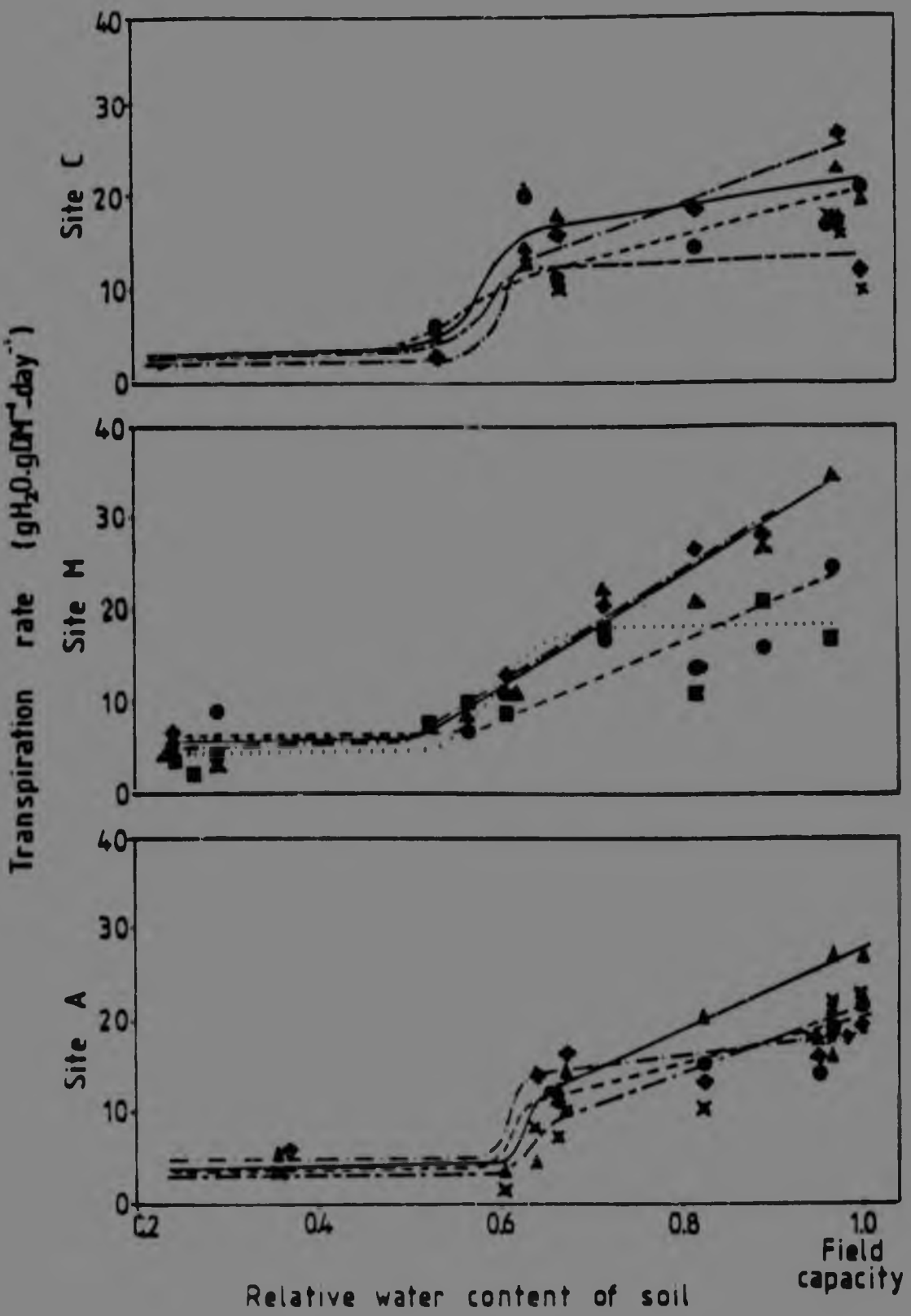

Figure 37 Relationship between daily transpiration and soil water potential. Soil moisture is weighted by root density in each layer ▲=Acacia nigrescens, ◆=Grewia bicolor, ■=Colophospermum mopane, ●=Combretum apiculatum, x=Sclerocarya birrea

Data from the cut-shoot method were used to calibrate the model because they were available for more species and a more complete range of soil moisture conditions. Daily transpiration was calculated as the area under the transpiration rate curve for a 24 hour period. Daily transpiration is plotted against an index of soil water availability in Figure 37 on page 113. Soil water availability was calculated by multiplying the relative water content (0=airdry, 1=field capacity) of each soil layer, as indicated by the mean soil moisture block reading, by the proportion of tree roots associated with that layer. The choice of a plausible function to express this relationship is not simple. Several forms have been suggested in the literature (Denmead & Shaw 1962). When the atmospheric demand is high, the transpiration rate is limited by the rate at which roots can extract water from the soil, which is in turn a function of the water potential gradient between the plant and soil, and the diffusive resistance in the soil and across the soil-root interface. Some workers (eg Feddes *et al* 1976) have therefore suggested a linear relationship between transpiration rate and soil water potential (ψ). As the soil dries, however, the cross sectional area of the diffusive pathway between soil and root declines as a function of the soil water content (θ) leading other workers to propose a linear dependence on relative water content (Hillel *et al* 1976), and yet others to use compound relationships of ψ and θ.

When the atmospheric moisture demand is low, then the transpiration rate tends to remain constant until the soil water potential falls to wilting point, when the transpiration rate drops abruptly. At intermediate atmospheric demand levels the relationship between soil moisture and transpiration rate can take on a variety of sigmoid forms. To avoid the introduction of arbitrary inflection points a complex curve was rejected for modelling purposes in favour of a simple one. Both trees and grasses were assumed to transpire at a maximum rate (E_{max}) until the relative soil moisture content ( ) fell below a given critical level (E_{crit}) whereafter the transpiration rate was a linear function of the difference between θ and the relative water content at wilting point (θ_{wilt}).

Transpiration rates of grasses (Table 3.8) were determined by repeatedly weighing pots in which grass tufts of known biomass were growing. Evaporation from the pots was suppressed by a 15mm mulch of 2mm di-

Table 3.8 Transpiration rates by *Panicum maximum* and *Schmidtia pappophoroides* measured by lysimetry over a two-week period (March 1985). Class A pan evaporation for the same period averaged 3.66 $mm.d^{-1}$. Data corrected for evaporation from the soil surface.

	Transpiration rate ($g.gDM^{-1}.d^{-1}$)			
	Panicum maximum		*Schmidtia pappophoroides*	
	Full sun	70% shade	Full sun	70% shade
Combretum site soil	7.81	9.35	3.47	4.22
Mopane site soil	7.68	5.17	7.72	4.65
Acacia site soil	7.36	7.14	1.73	(died)

ameter plastic spheres, and corrected for evaporation from the soil surface by reference to the mass loss from control pots having no grass tufts. For details of the pot sizes and weighing, see the section on "pot experiment" in chapter 4.

4.0 PRIMARY PRODUCTION AND PLANT DEMOGRAPHY

In the absence of other limiting factors, the dependence of primary production on water availability should be linear over the range of water limitation. Many such relationships between annual production and various indices of moisture (usually annual precipitation) have been published for the grass component of savannas (Walter 1939, Rosenzweig 1968, and Phillipson, 1975). A critique is given by Rutherford (1980)

This study seeks to construct a mechanistic model of the relationship between plant production and water availability. For this purpose the above studies are inadequate on two counts. As Bell (1982) has pointed out, the relationship is not independent of soil fertility (nor is it likely to be independent of soil physical factors). Thus the relationship is site specific and should be determined for each new case. Secondly, the causal relationship is between plant available water and production. Mean annual precipitation, potential evapotranspiration and even soil moisture status are at best crude estimators of this parameter because a significant portion of the water budget leaves the system through non-productive pathways such as runoff, evaporation from the soil surface, interception and deep leaching. The slope of the relationship between individual plant production and plant water use will be referred to in this study as plant water use efficiency (WUE, grams carbon fixed per gram water transpired), while the slope of the annual aboveground herbaceous layer production-annual rainfall regression will be referred to as the sward water use efficiency (WUE, kg ha^{-1} mm^{-1}).

Under conditions of equal and constant water availability and no nutrient deficiency, the competitive contest would be won by the plant with the highest water use efficiency However water availability fluctuates and is not equally accessible to all plants. Plant water use efficiency is probably not constant over all levels of water availability. Furthermore, as Cohen (1970) has pointed out, a high water use efficiency can be selected for only under conditions of exclusive water use, or where the

adaptations favouring high WUE does not reduce the transpiration rate disproportionately. Where soil moisture is a resource common to several competitors, water conservation at the expense of water uptake is not rewarded. The interaction of a variable moisture availability and a variety of water-use strategies provides opportunities for coexistence in semi-arid savannas (Westoby 1980).

Under conditions of extreme water stress, when water availability is practically nil, the competitive outcome is determined by neither water use efficiency nor transpiration rate but by the ability to survive until the next period of water availability, either by avoiding or by tolerating the drought. Thus drought mortality data are also relevant to understanding the co-existence of savanna species.

In this chapter the methods and results of determining grass production under conditions of known water use (see chapter three) are described. In order to construct a system water budget, the biomass contribution of each transpiring component must be known. In a monitoring programme it is desirable that the biomass be estimated non-destructively, which limits the methods applicable. They were further restricted by the low production levels during the first two years of the study.

An increase in grass production is the most conspicuous consequence of woody plant removal, and the one most commonly cited as a reason for bush clearing Grass production was therefore used as the major criterion for comparing the treatment (cleared) and control (uncleared) plots.

Changes in grass production are attributable to four sources, which operate sequentially at different time scales. The immediate response to improved growth opportunities is enhanced performance by individual tillers. Within weeks, the number of tillers per tuft increases, and if the resource levels are sustained, the number of tufts per unit area rises. Finally, all the above changes result in a species composition shift in favour of those species which perform better under the new resource regime; which may result in a higher system water use efficiency. All four sources were monitored (at their appropriate time scales) during this study.

Bush clearing is usually accompanied by a change in herbaceous species composition, often in the direction of lower palatability. The herbaceous layer species composition was therefore determined before clearing, two years after clearing and three years after clearing. Grass species normally confined to the sub-canopy habitat would be expected to decline following bush clearing, to be replaced by those normally found between canopies. One species from each of these groups was selected in each site for an intensive study of tiller dynamics and water use efficiency. Sub-canopy grasses were not conspicuous at the Acacia site before clearing, so representatives of the tall-grass/short-grass mosaic which occurs there were chosen. Number of tillers per tuft was recorded during the first two seasons, and tufts per hectare during the third. Herbaceous standing crop was measured at peak during the first two seasons, and monthly during the third

Production by trees was not monitored, but estimates of above-ground woody biomass and peak leaf biomass were made using allometric techniques.

4.1 WOODY-PLANT BIOMASS

One of the main determinants of the magnitude of the herbaceous response to bush clearing is the pre-clearing woody biomass None of the published bush clearing trials in Southern and East Africa report the pre-clearing biomass, and most neglect to report even the woody plant density or basal area. Woody plant biomass can be divided into above- and below-ground portions, and the above-ground portion into wood and leaf biomass (Rutherford 1979) The below-ground biomass is extremely difficult to measure, is not available to above-ground herbivores, is only indirectlly related to below-ground competition (root length or root activity would be better indices) and remains in the ground after clearing. For these reasons it was not measured in this study.

The leaf biomass is directly related to the leaf surface area, which in turn directly controls the rate at which water is transpired and energy is fixed by photosynthesis. It is therefore regarded in this study as the principle index of the influence of woody plants on grasses. Furthermore it represents a food resource to browsing herbivores. Only a small proportion of the wood biomass (the soft terminal twigs) is available to browsers. The principle importance of the wood biomass to bush clearing is as a nutrient pool which may be removed during the clearing operation. In some areas it may represent an economic resource which can help to balance the cost of bush clearing.

The total leaf mass of an individual woody plant is strongly related to the cross-sectional area of the stem (Barnes, Lloyd & McNeill 1976, Dayton, 1978). This relationship was determined for each dominant species by completely stripping the leaves of at least fifteen plants at peak leaf biomass, drying and weighing the leaves and regressing the dry leaf masses against the stem basal areas. This was possible for all species except *Acacia nigrescens*, where the regression was established for secondary branches. The cross-sectional area of secondary branches was then allometrically related to the stem basal area and the leaf mass versus stem area relationship was substituted into this second relationship.

Allometric regressions were also established between above-ground woody biomass (corrected for moisture content) and stem basal area. Again in the case of *A. nigrescens* it was not possible to weigh the entire tree, so the wood volume was allometrically determined, and multiplied by the wood density. The regressions (Table 4.1) are in reasonable agreement with relationships published by other workers (McNeill & Barnes 1976, Dayton 1978).

In order to determine the pre-clearing aboveground woody biomass, the allometric relations for woody and leaf tissue were applied to the frequency distributions of stem diameters obtained during the initial survey (Figure 13 on page 58). The values obtained (Figure 38 on page 121) agree quite well with estimates from savannas elsewhere (Rutherford,

Table 4.1 Allometric relationships in woody plants. Equations given are not necessarily the best fit in each case, but are of the class of equations which provide the best fit in the general case.

1. Leaf dry mass (L(kg)) versus Stem basal diameter (D (cm))

General form: $L=aD^2+b$

	a	*b*	r^2
Colophospermum mopane	0.0067	0.0290	0.94
Combretum apiculatum	0.0109	0.0520	0.98
Sclerocarya birrea	0.0074	0.0038	0.79
Grewia bicolor	0.0066	0.0019	0.65
Acacia nigrescens	0.0184	-0.0120	0.96

2. Woody dry mass (W (kg)) versus Stem basal diameter (D (cm))

General form: $\ln W=a\ln D+b$

	a	*b*	r^2
Colophospermum mopane	1.2780	-3.04	0.99
Combretum apiculatum	1.4015	-3.27	0.99
Sclerocarya birrea	1.3086	-3.52	0.99
Grewia bicolor	1.1024	-2.09	0.99
Acacia nigrescens	1.2723	-3.61	0.97

3. Bark surface area (B (cm^2)) versus Stem basal diameter (D (cm))

General form: $\ln B=a\ln D+b$

	a	*b*	
Colophospermum mopane	0.778	5.0553	*Equations derived*
Combretum apiculatum	0.902	4.8138	*on the assumption*
Sclerocarya birrea	0.809	4.9170	*that stems take the*
Grewia bicolor	0.602	6.2417	*form of a cylinder.*
Acacia nigrescens	0.772	4.5675	

1978). They are on the low side due to the fact that the published data mostly come from slightly moister savannas. The Mopane site has the highest woody-plant biomass, mainly due to the large wood biomass. This site is a multi-stemmed thicket rather than a woodland like the other two sites. Kelly (1973) estimated the woody-plant biomass in *C. mopane* woodlands and thickets to be 8700-30800 $kg.ha^{-1}$, with the leaf biomass contributing 590-2120 $kg.ha^{-1}$. Kennan (1969a) gives the leaf biomass in *C. mopane* thicket as 1490 $kg.ha^{-1}$. The thicket growth-form overrides



Figure 38 Pre-clearing aboveground standing crop of woody plants

the general tendency, as displayed by the Combretum and Acacia sites, for increasing woody biomass with decreasing clay content in the soil.

For all sites the standing crop of woody plants considerably exceeds the peak herbaceous standing crop, which is however of the same order as the tree leaf biomass alone

For modelling purposes it was assumed that the woody-plant leaf biomass developed during the first three weeks following the commencement of the rainy season, and then remained constant until the soil dried out, at which stage leaf fall began in proportion to the water deficit. Thus more than one leaf flush per year could occur, as was observed following the intra-seasonal drought of 1983/4 During the drought years of 1981/2 and 1982/3 the assumption that woody-plant leaf biomass is independent of rainfall was incorrect for *C. mopane* coppice. During wet years the coppice

form of *C. mopane* bore a much higher leaf biomass per unit stem cross-section than the thicket form from which it was derived.

Rainfall interception by the stems of woody plants is partly dependent on the bark surface area of the plant. This was approximated for the dominant species by assuming that the form of a stem is cylindrical, and by using the wood density data published by van Wyk (1972) to calculate the stem volume from the stem mass. The regressions are presented in Table 4.1.

The specific leaf area for each species was determined by dividing the leaf area of a large number of leaf samples (as determined planimetry, i.e. one side of the leaf only) by the dry mass of the samples. The results are presented in Table 3.8. In the case of grasses, the specific leaf area is the leaf area divided by the mass of the entire tiller. The leaf area indices for the Combretum, Mopane and Acacia sites works out to 1.4, 0.6 and 0.7 respectively if only woody plants are considered, and up to about 1.5, 1.6 and 2.4 if grasses are included.

4.2 MONITORING OF HERBACEOUS PRODUCTION

The herbaceous layer species composition survey (dry-weight ranking method as modified by Barnes, Odendaal & Beukes 1982) done before clearing began was repeated in January 1984 and January 1985. The results, presented in Figure 39 on page 123 and Table 4.2, show a change to dominance by forbs on the cleared and uncleared plots of all sites. The change was most conspicuous on the Combretum and Mopane sites. Forbs were an insignificant proportion of the standing crop before the drought and were therefore not registered by the dry-weight- ranking technique. The overwhelming proliferation of forbs in 1984 also tended to conceal the differences between the control and cleared sites. O'Connor (1985) notes that the effects of climatic fluctuations tend to override the differences brought about by the bush clearing treatment.

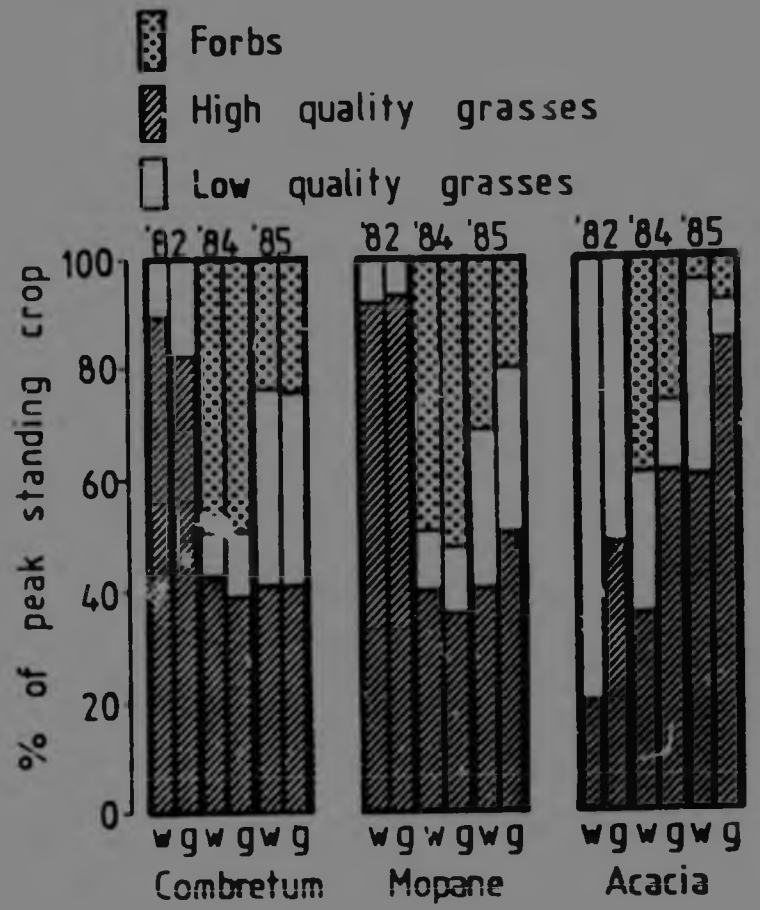

Figure 39 Herbaceous layer composition changes: % of the standing crop in March of each year. 1982 was the preclearing season.

Grass species were divided into two groups on the basis of a subjective assessment of their palatability. All *Panicum* species, *Urochloa mosambicensis* and *Digitaria eriantha* were considered to be of high quality, the rest low quality. The ratio of highly acceptable forage to poorly acceptable forage is nearly the same in the cleared and uncleared treatment on all except the Acacia site, where the cleared plot showed an increase in quality due to the proliferation of *Panicum maximum* and *Urochloa mosambicensis*. This site had a high quality sward in the un-

cleared treatment as well which showed a consistent quality increase over the period of the study, while sward quality in the uncleared treatment of the other two sites declined. It must be born in mind that the total herbage biomass in the cleared treatments increased relative to the uncleared treatment in all sites. Therefore no change in the

Table 4.2 Grass sward species composition by percentage bulk contribution in each study site and treatment before the clearing and during the second cleared season. Based on 100 0.5x0.5 m quadrats per plot ranked according to Barnes, Odendaal & Beukes (1982).

Species	*1981/1982*		*1983/1984*	
	Clear	*Control*	*Clear*	*Control*
1. Combretum site				
Aristida congesta	16	10	7	4
Bothriochloa radicans	1	-	1	1
Cyperaceae	4	3	23	26
Digitaria eriantha	18	39	2	1
Panicum coloratum	21	3	3	1
Panicum deustum	-	-	5	10
Panicum maximum	10	9	2	2
Schmidtia pappophoroides	12	9	4	1
Other grasses	2	-	4	1
Forbs	16	27	48	49
2. Mopane site				
Aristida congesta	7	8	6	7
Cyperaceae	28	29	16	24
Digitaria eriantha	48	45	14	8
Panicum maximum	5	6	1	1
Schmidtia pappophoroides	12	12	5	7
Other grasses	-	-	6	4
Forbs	-	-	52	49
3. Acacia site				
Aristida congesta	1	1	2	2
Bothriochloa radicans	50	76	5	14
Panicum coloratum	20	8	4	4
Urochloa mosambicensis	12	10	26	23
Panicum maximum	17	-	-	1
Other grasses	-	3	8	9
Panicum deustum	-	2	30	9
Forbs	-	-	25	38

palatable/unpalatable ratio nevertheless indicates an increase in the supply of palatable species. Similarly, the apparent decrease in the proportion of forbs between 1984 and 1985 is caused by an increase in the other categories. The forb biomass remained fairly constant, and observations in 1986 indicate that they persisted as a major component of the sward. The forb biomass in 1984 was dominated by *Heliotropium* sp, which was replaced by *Indigophora* sp. and *Sida* sp. in the subsequent years.

Standing crop estimates were obtained by clipping twenty 0.5x0.5m quadrats per treatment, separating the clippings into forb and grass components, drying and weighing. During the 1984/5 season standing crop estimates were made once a month for the duration of the wet season, and herbaceous layer production was calculated as the sum of the positive increments. Consumption by grazing was very low by comparison to herbage production during this and the 1983/4 season, following the large decrease in herbivore numbers due to drought mortality in November 1982 (Scholes 1985). Herbage production was too low during the 1982/3 and 1983/4 seasons to allow the sequential clipping method to be applied usefully. Herbage production in those years was equated to the peak herbaceous standing crop (March sample), since carry-over from the previous season was effectively zero. The peak aboveground herbaceous layer biomasses are given in Table 4.3, and annual herbaceous aboveground production (peak minus carryover from previous season) is plotted in relation to seasonal rainfall in Figure 40 on page 126. The data points marked Winter '84 refer to a second growth flush which occurred following unseasonal rainfall in that year. Total herbaceous layer production was greater on cleared than uncleared treatments at all sites. When grass production alone was considered, only the Mopane and Acacia sites showed a large increase. On the Combretum site the increase in herbaceous production on the cleared plot was almost entirely due to a proliferation of forbs, mostly unpalatable. The Acacia site showed an increase in both grasses and forbs.

Too few data points are available to allow a regression model to be fitted to the relation between herbaceous layer production and annual rainfall. The data from the two post-clearing seasons seem to follow the pattern

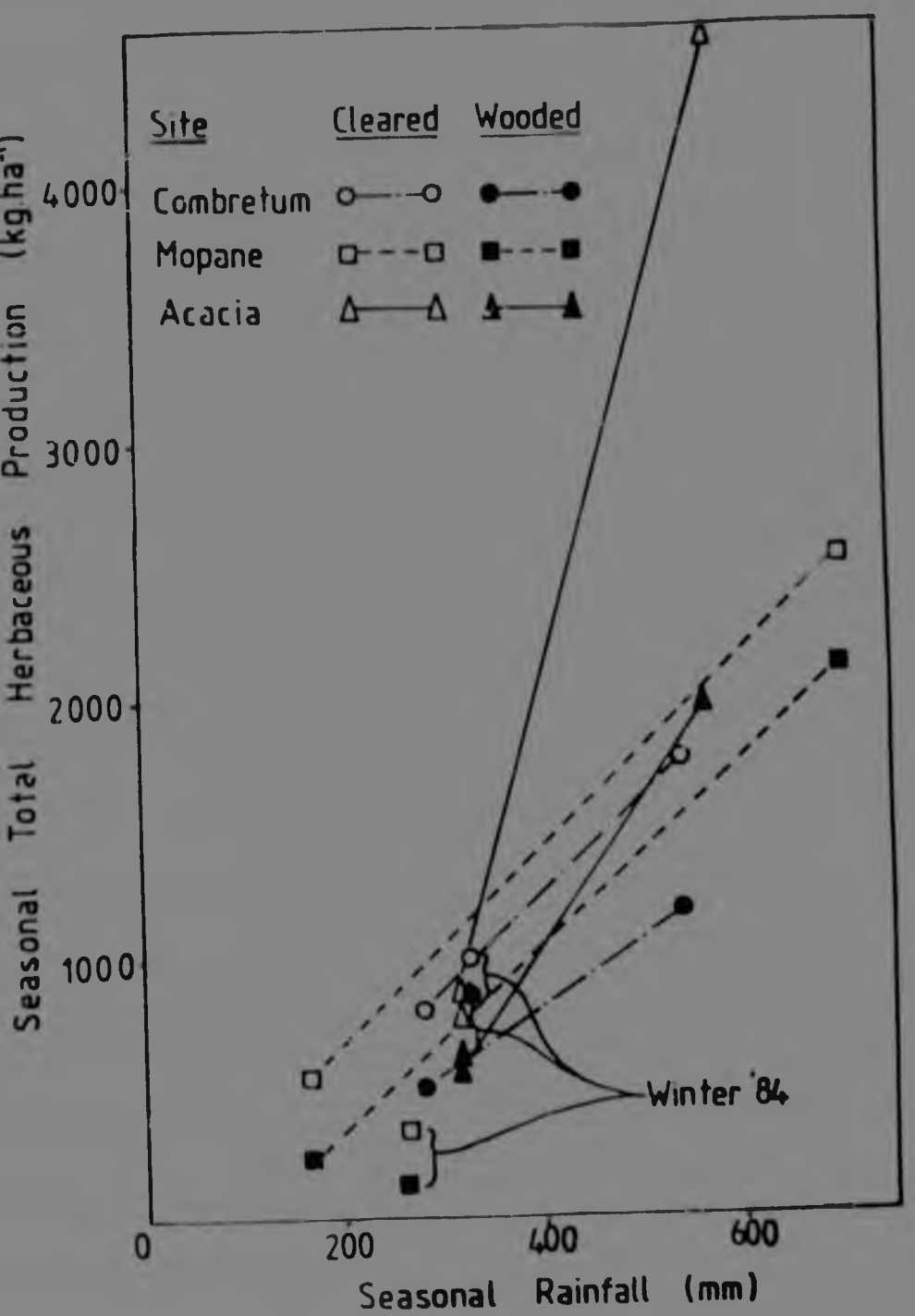

Figure 40. Herbaceous layer production related to rainfall: growing season rainfall only. The sample is too small to apply regression analysis; lines are for clarity only.

of the Dye & Spear (1982) study, wherein the absolute increase in herbage production between cleared and uncleared treatments is relatively

Table 4.3 Peak herbaceous layer aboveground biomass (kg.ha^{-1}) for each growing season. The January 1982 records preceeded clearing. Drought conditions in 1983 prevented a meaningful measurement from being taken (biomass was effectively zero). Values in parentheses are standard errors for 20 samples.

	Grass		Forbs		Total	
	Control	Cleared	Control	Cleared	Control	Cleared
Combretum site						
Jan 1982	210	250	0	0	210	250
Jan 1984	240	260	258	550	498	810
Mar 1985	2091	2734	441	832	2533	3566
	(376)	(590)	(94)	(210)	(406)	(623)
Mopane site						
Jan 1982	914	669	0	0	914	669
Jan 1984	70	232	169	311	239	543
Mar 1985	1843	2748	634	676	2478	3425
	(216)	(187)	(230)	(264)	(442)	(467)
Acacia site						
Jan 1982	994	637	0	0	994	637
Jan 1984	460	705	131	175	591	880
Mar 1985	2969	6004	362	111	3347	6115
	(432)	(1005)	(143)	(100)	(429)	(885)

independent of the seasonal rainfall; in other words, the sward water use efficiency is unchanged, but the water supply is increased. The exception to this pattern is the Acacia site where the increase due to clearing is much greater in the 1984/5 season (c.550 mm effective rainfall) than in the 1983/4 season (c.320 mm). The species composition data (Table 4.2) show that the cleared treatment had a much higher proportion of of *P.maximum* and *Urochloa mosambicensis*. Both of these species have a relatively mesic distribution. It is suggested that their contribution raised the sward water use efficiency in the cleared treatment above that in the wooded treatment. The dense sward suppresses evaporation from the soil surface which further increases the WUE'.

The absolute increase in herbaceous layer production following clearing was 300-500 kg ha^{-1} (60-56%) in the Combretum site, 300-350 kg.ha^{-1} (150-25%) in the Mopane site and 300-2500 kg.ha^{-1} (120-80%)in the Acacia site. The expression of the bush-clearing response as a percentage increase in grass production is misleading, since the absolute increase is fairly constant between years, but the reference level (uncleared) is highly variable between both sites and years.

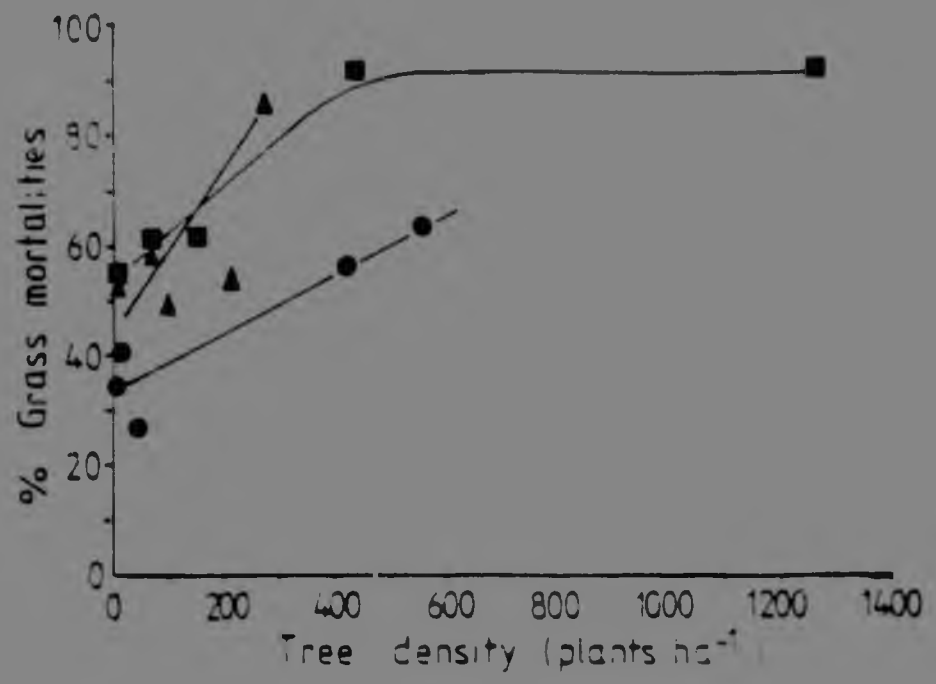

Figure 41. Influence of tree density on grass mortality: A=*A. nigrescens* woodland M=*C. Mopane* woodland O=*Combretum apiculatum* woodland. Curves fitted by eye.

A combination of high grazing pressure and drought during 1981/2 and 1982/3 reduced the grass standing crop to a level where its measurement was impractical and largely irrelevant, since the outcome of competition at this stage was determined not by which species produced the most but by which survived. Effort was therefore directed into determining grass mortality. The density of live and apparently dead grass tufts in relation to forb and tree density was determined by the point-centre-quarter method (Cottam & Curtis 1956) at five sites of differing tree density in each vegetation type. Twenty five points spaced 20 m apart were assessed at each site. A plotless method was chosen because of the order of magnitude differences between the densities of the components recorded. The influence of tree density on grass mortality in each vegetation type is illustrated in Figure 41. The presence of trees increased grass tuft mortality during a period of prolonged water stress. The effect was greatest on soils with a fine texture (the Acacia and Mopane sites)

and least on sandy soils (Combretum site), and was related to the tree density. There was relatively little tree mortality during the same period, and most of it could be ascribed to ring-barking by elephants (Scholes 1985). About 5% of the individuals in an extremely dense *Colophospermum mopane* thicket were killed by the drought, although many more showed some die-back followed by epicormic budding once the drought was over.

The intent was to monitor changes in grass standing crop non-destructively by the spectroreflectance method (Pearson, Miller & Tucker 1976). However during most of the study the green biomass was below the threshold for accurate measurement by this method. Low biomass and abundant forbs precluded the use of other indirect non-destructive methods such as the disc pasture meter (Bransby & Tainton, 1977). The marked tiller method of grass production estimation was therefore selected. One hundred and twenty eight individual tufts of each of the two dominant grass species in each plot were located within a grid system and marked with numbered metal tags. Every four weeks tiller length was measured from the ground to the extended tip of the highest leaf. During the 1982/3 season only the length of the tallest tiller per tuft was measured, but during the following season three individually marked tillers per tuft were measured, and the total number of tillers per tuft was recorded.

In order to assess grass production it was necessary to exclude grazing for a period. One quarter of the marked tillers were covered by a movable herbivore exclusion cage at any given time. The cage was moved to a new position once every four weeks. Additional tillers were marked to preserve the sample size when tillers died. A record was kept of tiller and tuft mortality, since sward productivity depends not only on production per tiller, but also on the number of tillers present. Cumulative tiller extension data are graphically presented in Figure 42 on page 130. Comparisons of tiller number between control and cleared treatments are given in Table 4.4. The experimental design is pseudoreplicated but not autocorrelated, since tillers were measured only during the period

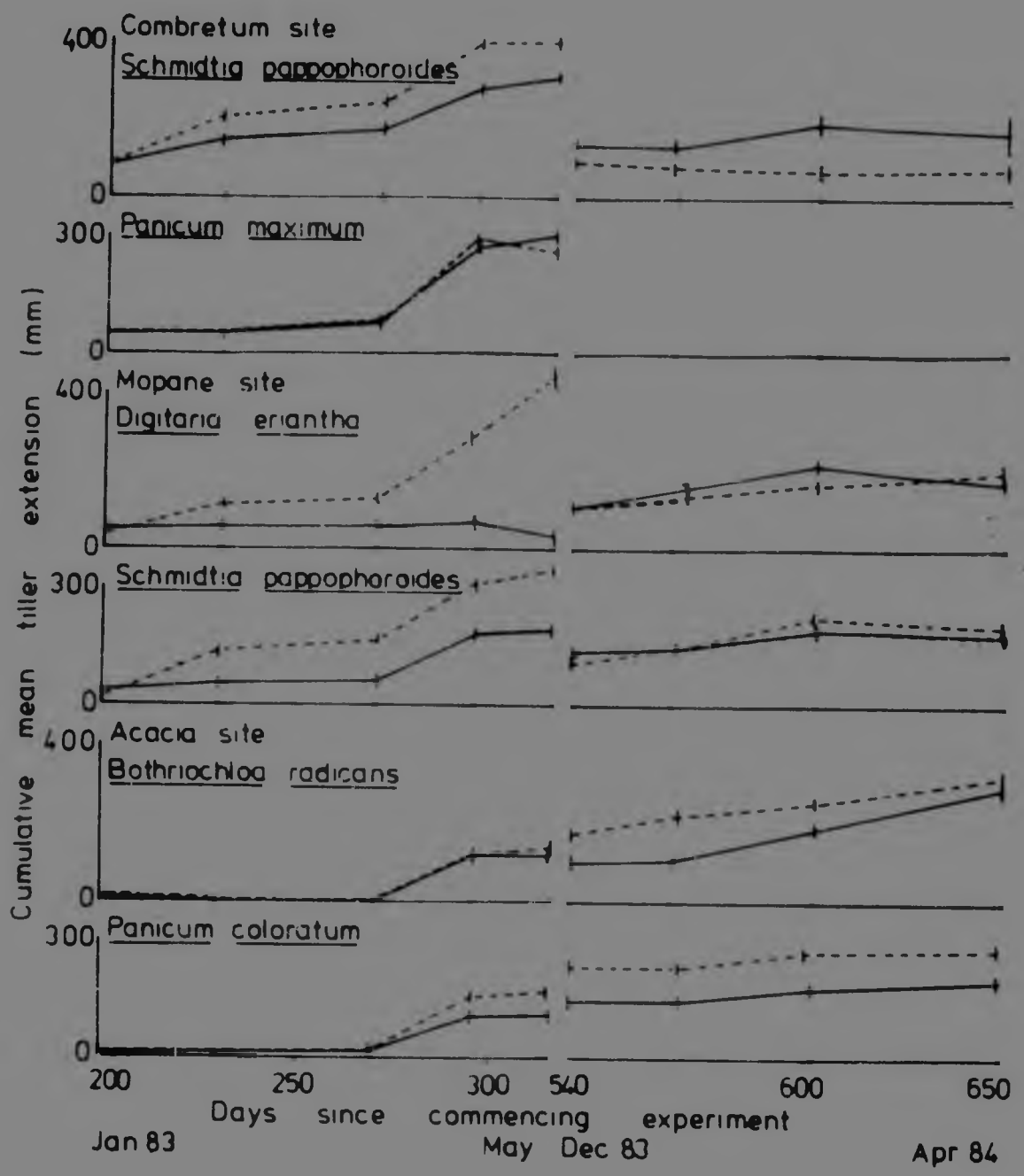

Figure 42. Cumulative tiller extension by site, species & treatment: broken lines are cleared treatments. solid lines wooded controls. Bars are standard errors.

Table 4.4 Mean number of tillers per tuft. Sample size is 64 in all cases but degrees of freedom for the t-tests may be less than 126 due to the assumption of unequal variances.

	Nov 1983		Dec 1983		Jan 1984		Feb 1984		Apr 1984	
1.Combretum site										
Schmidtia pappophoroides	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	5.92	0.31	5.66	0.29	5.56	0.30	4.73	0.28	4.75	0.31
control	4.97	0.29	4.73	0.33	4.42	0.34	4.17	0.36	3.75	0.42
t-statistic	2.238	*	2.117	*	2.514	*	1.228		1.916	
Panicum maximum	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	[illegible]	0.31	5.56	0.30	5.58	0.31	4.88	0.26	4.67	0.31
control		0.69	9.42	0.64	8.04	0.59	10.64	0.96	12.14	1.03
t-statistic	[illegible]	****	-5.461	****	-3.691	****	-5.791	****	-6.945	****
2.Mopane site										
Schmidtia pappophoroides	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	11.72	0.71	12.51	0.66	10.77	0.58	10.50	0.67	12.63	0.71
control	9.98	0.66	11.17	0.64	11.67	0.66	10.66	0.74	11.81	0.77
t-statistic	1.795		1.458		-1.024		-0.160		0.783	
Digitaria eriantha	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	7.67	0.53	8.43	0.51	9.00	0.65	11.01	0.77	10.34	0.80
control	3.61	0.26	4.81	0.33	5.86	0.38	7.33	0.45	7.48	0.44
t-statistic	6.877	****	5.959	****	4.170	****	4.126	****	3.132	**
3.Acacia site										
Bothriochloa radicans	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	3.06	0.55	15.72	0.83	17.11	0.84	15.92	0.82	13.13	0.70
control	6.34	0.38	15.06	0.98	14.09	0.90	15.23	0.96	14.23	0.75
t-statistic	1.077		0.514		2.453	**	0.547		-1.072	
Panicum coloratum	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	9.75	0.81	13.22	0.87	11.78	0.82	12.48	0.82	12.83	1.04
control	8.16	0.57	10.25	0.72	8.47	0.58	10.91	0.68	10.63	0.68
t-statistic	1.373		2.630	**	3.296	***	1.474		1.771	

*=90, **=95, ***=99 % level of confidence

of herbivore exclusion, which occurred only once per tiller per season, on average.

Tiller length is an extremely sensitive indicator of tiller growth and can be directly related to tiller mass (Sharrow 1981), but is a rather poor measure of sward standing crop since it is very difficult to get unbiased

estimates for all species and tiller sizes in the sward. The marked tillers are not necessarily representative of the entire tiller population since only two species were studied. The species composition of the sward changed radically during the course of the study, both as a consequence of climatic events and of the clearing manipulation. Thus the chosen species were in some cases no longer dominant at the conclusion of the study.

The most rapid tiller growth occurred during the first month of the 1983/4 wet season. At the Combretum site *Schmidtia pappophoroides* grew markedly more on the cleared than uncleared site, but *Panicum maximum* slightly less. *Digitaria eriantha*, a species mostly associated with sub-canopy areas, also grew taller in the uncleared plot of the Mopane site towards the end of the season, and *Schmidtia pappophoroides* in the beginning of the season. At the Acacia site *Bothriochloa radicans* grew taller on the cleared site in the first two months of the season following clearing, but less in the third month. *Panicum coloratum* grew more on the cleared than uncleared treatment during the first month

Differences in tiller number between treatments were more pronounced than differences in tiller length for most species, and persisted later in the season. The pattern at the Combretum site was the same as for tiller extension, with *S. pappophoroides* being favoured by clearing and *P. maximum* being disadvantaged. At the Mopane site, *S. pappophoroides* showed little difference between the plots, but *D. eriantha*, which showed less extension on the cleared treatment, nevertheless had consistently more tillers there. *B. radicans* showed little difference in tiller number between the treatments at the Acacia site, while *P. coloratum* had more tillers on the cleared plot during mid-season but by April the difference was small.

Three components of the grass production increase recorded as at the peak of the third post-clearing season are presented in Table 4.5. The fourth, change in sward water-use efficiency due to change in species composition, is a direct result of the changes in density and size of individual tillers. Mass per tiller (which is indexed by tiller length) increased more rapidly on the cleared than uncleared sites early in the first and second growing season (Table 4.3) but the difference was largely lost by the the third post-clearing season. The difference in tillers per

Table 4.5 The components of grass production increase, March 1985.

	Mass per tiller (g) Cleared	Uncleared	Tillers per tuft Cleared	Uncleared	Tufts per hectare Cleared	Uncleared
Combretum site						
A. congesta	26.80	30.13	3.75	3.30	3.55	2.28
P. maximum	18.46	16.33	25.01	33.64	1.08	2.63
P. squarrosa	46.46	31.33	14.78	2.35	4.32	4.38
U. mosambic.	21.06	20.00	12.51	17.12 *	1.39	0.53
Other					5.10	7.68
Total					15.44	17.50
Mopane site						
A. congesta	46.2	42.06	6.61	4.98 **	3.46	8 **
E. rigidior	16.73	10.53	10.22	6.33 **	8.22	5.
P. maximum	24.50	13.93 ***	34.10	35.03	1.73	0 00
P. squarrosa	33.66	49.80 ***	4.79	3.00 ****	3.89	5.61
S. pappoph.	19.60	18.86	6.15	4.94 *	9.95	9.35
U. mosambic.	29.46	24.46	16.42	14.77	0.43	1.87
Other					15.56	15.42
Total					43.24	46.74
Acacia site						
B. radicans	33.86	25.93	16.56	5.28 **	0.30	2.66
P. maximum	27.60	18.00 ***	27.05	31.33	1.36	0.02
U. mosambic.	24.73	32.53	14.83	16.85	7.09	7.78
Other					6.33	10.01
Total					15.08	20.47

*=90, **=95, ***=99 % level of confidence

tuft persisted in the third season on the Mopane site, but less so on the other sites The relative tardiness of this site in adjusting to the post-clearing environment is probably due to to the extremely low rainfall it received in 1982/3 In general the number of tufts per hectare decreased slightly (but not significantly) after clearing, while the performance per tuft had increased, largely due to increased tillering. The sub-canopy grass *P. maximum* increased in performance per tiller and decreased in tillers per tuft at all sites. The number of plants per hectare was lower on the cleared than uncleared treatment at the Combretum site, but higher at the Acacia site. Tuft density was measured in December 1984, using a plotless distance based method (Diggle 1975, Cox 1976). One hundred points were systematically located within a one hectare area, using a wheel-point apparatus (Tidmarsh & Havenga 1955). The distance

from each point to the centre of the nearest grass tuft was recorded to a resolution of 10mm (d_x) and from the centre to the centre of the nearest neighbouring tuft (d_y) The total tuft density was estimated using the compound estimator of Cox (1976), which is corrected for non-random dispersion. These data were also used to test for evidence of competition in the sward. The results are presented in Table 4.7.

4.3 ROOT DISTRIBUTIONS

The distribution of roots in the soil profile is of critical importance to the Walter hypothesis. Strang (1969a) includes some observations of rooting depth in savannas and notes that while grasses have prolific roots in the surface horizons, they also have deeper roots. This was confirmed by Dye (1984) who showed that a significant portion of the water requirement of grass plants can be met by roots deeper than 0.5 m, and that rooting depth varies between grass species. Knoop (1982) showed that the hypothesis of exclusive access to deeper soil horizons by tree roots was false.

This study made no attempt to determine the productivity of underground plant parts, but the vertical distribution of grass and tree roots was estimated by the profile method (Bohm 1979). Two 1 m deep pits were dug in each treatment plot before clearing, one under a tree canopy and one in the open (thus four pits per site). One face of the pit was cut to the vertical, smoothed and washed to a depth of approximately 10 mm with a fine water spray Care was taken to wash the entire profile evenly. A 0.5x1 0 m sheet of clear Perspex was fixed to the profile and covered with a thin sheet of clear acetate Grass and tree roots, which were morphologically distinct down to about 0 5 mm diameter, were traced onto the acetate using different coloured pens.

The centimetres of root length for each root type (grass or tree) were summed horizontally in 5 cm deep bands to the depth of the profile. The

scoring was aided by the use of a 5x5 cm reticule ruled into 1x1 cm grid squares. A root occurring in a square was scored as one centimetre of root length, irrespective of root diameter. Root scores per type per 5 cm depth class were expressed as proportions of the total score for that root type over the entire profile to remove the bias introduced by unequal washing depth between profiles These proportions are presented in Figure 43 on page 136.
The difference in proportions at each depth were tested for significance using the Mann-Whitney-Wilcoxon test for paired samples, since the root counts are non-normally distributed Since many tests were performed, a few of the individual test results are likely to be spurious. The overall trends, however, are clear.

Grass plants have proportionately more of their roots in the surface horisons than tree roots do, and *vice versa* in the deeper soil layers. In between is a zone in which there is no significant difference between the grass and tree root distributions. This zone extends from 300mm to 500mm in the sandy site, 150 to 500mm in the sandy loam site and from 100 to 900mm in the clayey site Therefore rooting depth differentiation is much clearer on soils with high infiltration rat s and low water-holding capacity.

The total counts for grass roots greatly exceeded those for tree roots at all sites (Combretum site 3:1; Mopane site 2:1; Acacia site 6:1). This does not necessarily mean that grass root activity exceeded tree root activity by the same amount, since root density is only one of the factors influencing activity. Resource concentration, radial and axial root resistances, mycorrhizal infection and temporal factors also influence root uptake rates.

A depth of 350 mm, corresponding approximately to the transition between the A and B horizons in all sites, and corresponding also to the horizons used by other workers (Knoop 1982), was chosen as the lower limit of the topsoil. The proportions of each type of root occurring in the topsoil was used to test for differences in root distribution between treatment plots, sub-habitats within sites, and between sites (Table 4.6).

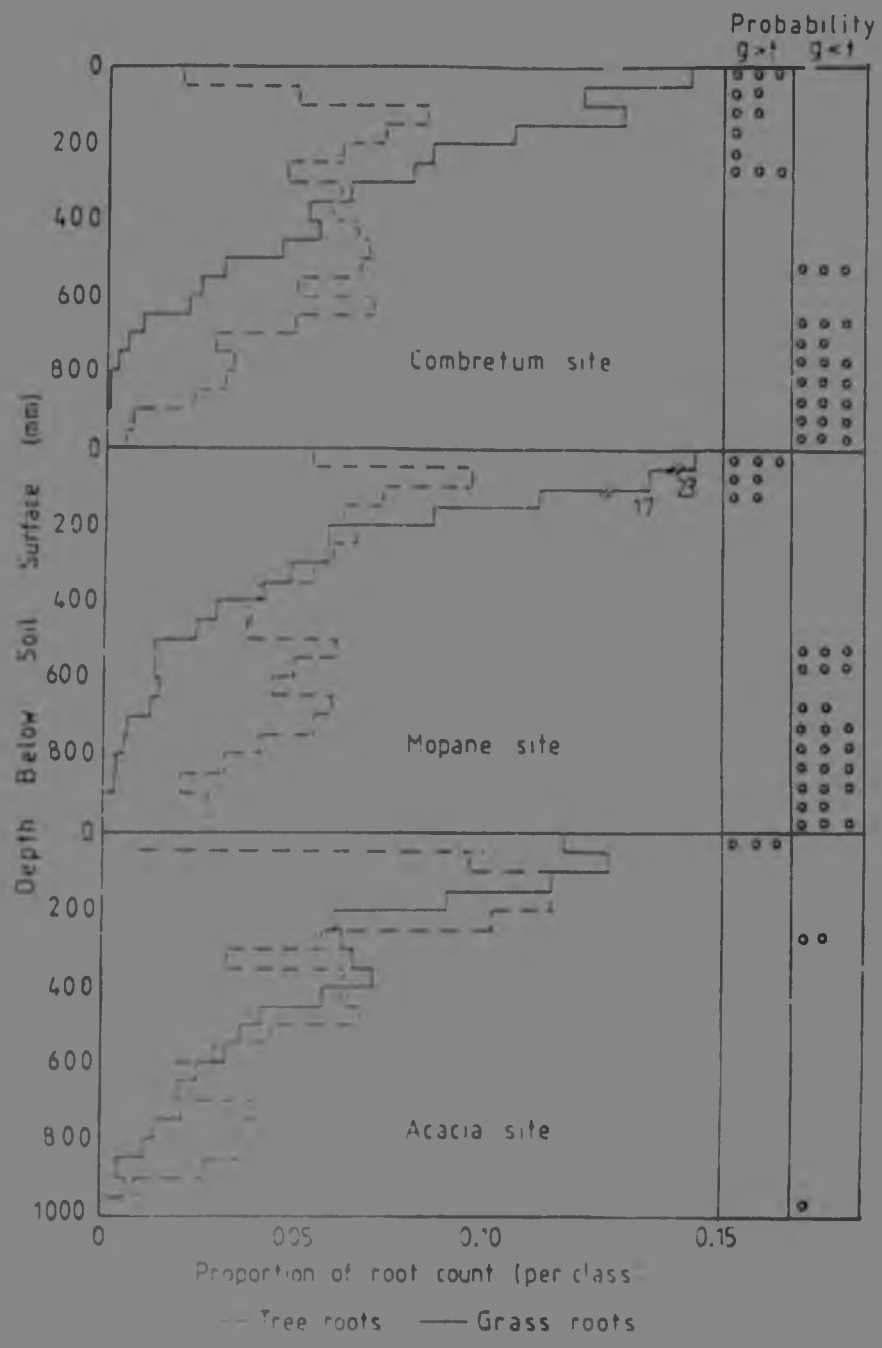

Figure 43 Root distributions Proportions of the total count for each root type encountered at each depth. Significance levels ◦ 90% oo 95% ooo-99%

Table 4.6. Tests of significance for differences in the proportions of grass and tree roots in the topsoil (< 350mm deep) between sites and subhabitats. O=between canopies, C=beneath canopy.

*=90% **=95% ***=99% significance level

Site	Acacia				Combretum				Mopane			
Root type	Grass		Woody		Grass		Woody		Grass		Woody	
Habitat	C	O	C	O	C	O	C	O	C	O	C	O
Code	a	b	c	d	e	f	g	h	i	j	k	l
Mean	55	73	51	69	76	74	72	69	77	85	70	81
sd	2.2	7.7	3.2	8.6	9.6	12.1	8.8	12.7	6.4	9.3	5.7	11.1
n	4	4	4	4	4	4	4	4	4	4	4	4
t-tests for	a-b		c-d		e-f		g-h		i-j		k-l	
Habitat												
|t|	4.607		3.916		0.259		0.387		1.377		1.876	
prob>|t|	.0147	*	.0196	*	.8049		.7135		.2240		.1275	
t-tests for	a-c		b-d		e-g		f-h		i-k		j-l	
Root types												
|t|	2.054		0.778		0.499		0.484		1.764		0.482	
prob>|t|	.0919		.4606		.6356		.6459		.1290		.6477	
t-tests for	a-e		b-f		a-i		b-j		e-i		f-j	
Sites (grass)												
|t|	4.216		0.035		6.615		1.904		0.260		1.474	
prob>|t|	.0209		.9736		.0039		.1074		.8043		.1945	
t-tests for	c-g		d-h		c-k		d-l		g-k		h-l	
Sites (trees)												
|t|	4.588		0.065		5.769		1.772		0.525		1.416	
prob>|t|	.0122	*	.9506		.0028	**	.1304		.6213		.2074	

Pooled habitat data

Root type	Grass	Woody	Grass	Woody	Grass	Woody
Code	A	B	C	D	E	F
mean	65	60	75	71	81	76
sd	11.2	11.3	10.1	10.2	8.5	7.5
n	8	8	8	8	8	8
t-tests for	A-B		C-D		E-F	
Root types						
|t|	.754		0.734		1.166	
prob>|t|	.634		.4750		.2640	
t-tests for	A-C	B-D	A-F	B-G	C-F	D-G
Sites						
|t|	1.763	2.033	3.402	2.880	1.364	0.898
prob>|t|	.0700	.0616	.0047	.0122	.1949	.3842
			**			

*=90% **=95% ***=99% significance level

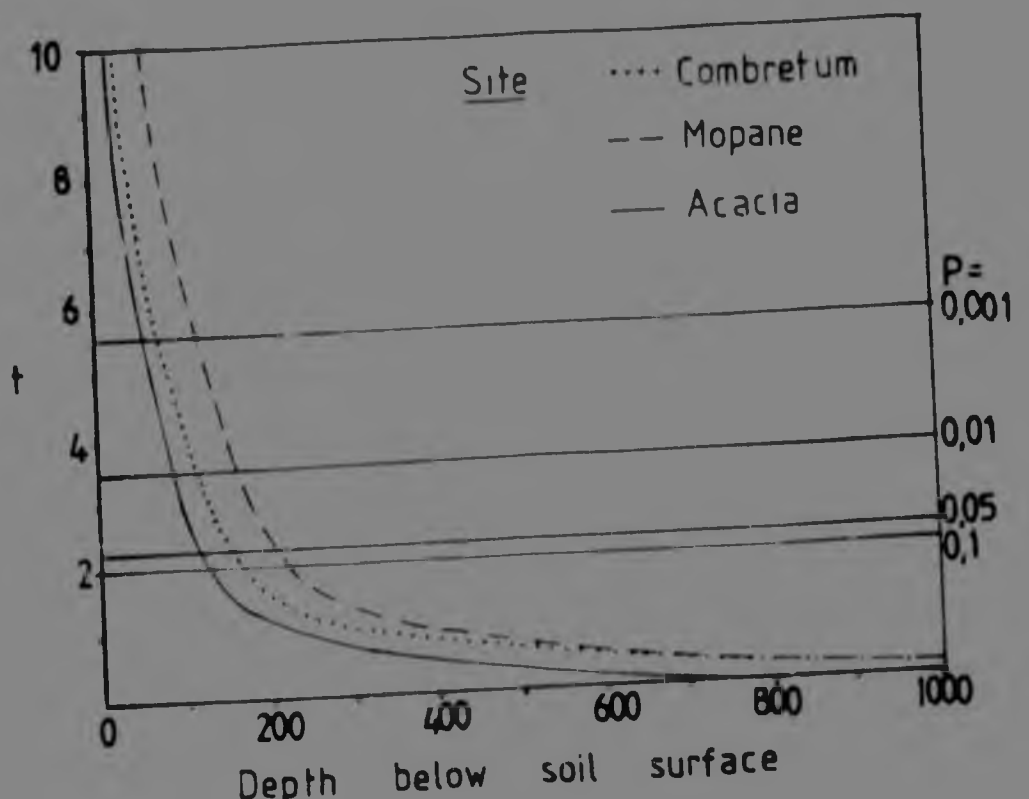

Figure 44 t Test values for differences between root types: Proportion of roots above the depth on the x-axis are compared for trees and grasses.

Statistical analysis by t-test showed no significant difference ($p<0.05$) between control and to-be-cleared plots at each site. A statistical difference between micro habitats (canopied and open) was demonstrated for the Acacia site, where rooting was deeper under the canopy for both trees and grasses. Contrary to expectation, no significant differences were found between root types within any sub-habitat, although grass roots had consistently higher proportions in the topsoil, especially under tree canopies. Testing for differences between sites revealed the Acacia under-canopy habitat to have a significantly lower proportion of tree roots in the topsoil than under-canopy habitats in the Mopane or Combretum sites.

When the micro-habitat data for each site were pooled, thus raising the sample number at each site to eight, there was still no significant difference between the proportions of tree and grass roots in the topsoil. A comparison of sites again showed the Acacia site to differ from the others, but only significantly so with respect to the Mopane site. In all cases rooting was deeper for both trees and grass in the Acacia site, a surprising finding given the poor drainage at this site.

To what extent is the failure to find a significant difference in rooting depth between trees and grasses a function of the depth chosen to represent the topsoil : subsoil interface? To answer this question, t values were calculated for differences in cumulative rooting proportion between trees and grass above various depth thresholds (Figure 44 on page 138). A significant difference between the two types occurred only in the top 250 mm for the Mopane site, 150 mm for the Combretum site and 100 mm for the Acacia site. These would be the appropriate topsoil depths for the application of the Walter hypothesis.

4.4 SPATIAL EVIDENCE FOR COMPETITION IN SEMI-ARID SAVANNAS

Spatial patterns can provide evidence for or against the importance of competition in structuring a community (Pielou 1977). It is suggested that when competition between individuals is intense, the distance between them would tend to be maximised, thus tending to regular distribution. A clumped distribution of individuals would indicate some other factor to be dominant, perhaps local microclimatic amelioration in the vicinity of other plants or uneven propagule distribution.

The two-distance method described in section 4.2 for determining tuft density can also yield information on the distribution of tufts (Cox 1976). In a completely randomly distributed population, d_y is expected to exceed

Table 4.7 Spatial pattern estimators. Values of p exceeding 0.25 indicate regular populations, less than 0.25 indicates clumped populations. Estimator p is binomially distributed with n=100.

	Combretum		Mopane		Acacia	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Grasses	0.26	0.34 *	0.24	0.22	0.24	0.46 ***
Forbs	0.14 **	0.44 **	0.30	0.22	0.18 *	0.30
Trees	-	0.22	-	0.30	-	-

* = 90% , ** = 95% , *** = 99% confidence level of significance

d_x one quarter of the time on average. In a clumped population the probability is lower, while in a dispersed population it is higher. The probability p that $d_y > d_x$ is binomially distributed, so the significance of a deviation from randomness can be tested. The pattern estimators are presented in Table 4.7. For grasses they indicate significant regularity of spacing in the wooded treatments of both the Combretum and Acacia sites. The implication is that competition between grass tufts is stronger in these two situations than in the cleared treatments. The Mopane site was greatly affected by the drought, and may not have stabilised sufficiently by the time these measurements were taken to display the spatial consequences of competition.

The spatial indicators for forbs showed significant deviations from randomness in several cases, but no interpretable trends. Both ephemeral and perennial forbs were included in the analysis, which may have obscured interactive effects between the perennial forbs.

The method was also applied to woody plants, with the modification that sum of the stem basal areas for each of the two plants was recorded as well as the point-to-plant and plant-to-nearest neighbour distances. The systematic points were located by laying down a regular 10m grid with the aid of a tape measure. The Cox (1976) pattern estimators for woody

plants did not deviate significantly from randomness. In addition to the pattern estimators the correlation between nearest-neighbour distances and an index of plant performance (the combined sum of the basal areas) could be calculated after the fashion of Yeaton & Cody (1976) and Smith & Walker (1983). The hypothesis is that competing plants crowded close to one another should perform more poorly than when spaced further apart and therefore have smaller basal areas. The only significant correlation discovered was for intraspecific interactions in *Colophospermum mopane* in a dense coppice site (r^2=0.50 n=85 p<0.05). This site was the one with the highest woody biomass, which was overwhelmingly dominated by *Colophospermum mopane*.

If competition between the "woody plant" and "grass" functional groups plays a role in determining their relative proportions in the community, then an inverse relationship should exist between their biomasses in samples from a range of comparable sites from the same community. Low tree biomass should be associated with high grass production, and in the absence of herbivory, greater grass standing crop Since there are finite limits to the performance of individual tillers and the number of tillers per tuft, and these limits are reached within a few seasons, increased grass production in the longer term should be related to an increase in tuft density per hectare, a measure which is furthermore less sensitive to herbivory than production itself. This hypothesis was tested by applying the two-distance method to woody plants and to grass tufts within areas with differing tree basal areas. Tree basal area is well correlated with tree biomass in the vegetation type studied. The study areas were located in woodlands dominated by *Colophospermum mopane*, all within a 2km radius of the Mopane study site. The low basal area sites had been cleared to different degrees. The relationship between tree basal area and grass tuft density is inversely concave (Figure 45 on page 142). Its form is reminiscent of the tree basal area-grass production curves presented by Beale (1973) and the general case for asymmetric competition as analysed by de Wit (1960) There is a slight tendency towards increased dispersion (implying increased inter tuft competition) as the woody basal area increases and the tuft density decreases.

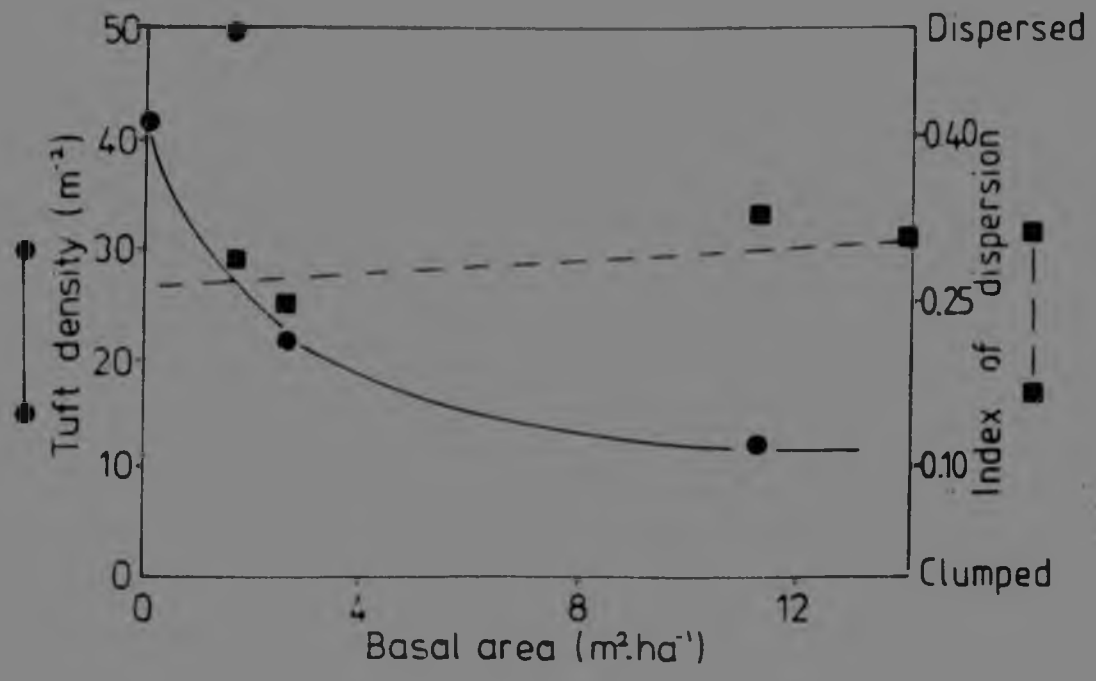

Figure 45. Relationship between tree basal area and grass tuft density: curves fitted by eye

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In summary, evidence for a competitive effect of trees on grasses was apparent for all sites, and grass on grass for some sites. There was no evidence of inter-tree competition except at the most densely wooded site, which suggests that the potential exists for increased woody density ("bush encroachment") at the other sites

4.5 WATER USE EFFICIENCY

Cohen (1970) observes that it is necessary to know both the amount of the limiting resource preempted by each competitor and the efficiencies with which the resource is translated into new growth to predict the outcome of a competitive interaction. Several lines of evidence point to the central importance of WUE as a determinant of herbaceous production in savannas.

1. The large production differences between eutrophic and dystrophic sites receiving the same rainfall (compare the Combretum and Acacia sites) implies that the latter have a higher WUE in the herbaceous layer as a whole.

2. Competition models, such as those of Walker & Noy-Meir (1982), McMurtrie & Wolf (1983) and this study, are highly sensitive to the values of WUE which they use.

3. The grass production beneath the tree canopy, where moisture and light are lower than between canopies, is frequently greater than in the open.

Water use efficiency can be directly and instantaneously measured using gas analysis techniques, or it can be inferred by monitoring the growth of a plant over a period of known water use. The former method requires sophisticated equipment which is difficult to use in the field. It is usually possible to measure the WUE of only a single leaf at a time by this method, making it inappropriate for estimating the long-term WUE of the vegetation as a whole. A large number of leaves of different species and at different times can however be measured fairly simply, and the technique therefore lends itself to comparative studies. Instantaneous WUE as measured by gas analysis overestimates the long-term WUE of the vegetation because it does not adequately account for respiration losses by organs not enclosed in the cuvette or at times not sampled. Long-term WUE (over the period of a growing season) are better approached by the harvest method, which is however slow and labour-intensive and must therefore

be restricted to a few key species. The main difficulty in this method lies in accurately estimating the water use by a particular plant. The most practical approach is to isolate the plant in a pot and give it a known amount of water. Loss by evaporation can be corrected for by reference to pots without plants. The unnaturalness of the pot environment is minimised by conducting the experiment under conditions approximating those in the field.

4.5.1 GAS ANALYSIS MEASUREMENTS

The aim of this experiment was to compare the relative changes in water use and water use efficiency by trees and grasses over a period of declining soil moisture levels. The hypothesis to be tested was that niche separation exists between trees and grasses along a soil water-potential axis. Relative differences in either transpiration rate or WUE with declining soil water potential would provide such separation.

Lof (1976) discusses the theoretical reasons why WUE should not be a constant over the full range of water potentials. Stomatal closure caused by water stress affects transpiration more than photosynthesis due to differences in the stomatal diffusive resistance to CO_2 and H_2O. Furthermore, the two fluxes respond to different variables: transpiration to temperature and water potential; and photosynthesis to stomatal resistance and radiant energy.

A LICOR-6000 portable photosynthesis unit equipped with a 0.25 litre cuvette was used to measure carbon fixation rates by individual leaves of four woody plant and one grass species through the duration of a drying cycle at the Mopane site. The transpiration rates were simultaneously measured on different leaves of the same plants using a LICOR-1600 steady-state porometer. The LICOR-6000 is able to simultaneously measure moisture and carbon fluxes, but the failure of the moisture sensor in the field required the above arrangement. The absolute

values of WUE obtained are therefore not reliable, although the absolute values of transpiration and photosynthesis are

The only grass species with leaves suitable for use with both instruments was *Panicum maximum*, and then only until water stress caused leaf rolling. Transpiration and carbon fixation were measured in the sun at two-hourly intervals from sunrise to sunset on four occasions during a three-week rainless period in December 1984. Over this period soil moisture conditions declined from near saturation to wilting point. A prior trial had shown dark respiration and transpiration to be low (<5%) relative to the daytime rates, a finding supported by Strain (1975).

The results are presented in Figure 46 on page 146. The instantaneous values recorded every two hours have been integrated to produce daily rates, which are plotted against the profile moisture content on that day, as determined from the arrays of moisture blocks. Daily transpiration rates show a similar course in relation to soil moisture in both trees and grasses: a fairly steep decline to a relatively constant low level at soil profile water contents below 50% of field capacity. Leaf rolling prevented transpiration measurements on *P. maximum* at the lowest water potentials. The low on day one for this species is attributed to a lag period while the grass leaf tissues rehydrate followinf a previous dry period. The highest transpiration rates per unit leaf area were consistently delivered by the shrub *Grewia bicolor*, which was also observed to be the first to show symptoms of water stress, both at midday when the soil was moist and over the course of the drying cycle. Moore (1980) reported *Grewia flava* to have the highest transpiration rate amoung the species which he studied. The lowest transpiration rates were recorded in *Combretum apiculatum*, which was also least sensitive to soil moisture levels.

Net photosynthetic rates by woody plants declined slightly over the course of the drying cycle, while those for *P. maximum* declined sharply, especially after the leaves had rolled and wilted While the soil was moist it had the highest photosynthetic rate, which is consistent with its C4 photosynthetic pathway. At lower soil moisture potentials the C3 tree *Colophospermum mopane* had the highest rates.

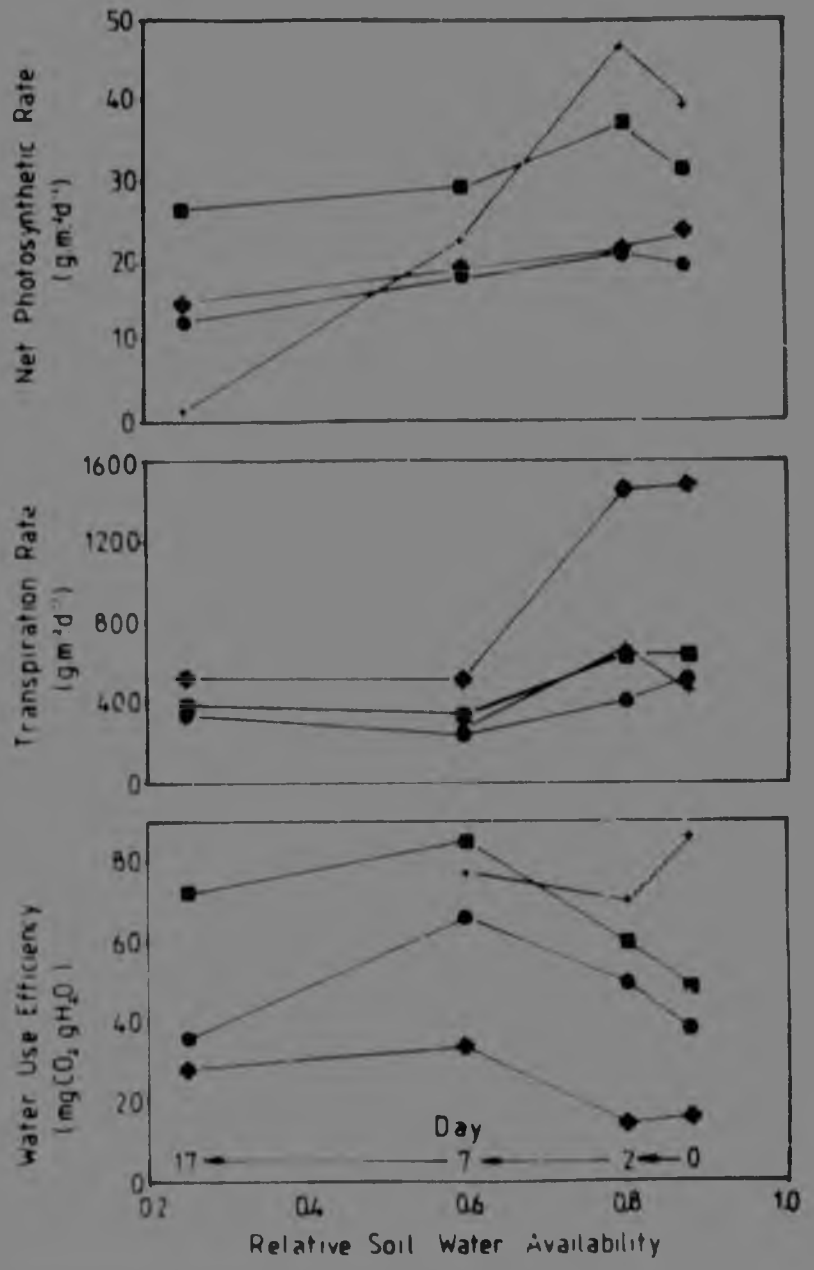

Figure 46. Water use efficiency in the field: Changes in transpiration and photosynthesis with decreasing soil moisture ◆=G bicolor; ■=C. mopane; ●=Combretum apiculatum; +=P maximum.

4.5.1.1 Discussion

The overall trend among woody plants was for WUE to increase slightly with increasing water stress. This trend has been observed by other workers in arid regions (Lof 1976). The trend in *Panicum maximum* is uncertain since transpiration could not be measured on the last day, but the rapid decline in photosynthetic rate suggests that WUE would decline also.

WUE of woody plants and grasses was of the same order, despite the difference in photosynthetic pathway. The values obtained are in broad agreement with those estimated by other workers (O'Leary 1975). The shrub with the highest transpiration rate (*G. bicolor*) had the lowest WUE, while that with the highest WUE had a relatively low transpiration rate (*Colophospermum mopane*). *G. bicolor* could be classified as a drought tolerater and water "spender" relative to the sclerophyllous drought avoider water "savers", *Colophospermum mopane* and *Combretum apiculatum*.

Thus a variety of strategies is discernable both between the tree and grass functional groups, and within the tree group. The possible tendency for grasses to have a higher WUE than trees at high water potentials but lower WUE at low water potentials (as shown in this experiment) permits a degree of niche separation between these potential competitors. Further studies are required to establish whether this is the general case. This study shows that changes in WUE over the course of a drying cycle are relatively small, which is an assumption used in the model of savanna production.

4.5.2 POT EXPERIMENT

The tendency for certain grass species (usually highly productive and palatable ones) to be restricted to the area below the canopy of trees

has been noted and investigated by several authors (Bosch & van Wyk 1970, Kennard & Walker 1973). Lower light levels, improved water and nutrient status and enhanced seedling establishment have all been suggested as explanations for this pheromenon, which has important implications for the productivity and quality of the herbaceous layer. The desirable sub-canopy grasses have been observed to disappear after tree removal (Dye & Spear 1984).

Savanna grasses have a C4 photosynthetic pathway and therefore do not reach light saturation point even in bright sunshine. If light were the dominant factor in delimiting the habitat preference of the sub-canopy species, then their performance in shade should be better than in the sun, all other factors being equal. However *Panicum maximum*, the principle sub-canopy species, performed better in the sun than in the shade when grown in pots by Kennard & Walker (1973).

An analysis of the relative moisture status of the sub-canopy and between-canopy habitats is given in Chapter 3. The sub-canopy habitat receives less moisture overall than the inter-canopy areas, due to interception losses by the trees. This is balanced in the immediate vicinity of the tree stem by the stemflow contribution, which can be considerable. Water status depends also on the transpirational demand imposed on the plant. Sunlit leaves undergo a rapid and detrimental increase in temperature if they do not cool their leaves by transpiration. Shaded leaves do not receive the same radiation load, and therefore are free to control their water use and thus raise their WUE. The sub-canopy grasses, which tend to be more mesic species than those of the inter-canopy, have been observed to wilt later than those exposed to the full sun.

The sub-canopy habitat tends to be a zone of nutrient enrichment, due to the deposition there by leaf-fall, leaching and stemflow of nutrients assimilated in the intercanopy regions (Kellman 1979). It also has a higher percentage of organic matter in the soil, which improves the moisture status by increasing infiltration and decreasing evaporation, and provides favourable microsites for seedling germination. If nutrient status was the only factor involved, fertilisation should lead to an increase in the sub-canopy grasses, which it does (Donaldson, Rootman & Grossman 1984).

In the course of this study the following additional observations were made:

1. Prior to clearing, the sub-canopy habitats were most clearly evident on the sites of lowest fertility (Combretum and Mopane) and were not at all apparent on the Acacia site.

2. The subcanopy habitats persisted in the Combretum and Mopane sites after clearing.

3. On the Acacia site typical sub-canopy grasses (*P. maximum, P. deustum*) germinated in the first season following clearing in the areas previously covered by tree canopies.

It is suggested that light, moisture, and nutrients are all involved in the delimitation of the habitat requirements of sub-canopy grasses. An experiment was designed using a typical sub-canopy grass (*Panicum maximum*) and a typical intercanopy grass (*Schmidtia pappophoroides*) to test this idea

The aim of the experiment was to estimate and compare the transpiration rate and water use efficiency of the two species grown in all combinations of high and low light, stressed and non-stressed water supply and three different soils. The hypotheses to be tested were that *P. maximum* grows best in the shade on nutrient poor soils, but best in the sun on nutrient rich soils, provided that the water supply is non-limiting, and outcompetes *Schmidtia pappophoroides* under these conditions due to higher transpiration rates or WUE

4.5.2.1 Procedure

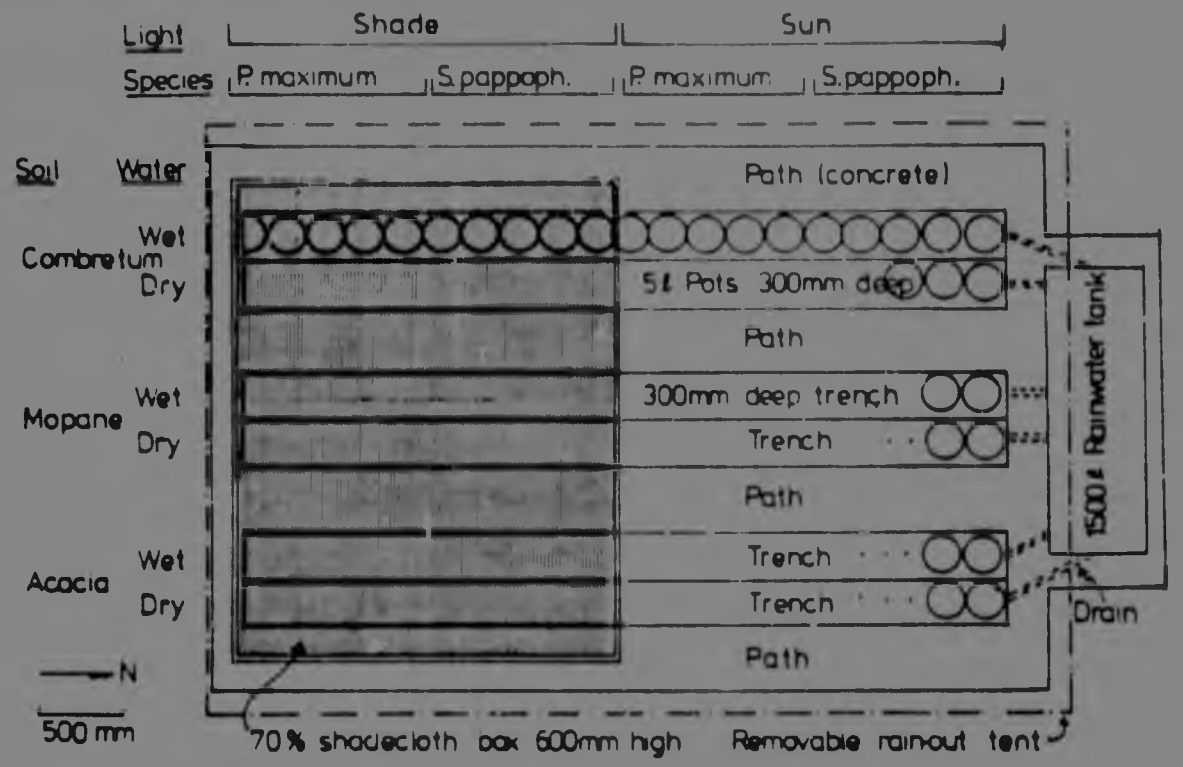

Figure 47. Layout of the pot experiment

The layout of the experiment is illustrated in Figure 47 on page 150. In principle it is a complete factorial experiment with three treatments: light (sun and shade); water (wet and dry) and soil (Combretum, Mopane and Acacia). Practical limitations prevented complete randomisation. Where possible, treatments were interspersed. Each treatment level had five replicates. The experiment was conducted in 5ℓ plastic pots filled to a depth of 300mm with sieved topsoil from each of the study sites. The pots were planted in March 1985 with one new tiller each, stimulated from a small number of parent plants growing at the Mopane site by severe clipping two weeks previously. The soil surface was covered with a mulch of black plastic spheres 2mm in diameter to a depth of 20mm, in order to suppress evaporation. The pots were placed in trenches 300mm wide and 300mm deep in order to keep the soil in the pots at approximately

the same temperature as soil in the field. Irrigation was with rain-water delivered by flooding the trenches to a depth of 50mm and allowing the soil in the pots to soak up the moisture through three 10mm holes in the base of the pots. Thereafter the trenches and pots were drained and the pots individually weighed to the nearest 0.1g in order to determine their moisture content. This irrigation method was adopted to ensure an even initial wetting of the pot soil to field capacity. The pots in the "wet" treatment were re-irrigated whenever the moisture had dropped to 50% of field capacity. These plants therefore never showed signs of more than transient water stress. The plants in the "dry" treatment were not re-watered until most of them were showing severe wilting, when the pots were brought back up to field capacity. This occurred twice during the two-month duration of the experiment. The wet treatment received water on average every 10 days.

The pots were individually weighed every three days at 08h00. Irrigation was done at 17h00, and the pots were weighed the next morning after draining during the night. The entire experiment was covered with a tarpaulin tent when rain was imminent.

One half of the experiment was shaded with commercial shadecloth which reduced the light intensity by 70%, which is comparable to the mean reduction beneath a tree canopy. The shadecloth enclosed the "shade" pots on all sides except the south, and was suspended 0.6m above them.

Each replicate included a control pot which had no plant in it, in order to correct for evaporation from the soil surface.

The plants were harvested after 60 days, and the roots were washed out of the soil with a water spray. The dry mass of the above- and belowground parts was determined to the nearest 0.01g after drying for 24 hours at 70°C. Water use by each plant was determined by summing all the decrements in pot mass over the duration of the experiment and correcting for evaporation from the soil surface. The correction was made by relating evaporation rate to soil moisture content for each light and soil combination and then applying this model to each pot individually,

according to its known moisture content. The corrections, especially in the case of *Schmidtia pappophoroides*, were significant.

Data analyses were by pairwise t-tests and regression analysis (homogeneity of slope tests), using the SAS statistical package (SAS Institute, 1982).

4.5.2.2 Results

The following observations can be drawn from the results presented in Figure 48

1. Production, transpiration and WUE were much higher in *Panicum maximum* than *Schmidtia pappophoroides* in all treatments. Based on these data, *P. maximum* would out-compete *S. pappophoroides* in all habitats.

2. The linear regression between dry matter accumulation and water use was significant at the 90% level for all treatments in *P. maximum*, but only in the sunlight for *S. pappophoroides* (except in the Combretum soil, where the regressions for the sun and shade treatments were both significant).

3. There is no significant difference in WUE (as measured by the slopes of the above regressions), transpiration rate or production between soils in *P. maximum*

4. There is no significant difference (at the 10% level) between the slopes of the regressions relating dry matter accumulation to water use for shaded and sunlit plants in either species on any soil, except for *S. pappophoroides* on clay soils, where the shaded plants performed very poorly In general, however, the slopes (equivalent to WUE) are lower in shaded than sunlit plants in both species. There

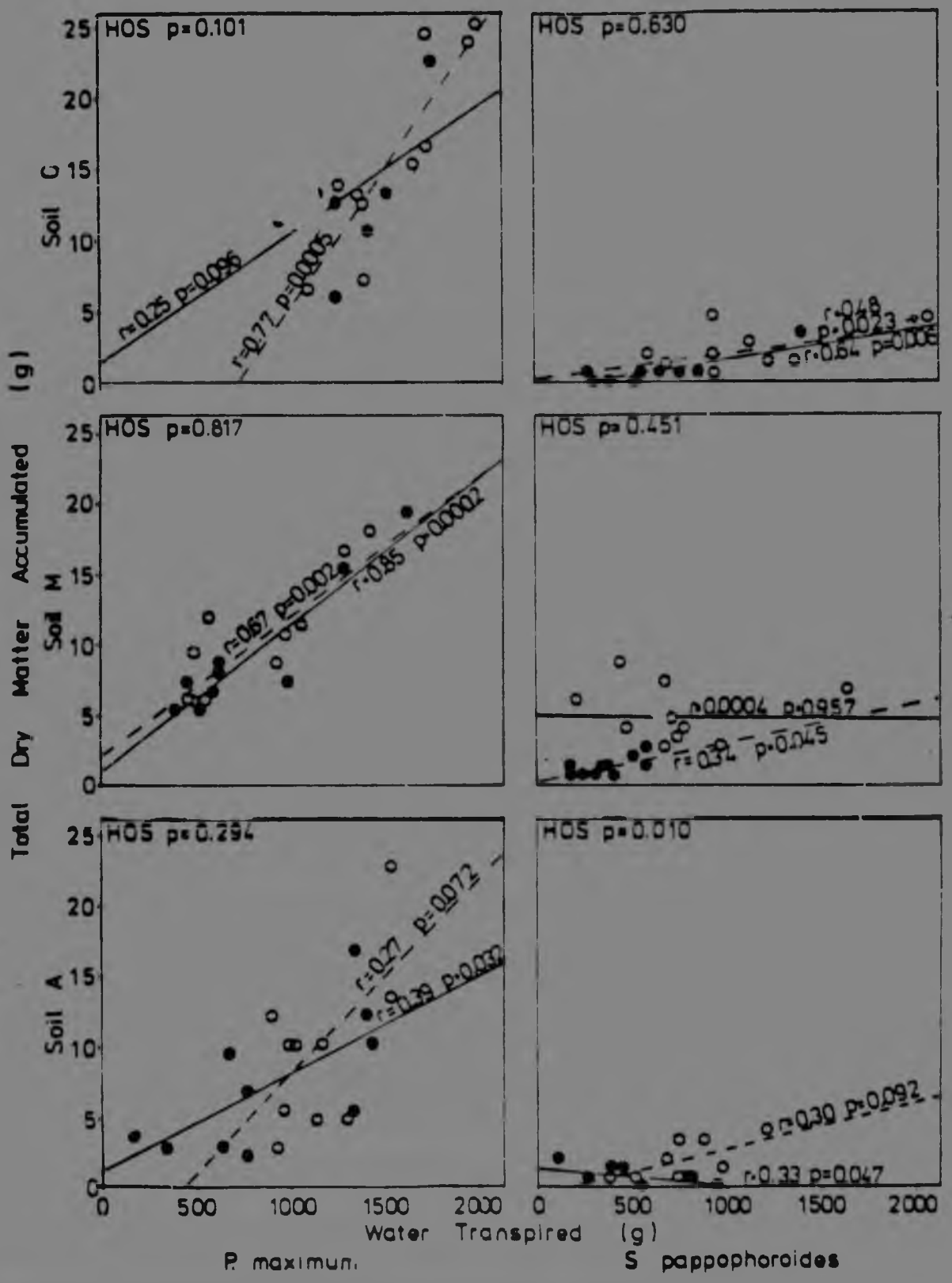

Figure 48. Regressions of net production on water usage: Sun (o-- o), Shade •___•, HOS=Homogeneity of Slope test.

is an indication (replication is too low for a meaningful statistical test) that the WUE of shaded, water-stressed individuals of *P. maximum* is lower than that of unstressed plants (see soil C).

5. Dry matter accumulation is significantly lower in the shade than the sun in *Schmidtia pappophoroides*.

6. The above findings are true for total dry matter (above plus belowground) as well as for aboveground accumulation alone.

4.5 2.3 Discussion

P. maximum can grow equally well under high and low light intensities, but is sensitive to water stress. *Schmidtia pappophoroides* cannot grow successfully in the shade, especially on clayey soils, which were permanently saturated due to its inability to extract the water. It grows best on loamy sands (Mopane soil) in the sun, but its growth there is poorly correlated with water use. This poor correlation could be due to inaccurate correction for evaporation, since evaporation rates were high on this soil but transpiration rates low in this species. The relative inaccuracy is therefore large. The experiment cannot fully account for the strange behaviour of *P. maximum* in the field but does account for the absence of *S. pappophoroides* under tree canopies. This raises the possibility that the sub-canopy grass species grow there because they can rather than because they are restricted to this habitat. Other factors, such as sensitivity to drought (Scholes 1985), especially as seedlings (Kennard & Walker 1973), may prevent them from dominating the inter-canopy habitat.

The WUE value for *Panicum maximum* in the pot experiment (10 mg $CO_2.gH_2O^{-1}$) is of the same order as the values determined by gas analysis (10-90 mg $CO_2.gH_2O^{-1}$). That they are on the low side is to be expected due to the probable dry matter losses, especially of roots, incurred during harvesting and the effects of dark respiration and root

turnover which are not included in the gas-exchange measurement. The WUE of *Schmidtia pappophoroides* is considerably lower (2.5 mg $CO_2.gH_2O^{-1}$). By comparison, the WUE for the entire sward at each study site, as estimated by the slope of the lines for cleared treatments in Figure 40 on page 126, is in the region of 0.4 (Combretum and Mopane sites) to 1.5 mg $CO_2.gH_2O^{-1}$ (Acacia site). This is because the latter figures are for aboveground production only and include some losses due to grazing and decay before harvest. They are also only partly corrected for evaporation from the soil surface. The data from this experiment suggest that differences in herbaceous layer productivity between sites with different soils are not due to differences in the performance of individual species, but due to differences in species composition between the sites. The highest productivity site (Acacia) has a preponderance of grass species with high water use efficiency, such as *P. maximum*, while the lowest productivity site has mostly grasses with a low WUE, such as *S. pappophoroides*. Whether this trend is due to differences in nutrient status at the sites or due to differences in water availability would need to be tested with a fertilisation experiment. Another hypothesis arising from this experiment is that grasses with a mesic distribution have a higher WUE than those with a xeric distribution.

5.0 A MODEL OF HYDROLOGY AND PRIMARY PRODUCTION IN SAVANNAS

5.1 MODELLING PHILOSOPHY

The construction of conceptual models to explain observations is fundamental to scientific method at all levels. In this sense a "model" is a hypothesis; a set of precise statements providing a link between two sets of observations. Simple qualitative models can be concisely stated in words, but when the model involves several quantitatively interacting factors it is more precise and concise to state it in mathematical form. When the relationships between the variables are mathematically uncomplicated they can be analysed with the tools of symbolic algebra. Frequently, however, the complexities of nature demand functions which are mathematically intractable The model is explored in this case by numerical simulation

Numerical simulation was adopted as an approach for this study for the following reasons.

1. It acts as a framework within which the various facets of the study could be integrated.

2. It allows specific hypotheses regarding the interaction between woody plants and grasses in a savanna to be tested.

3. It generalises the study by interpolating within the limits of the data base Thus while field data were limited to three soil/vegetation associations, two seasons and two treatments (cleared and uncleared), the model provides a basis for making predictions of, for instance, the system response to partial clearing on intermediate soil types under various rainfall regimes.

5.C A MODEL OF HYDROLOGY AND PRIMARY PRODUCTION IN SAVANNAS

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Models are approximations to nature. Thus modelling is a process rather than an end. The fit of prediction to observation can usually be improved by the inclusion of further factors and more complex interactions, but at the expense of causal clarity. Since the model is only as good as the observations on which it is based, the complexity should be at a level compatible with the precision of the data. The modelling philosophy has been to introduce the minimum level of complexity necessary to explain the major trends in the data while maintaining the mechanistic structure of the model. In accordance with this principle, three models relating to three different aspects of savanna function are proposed independently, rather than in one overall model. The first is a model of hydrology and primary production in a semi-arid savanna, and is discussed in this chapter. The second, in chapter 6, examines the conditions under which savannas can be kept in an open condition by the use of fire. The third, in chapter 7, simulates the regrowth of woody plants following bush clearing.

5.2 SAVANNA

5.2.1 GENERAL STRUCTURE

SAVANNA is a simulation of the hydrological cycle of a terrestrial system having trees and grasses as its only transpiring components, linked to a plant production simulation model in which tree and grass leaf growth is a function of soil moisture. The iteration period is one day and the driving variable is rainfall. The model is not directly patterned on any single model reported in the literature but has been influenced by those of Walker *et al* (1981), McMurtrie and Wolf (1983) and the ELM project (Innis 1978). The general structure of SAVANNA and its computer environment is illustrated in Figure 49 on page 159.

Numerous assumptions and simplifications are made in the construction of a model such as this. Some have been dealt with in the description of the hydrological system, and most others are revealed by the model structure (following section). The major simplifying assumptions are as follows.

1. All woody plants regardless of species or phenological stage are treated as a single functional group, whose parameters can be varied as a whole. The same applies to all grasses No other plant forms are considered. In each simulation the woody and grass components are given the parameters representing the tree and grass species dominant at the site which provided the hydrological parameters. The model does not allow for species composition changes during the simulation period.

2. Woody tissue growth rates are assumed to be slow by comparison to leaf tissue production, and thus woody standing crop is treated as a constant (although woody plant leaf tissue is treated dynamically).

3. The interactive effects of herbivory on plant productivity (such as stimulation of compensatory growth (McNaughton 1983)) are ignored since they could not be quantified.

4. Additional water inputs such as run-on or lateral subsurface flow from adjacent areas are not considered

5. The soil and vegetation are considered to be spatially homogeneous in the horizontal dimensions. There is no consideration of the sub-canopy habitat.

Water enters the model system as rainfall, a portion of which is lost by interception and runoff. The remainder percolates into the soil and is lost by evaporation, transpiration by trees and grass and deep drainage from the bottom of the soil profile Two soil horizons are defined (topsoil and subsoil) within which soil properties are homogeneous. The profile is divided into an arbitrary number of soil layers (10 layers, each 100mm

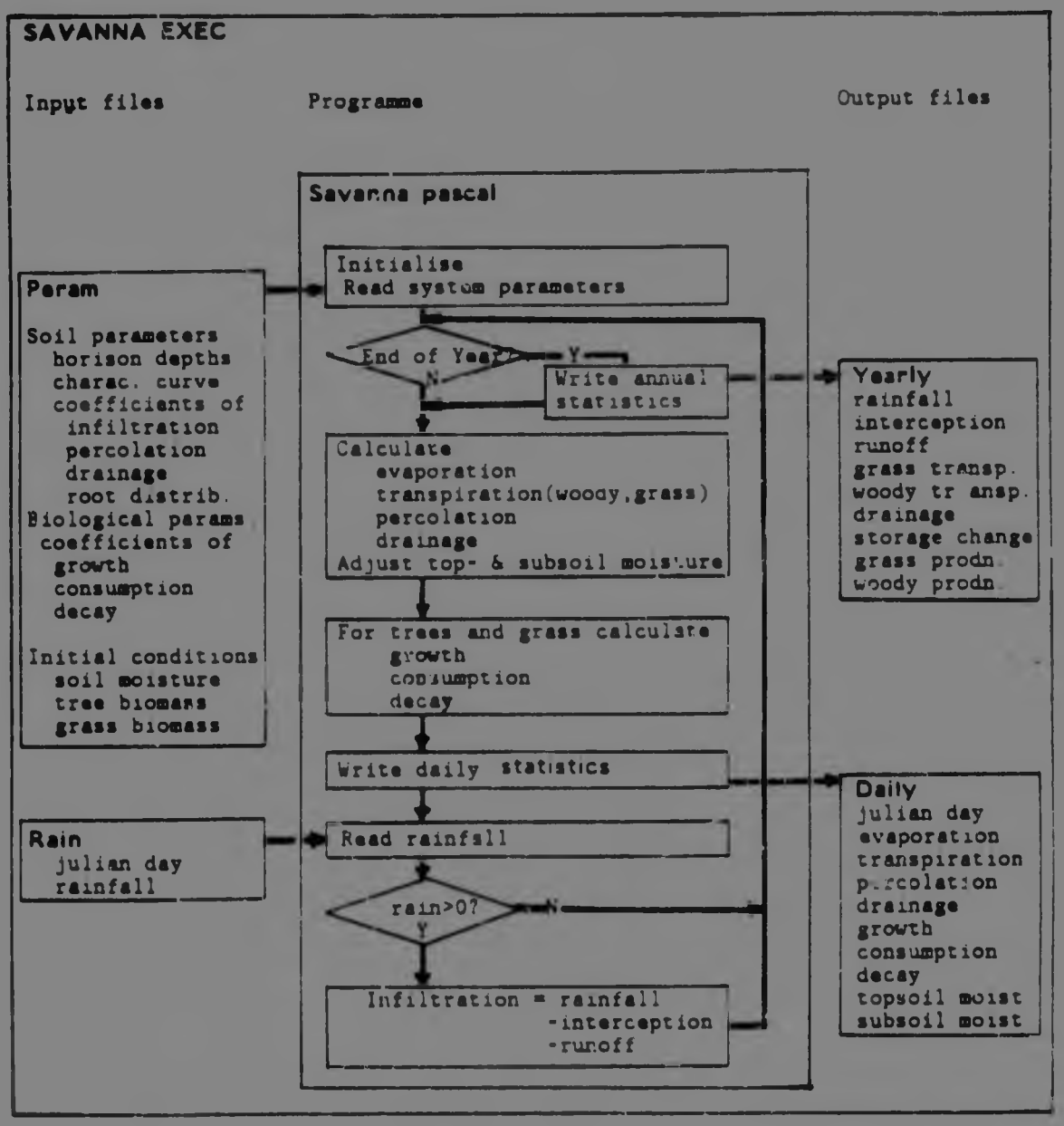

Figure 49. General structure of the model: Items in bold are the file names used.

deep). Evaporation from the soil surface is extracted from the upper layers; deep drainage is removed from the lowest layer. The transpiration rate of grasses and trees are controlled by the moisture content of all layers, weighted by the density of roots within each layer. Moisture transfer between layers is a function of their relative water potentials.

Grass and tree growth are controlled by the amount of water which they transpire and the efficiency with which it is translated into dry matter. Grass biomass has no upper limit, but tree leaf biomass has a maximum total determined by the rooted basal area of woody plants. Tree leaf expansion ("flushing") is rapid if the soil is moist and the temperature warm. Grasses have a much smaller carbohydrate reserve and therefore the magnitude of the flush is smaller, but can occur in any season, provided the soil is wet. Grass leaf expansion depends mostly on new photosynthates and is therefore limited by the growth rate. In both cases, if soil moisture is insufficient for growth, a portion of the live leaf mass is transferred to the dead leaf mass compartment, which decays by a constant proportion daily. Consumption of the leaf mass by herbivores occurs at a fixed rate until the leaf mass is reduced to zero.

Hydrological, production and water use statistics are accumulated daily and yearly.

5.2.2 DETAILED MODEL DESCRIPTION

5.2.2.1 Symbolic conventions

The symbols used in this section and their computer mnemonic equivalents are listed in Table 5.1. The two types of plants, woody and grass, are denoted with the subscripts w and g. Where a parameter can apply to either type, it is subscripted with i. Similarly there are two soil horizons, topsoil and subsoil. A specific horizon is subscripted t or s, but a soil layer in general by j. The present time step is denoted by subscript n. In the model, the mnemonics are prefixed with g-, w-, top- or sub- to reflect the same distinctions.

Table 5.1 Symbols used in the equations and their model mnemonics.

Symbol	Mnemonic	Description	Units
a	a,	Parameter of soil characteristic curve	
C	gra...ov	Projected aerial cover by grasses (proportion)	ND
d_i	-decay	Proportion of dead mass decaying daily	ND
D_i	-dead	Dry mass of dead leaf tissue	kg
E_{soil}	esoil	Daily evaporation from the bare soil	mm
e_{soil}	ecoef	Coefficient of evaporation for falling rate phase	ND
E_i	-trans	Daily transpiration by plant i	mm
e_i	-tmax	Maximum transpiration rate of plant i	mmd
E_{max}	emax	Maximum daily evaporation from bare soil	mm
F_t	perc	Daily moisture flux between top- and subsoil	mm
h_i	grazing	Dry mass of live leaf grazed daily	kg
I	intercep	Total interception by plants during a storm	mm
WUE	wue	Water use efficiency	$g \cdot g^{-1}$
$K(\theta)$	ktheta	Soil hydraulic conductivity function	mm^2
K_{sat}	ksat	Saturated flow rate	ND
L_i	-leaf	Dry mass live leaf tissue	kg
L_{max}	tleafmax	Woody leaf mass per ha at full expansion	kgh
M_g	gmass	Dry mass of above-ground dead and live grass	kg
m	topm subm	Parameter of soil characteristic curve	
	-mm	Water stored in soil layer	mm
n	topn,subn	Parameter of soil characteristic curve	
P_{sat}	poros	Proportion of pore space filled at field capacity	
$r_{i,j}$	-root-	Proportion of roots of plant i in layer j	ND
z_j	-z	Depth below the soil surface of bottom of layer	mm
θ_j	-theta	Relative water content (v/v) of soil layer	
θ		Volumetric soil moisture content	$m^3 m$
θ_{sat}	thetasat	Volumetric water content at field capacity	
θ_{rel}	thetares	Volumetric water content at air-dryness	
Ψ_j	cm(.j.)	Total water potential in soil layer j	

5.2.2.2 Soil moisture parameters

Each soil layer has a thickness (T) in mm, a lower depth measured from the surface (z) in cm and a moisture content (depth in mm, or as a proportion of the soil volume, θ). The total water capacity of the layer (TWC) is the moisture content at which all the available pore space is filled with water. A portion of this water will rapidly drain out of the soil under the influence of gravity (saturated flow) The moisture content which can be held against the gravitational force is the field capacity (θ_{sat}), below which point moisture moves by unsaturated flow until air-dryness is reached (θ_{res}). The TWC and field capacity are related by the proportion of the pore space occupied by water at field capacity (P_{sat})

$$TWC=\theta_{sat} P_{sat} \quad ...5\ 1a$$

The TWC is calculated from the soil bulk density, on the assumption that soil particles have a bulk density of 2.4 $g.cm^{-2}$

$$TWC=1-(Bulk\ density/2.4) \quad ...5.1b$$

The relative moisture content (θ) is zero when the soil is air-dry and one when at or above field capacity

$$\theta=(\theta-\theta_{res})/(\theta_{sat}-\theta_{res}) \quad ...5.2$$

Each moisture content is associated with a unique total water potential. The equation suggested by van Genuchten (1980), modified to include gravitational potential in $cm(H_2O)$ is

$$\psi=10.2[(\theta^{-1/m}-1)^{1/n}]/a + (z/10)...5.3$$

where

$$n=1/(1-m) \quad ...5.3a$$

Values for the constants m and a are given in Table 3.4.

5.2.2.3 Water Fluxes

An electrical analog model is adopted to predict the contribution of each soil layer to evaporation from the soil surface. The moisture content of each layer is weighted by the inverse of the distance to the soil surface, assuming that diffusive resistance to water vapour in the soil is proportional to the length of the diffusive pathway. Strictly speaking, water potential rather than water content should be used when applying the electrical analog, but since in this case the potential of the sink (the atmosphere) is unknown the potential difference cannot be calculated. Water content is used as a simplifying approximation. The effective moisture content for evaporation (θ_E) is calculated as

$$\theta_E=\Sigma(\theta_i/z_i) \quad ...5.4$$

Potential evaporation from bare soil is a constant proportion (e_{soil}) of the effective soil moisture during the falling-rate phase, but cannot exceed a maximum rate during the initial phase.

$$E_{soil}=e_{soil}\theta_E \; ; \quad E_s<E_{max} \quad ...5.5a$$

otherwise

$$E_s=E_{max} \quad ...5.5b$$

The potential rate is reduced by the proportion of grass cover (C) (Tanner & Jury 1976)

$$E_{soil}'=E_{soil}(1-C) \quad ...5.6$$

where, following Dye (1984), cover is related to grass standing crop (M_g)

$$C=(4.22+15.37\ln(M_g))/1000 \quad ...5.7$$

The evaporative flux is removed from all soil layers in proportion to their contribution to θ_E.

Transpiration rates of trees and grasses are calculated by assuming maximum transpiration (e_i) at and above field capacity and zero transpiration at air-dryness with a linear relationship to soil water content between. Molz (1981) reviews a large number of extraction terms, and concludes that the simplest perform as well as the most complex and at present there is little theoretical ground for choosing the latter. Although water potential provides the gradient that drives the flux it is water content that controls the resistance to flow. Given that the moisture distribution in the profile is usually uneven, as is the distribution of roots, the contribution of each soil layer to the soil moisture as it appears to the plant is approximated (again by electrical analog, assuming root resistance to be inversely proportional to the number of roots in a layer (Gardner 1964, Lascano & van Bavel 1984), and simplifying by using θ instead of water potential) by

$$\theta'_i = \Sigma_j \theta_j R_{i,j} \quad \ldots 5.8$$

where θ'_i is the relative water content weighted by the proportion of roots of plant type i in each layer j ($R_{i,j}$). The rate in $g(H_2O).g(\text{leaf mass})^{-1}.d^{-1}$ is multiplied by the leaf mass per hectare (L_i) in kilograms to yield litres per hectare per day, which is converted to millimeters of water by division by 10000.

$$E_i = (\theta'_i e_i L_i)/10000 \quad \ldots 5.9$$

Transpired water is removed from each layer in the proportion by which it contributed to θ'.

Transfer between soil layers is determined by the water potential gradient between them, multiplied by the hydraulic conductivity ($K(\theta)$) (Millington & Quirk 1961)

$$F_j = K(\theta)(\psi_j - \psi_{j+1})/z \quad \ldots 5.10$$

where the hydraulic conductivity function is related to the saturated hydraulic conductivity (K_{sat}) by (van Genuchten 1980)

Transpiration rates of trees and grasses are calculated by assuming maximum transpiration (e_i) at and above field capacity and zero transpiration at air-dryness with a linear relationship to soil water content between. Molz (1981) reviews a large number of extraction terms, and concludes that the simplest perform as well as the most complex and at present there is little theoretical ground for choosing the latter. Although water potential provides the gradient tnat drives the flux it is water content that controls the resistance to flow. Given that the moisture distribution in the profile is usually uneven, as is the distribution of roots, the contribution of each soil layer to the soil moisture as it appears to the plant is approximated (again by electrical analog, assuming root resistance to be inversely proportional to the number of roots in a layer (Gardner 1964, Lascano & van Bavel 1984), and simplifying by using θ instead of water potential) by

$$\theta'_i = \Sigma \theta_j R_{i,j} \quad \ldots 5.8$$

where θ'_i is the relative water content weighted by the proportion of roots of plant type i in each layer j ($R_{i,j}$). The rate in $g(H_2O).g(\text{leaf mass})^{-1}.d^{-1}$ is multiplied by the leaf mass per hectare (L_i) in kilograms to yield litres per hectare per day, which is converted to millimeters of water by division by 10000.

$$E_i = (\theta'_i e_i L_i)/10000 \quad \ldots 5.9$$

Transpired water is removed from each layer in the proportion by which it contributed to θ'.

Transfer between soil layers is determined by the water potential gradient between them, multiplied by the hydraulic conductivity ($K(\theta)$) (Millington & Quirk 1961)

$$F_j = K(\theta)(\psi_j - \psi_{j+1})/z \quad \ldots 5.10$$

where the hydraulic conductivity function is related to the saturated hydraulic conductivity (K_{sat}) by (van Genuchten 1980)

$$K(0)=K_{rel}(0)K_{sat} \quad ...5.11$$

where

$$K_{rel}(0)=0^{\frac{1}{2}}[1-(1-0^{1/m})^{m}]^{2} \quad ...5.12$$

Moisture drains from the lowermost soil layer on the assumption that the deep soil pool is effectively infinite. Its water potential is set to an arbitrarily small value. In effect this means that all moisture entering the lowest soil layer and which is not used by plants is lost to deep drainage.

The resultant of these fluxes is

$$mm_{j,n}=mm_{j,n-1}-E_{soil,j}-F_{j}-E_{g,j}-E_{w,j} \quad ...5.13$$

In the event that the sum of the fluxes exceeds the available moisture in the soil layer ($\theta_{j}-\theta_{sat,j}$) then each flux is reduced in proportion to its contribution to the sum, such that the sum equals the available moisture. This situation can arise due to the use of the finite difference approach; a time or depth increment may be too large for stability.

5.2.2.4 Plant production, consumption and decay

Daily plant production (P_{l}) is in direct proportion to the amount of moisture transpired by the plant type. The proportionality constant is the water use efficiency (WUE), expressed in $kg.mm^{-1}$

$$P_{l}=E_{l}WUE_{l} \quad ...5.14$$

If transpiration per unit leaf mass (E_{l}/L_{l}) falls below a minimum maintenance level ($E_{min,l}$), a portion of the live leaf becomes dead leaf. The minimum maintenance level is calculated as the transpiration rate when the entire soil profile is dried to wilting point (-1500 kPa). The size of the portion depends on the difference between the minimum maintenance transpiration and the actual transpiration, and a constant (s_{l}) which

$$K(0)=K_{rel}(0)K_{sat} \quad ...5.11$$

where

$$K_{rel}(0)=\theta^{\frac{1}{2}}[1-(1-\theta^{1/m})^{m}]^{2} \quad ...5.12$$

Moisture drains from the lowermost soil layer on the assumption that the deep soil pool is effectively infinite. Its water potential is set to an arbitrarily small value. In effect this means that all moisture entering the lowest soil layer and which is not used by plants is lost to deep drainage.

The resultant of these fluxes is

$$mm_{j,n}=mm_{j,n-1}-E_{soil,j}-F_{j}-E_{g,j}-E_{w,j} \quad ...5.13$$

In the event that the sum of the fluxes exceeds the available moisture in the soil layer ($\theta_{j}-\theta_{sat,j}$) then each flux is reduced in proportion to its contribution to the sum, such that the sum equals the available moisture. This situation can arise due to the use of the finite difference approach; a time or depth increment may be too large for stability.

5.2.2.4 Plant production, consumption and decay

Daily plant production (I_{i}) is in direct proportion to the amount of moisture transpired by the plant type. The proportionality constant is the water use efficiency (WUE), expressed in $kg.mm^{-1}$.

$$I_{i}=E_{i}WUE_{i} \quad ...5.14$$

If transpiration per unit leaf mass (E_{i}/L_{i}) falls below a minimum maintenance level ($E_{min,i}$), a portion of the live leaf becomes dead leaf. The minimum maintenance level is calculated as the transpiration rate when the entire soil profile is dried to wilting point (-1500 kPa). The size of the portion depends on the difference between the minimum maintenance transpiration and the actual transpiration, and a constant (s_{i}) which

expresses the ability of the plant type to tolerate desiccation. It can be interpreted as the number of days of zero transpiration which plant i can tolerate before it loses all its green leaf, and its value is based on field observations. Typically tree leaves tolerate longer periods of drought (14 days) before dying than grass leaves do (5 days).

Therefore, if $E_i < E_{min,i}$ then

$$x_i = [(E_{min,i} - E_i)/E_{min}][L_i/s_i] \quad \ldots 5.15$$

The dying portion (x_i) is transferred to the dead leaf compartment

$$D_{i,n} = D_{i,n-1} * x_i \quad \ldots 5.16$$

which decays by a constant fraction daily (that is, exponentially). The magnitude of the fraction (d_i) is approximated from half-life estimates in the literature (Bezuidenhout 1980, Grunow, Groeneveld & du Toit 1980).

$$D_{i,n} = D_{i,n-1} d_i \; ; \quad 0 < d_i < 1 \quad \ldots 5.17$$

The initial leaf expansion following rainfall must use stored rather than new photosynthates. This phase of rapid leaf expansion is known as leaf flush. Woody plants in semi-arid savannas can be observed flush almost to full leaf expansion within two weeks of receiving adequate rainfall. It is assumed that this growth is entirely due to the reallocation of reserves and cell expansion rather than synthesis. This behaviour is modelled for trees with the following functions.

If there is sufficient moisture present in the soil ($\theta_t > \theta_{min,t}$) and the mean air temperature exceeds a given minimum (modelled by assuming that the mean air temperature follows the same annual course as pan evaporation, Figure 31 on page 102
and that the critical temperature is the mean air temperature on the first of September) then provided that L_i does not exceed L_{max}

$$Flush_t = L_{t,n-1} * (L_{max,t}/f_t) \quad \ldots 5.17$$

where f_t is the time in days to full flush. Maximum leaf mass per hectare ($L_{max,i}$) is calculated from a knowledge of the relationship between stem basal diameter and peak leaf mass, and the distribution of stem diameters per hectare. It is specified as an input parameter.

The photosynthetic reserves available to grasses are much smaller than those available to trees. Only a small portion of the full leaf expansion is due to flushing, and the remainder depends on photosynthesis. The initial flush is set to an arbitrary value of 50kg ha^{-1} (about 5 % af the annual production). Thus, if $L_g<50$ and $0_g>0_{min,g}$ then

$$Flush_g=50 \quad ...5.18$$

There is no maximum grass leaf mass. Flushing increments in both trees and grasses are not accumulated as annual production, which is calculated as the sum of l_i only.

Consumption by herbivores of live leaf material occurs at a constant rate (h_i). The option of herbivory was not used in this study, so $h_i=0$ Daily changes in tree and grass leaf biomass are therefore expressed by

$$L_{i,n}=L_{i,n-1}l_i-x_i*Flush_i-h_i \quad ...5.19$$

5.2.2.5 Partitioning of rainfall

Rainfall is decreased by interception and runoff before being added to the soil store Interception has three components: grass leaves, woody plant leaves and woody stems Preliminary modelling showed the contribution by woody stems to be less than one percent of that of either grass or tree leaves, so it was ignored in further modelling.

Interception by the canopy of plants (I) is given by the leaf mass multiplied by the storage capacity per gram of leaf tissue (i_l) given in Table 3.8, and converted to millimetres. A more sophisticated approach to interception (for example Rutter *et al* 1971 or Parton 1978) cannot be supported either by the data available or the time step of the model.

$$I=(L_w i_w * L_g i_g)/10\ 000 \quad \ldots 5.20$$

The model can either be provided with the measured runoff volumes associated with given storm events, or if provided with a historical sequence of storms, can estimate the runoff (R) associated with each on the basis of its depth (P) and the grass cover when it occurred. It is assumed that the maximum runoff occurs when grass cover is zero, and the minimum when grass cover is 100%. The maximum and minimum runoff envelopes are given in Figure 23 on page 83, and grass cover (C) is calculated in equation 5.7.

$$R_{max}=r_{max}(P-I)+c_{max} \quad \ldots 5.21a$$

$$R_{min}=r_{min}(P-I)+c_{min} \quad \ldots 5.21b$$

$$R=R_{min}+C(R_{max}-R_{min}) \quad \ldots 5\ 22$$

provided that $0<R<(P-I)$, where r and c are the slopes and intercepts of the maximum and minimum runoff envelopes.

The rainfall remaining after the subtraction of interception and runoff percolates rapidly (saturated flow) into the soil. Each soil layer is sequentially filled to field capacity until all the rainfall has been used up. If there is excess rainfall remaining once the lowermost soil layer has been filled, each layer is filled (sequentially from the bottom upward) to its TWC. Any excess rainfall is added to the runoff.

5.2.2.6 Model input and output

Input to the model is in the form of a file containing all the soil and biological parameters and the initial values of the variables (Appendix 3) and another containing rainfall dates and depths. The rainfall file can have two possible formats, corresponding to long- and short-term data.

Output can be specified as daily or yearly, and consists of all the major variables. In addition, water-use niche overlap statistics for trees and grasses can be requested. They are calculated independently for the soil depth and time niche axes and also for both axes considered simultaneously. Levins' (1968) asymmetric niche overlap measure (here specified for grass, all axes simultaneously)

$$O_{j,n} = \Sigma_j \Sigma_n (E'_g E'_t / \Sigma_{j,n} E'^2_g) \quad \ldots 5.23$$

as well as Pianka's (1974) symmetric (canonical) measure

$$O_{j,n} = \Sigma_j \Sigma_n E_g E'_t / \sqrt{(\Sigma_{j,n} E_g^2 \; \Sigma_{j,n} E'^2_t)} \quad \ldots 5.24$$

are calculated. The equations both use transpiration (E'_g for grass and E'_t for trees) per soil layer per day to calculate the degree to which the two plant forms use the same resource. The difference between them is that the symmetrical measure normalises the total resource use by trees and grass to be equal to one another, which causes the overlap by species A on species B to be equal to the overlap of B on A.

5.2.3 MODEL CALIBRATION

All of the parameters used in the model have a physical or biological meaning and were determined from field data gathered during the 1982/3 and 1983/4 seasons. The fit (measured by the correlation coefficient) of the simulated soil moisture contents to the observed data for these

seasons was maximised by adjusting the values of key parameters, selected for their linear influence on the model output and their relative independence from one another. The initial estimates were those determined from field data. The soil moisture portion of the model was calibrated first by setting plant growth to zero, and using the 1983/4 rainfall records as input data. The model output was matched to the data from the poisoned root free columns by adjusting E_{max}, e_{soil} K_{sat} and θsat.

The production model was then calibrated against the 1983/4 tiller length and grass biomass data by adjusting e_g, and WUE_g, checking the soil moisture depletion against the data from the moisture blocks in the cleared treatments. Finally, the parameters relating to woody plants e_w and WUE_w) were set to appropriate values and calibrated against the moisture data from the wooded treatments. In most cases the necessary adjustments were small, but in the case of $E_{max,g}$ on the Combretum site, the field estimates were doubled to give satisfactory fits to the observed data.

5.2.4 MODEL TESTING

The model soil moisture and grass production predictions were tested against the independent data set gathered during the 1984/5 season. The correlation coefficients for observed versus simulated data are presented in Table 5.2. Graphical comparisons of the simulated and observed data are shown in Figure 50 on page 171 and Figure 51 on page 172.

The qualitative behaviour of the soil moisture portion of the model simulated the observed trends fairly well. The poor correlation coefficient values are at least partly due to the high variability of the observed data (as evidenced by poor correlations between replicate soil moisture blocks). Furthermore, 1981-83 were extreme drought years; the 1983/4 season, despite receiving near-average rainfall still reflected the effects of drought stress. On the other hand 1984/5 was an exceptionally wet season and unseasonal rainfall in July 1984 made the 1983/4 and 1984/5 seasons functionally continuous. An alternative approach would have been

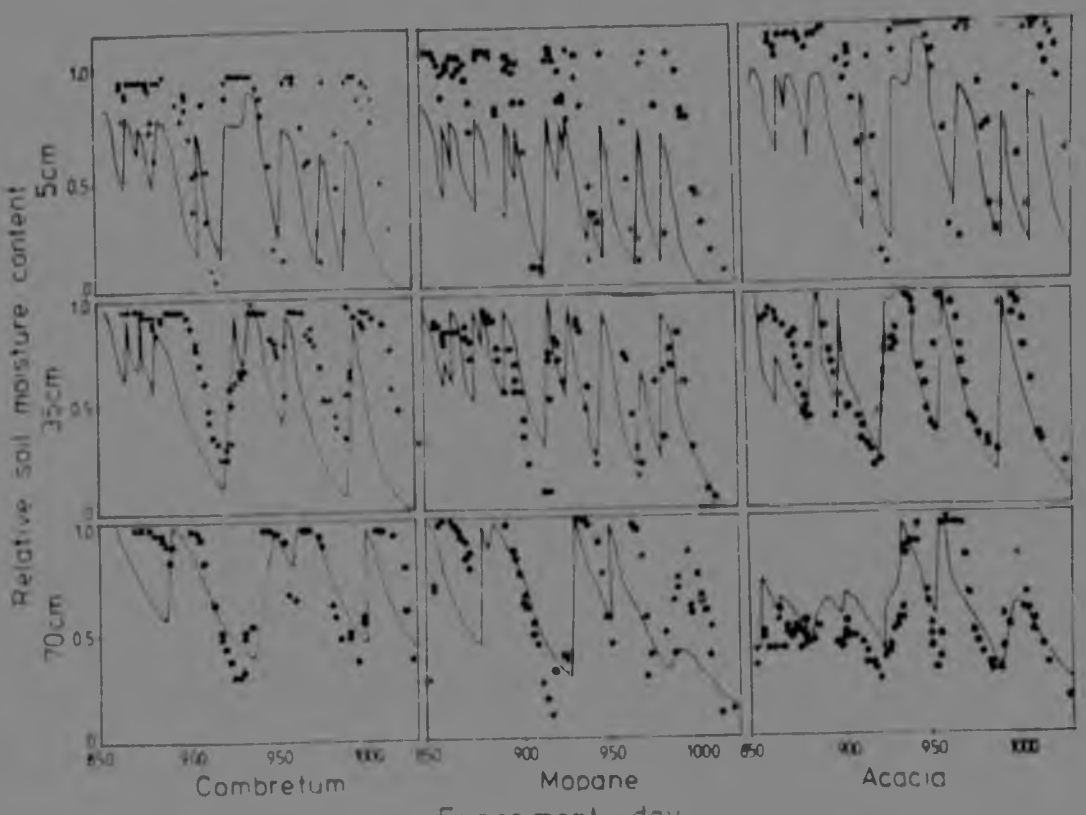

Figure 50. Observed and simulated soil moisture data for 1984/5

to use the 1983/4/5 data for calibration, and the 1982/3 for verification. It was considered unwise, however, to use an extreme year as a test of the model. Using the middle season (1983/4) for verification would not have allowed two consecutive seasons to be used for calibration.

Despite the inherent problems with the calibration and test data sets, the models are all significant at the 99 9% probability level.

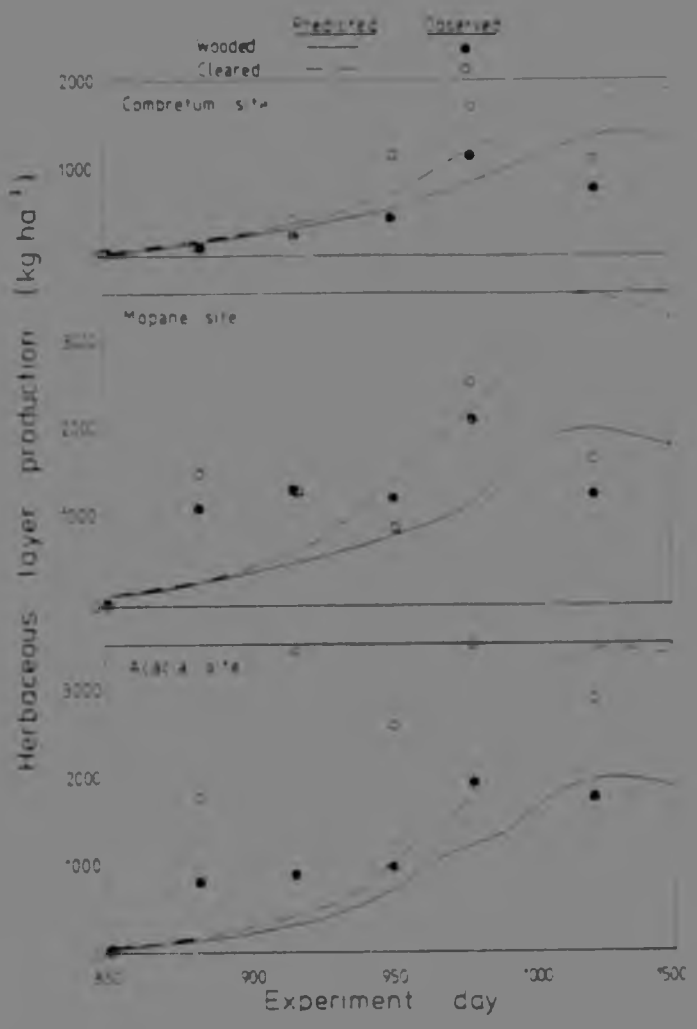

Figure 51. Observed and simulated grass standing crops for 1984/5

The grass production simulations are in fair agreement with harvest data at the scale of a full season, but drastically underestimate production during the early part of the growing season. This suggests that WUE is not a constant over the period of a growing season. It is higher during the early part of the season. There are several possible reasons for this.

Table 5.2 Correlation (r^2) between observed and predicted soil moisture data.

Depth	Uncleared 5mm	Uncleared 350mm	Uncleared 700mm	Cleared 5mm	Cleared 350mm	Cleared 700mm
"Combretum site"						
Between observed reps.	0.9180	0.7620	0.7607	0.8396	0.7269	0.6358
Calibration	0.4227	0.6312	0.6221	0.4767	0.5880	0.6897
Validation	0.5536	0.2701	0.3646	0.3847	0.3657	0.2531
"Mopane site"						
Between observed reps.	0.8871	0.6294	0.5180	0.7734	0.6795	0.4952
Calibration	0.7943	0.7226	0.5640	0.5736	0.5852	0.8004
Validation	0.5409	0.4307	0.4806	0.3545	0.2634	0.3693
"Acacia site"						
Between observed reps.	0.8682	0.7494	0.4345	0.8631	0.8854	0.7534
Calibration	0.4595	0.4806	0.2554	0.5488	0.6533	0.2651
Validation	0.4662	.4777	0.4208	0.2932	0.3753	0.2688

1. WUE may decline with physiological age of the tillers, due to self-shading or an increase in respiration.

2. The phenology of grass species within the sward may differ from one another, with the high WUE species being active in the early part of the season, and the low WUE species active late in the season.

3. Retranslocation of reserves may play a larger role in the initial growth flush than is currently believed.

5.2.5 FORTY-YEAR SIMULATIONS

Rainfall records from Skukuza for the period 1930 to 1970 (reduced by 10% on each storm to match the annual rainfall at Klaserie) were used as

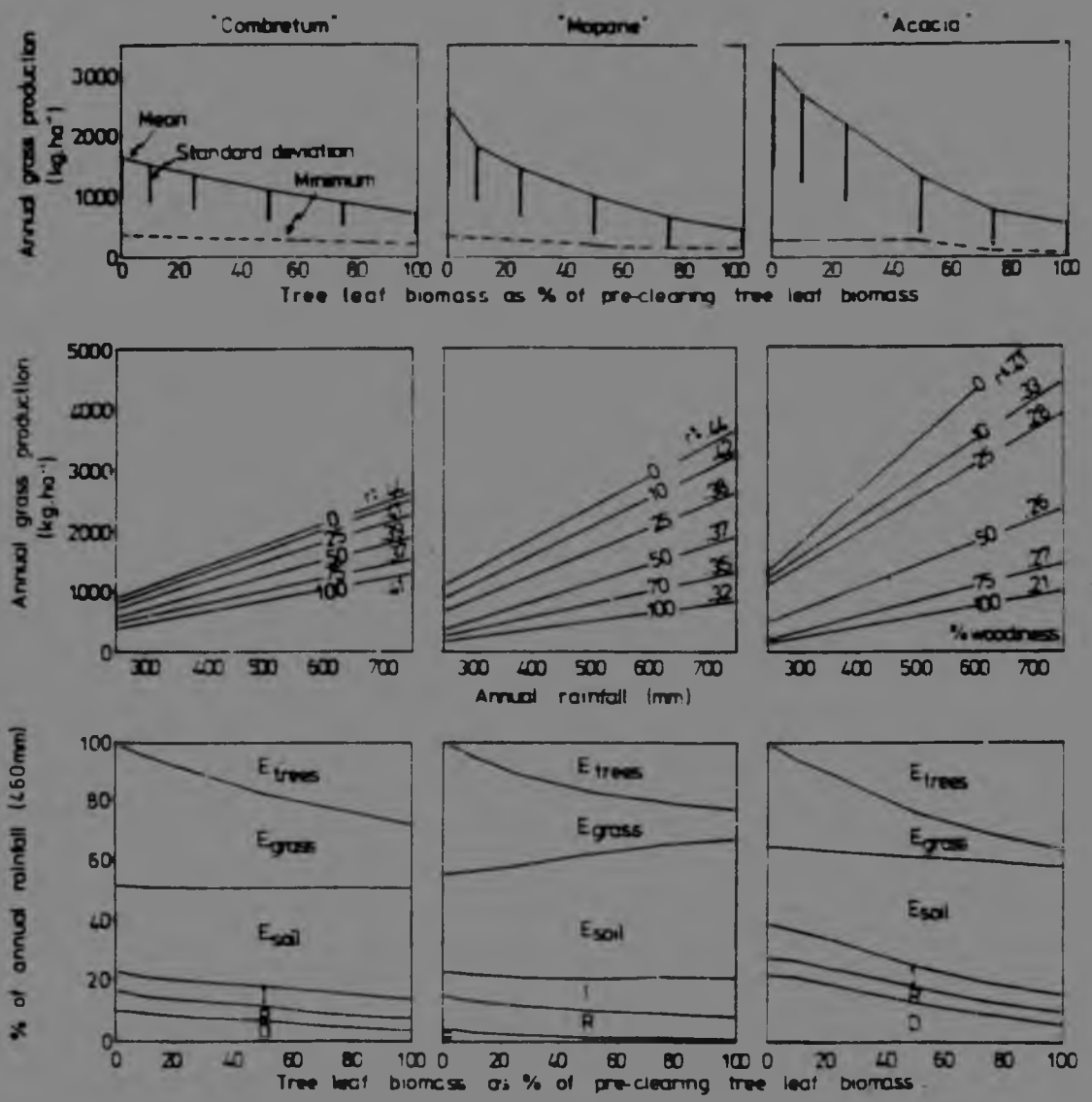

Figure 52. The effect of trees on water budgets and herbaceous production: means of 40-year simulations using rainfall data from Skukuza and model parameters from the study sites at six levels of removal of woody plants. R=runoff, I=interception, E=evapotranspiration.

input data for the model The model parameters used were those determined for each of the study sites. For each site six separate simulations

were run; one with the current woody plant density and basal area, one with no woody plants and four with intermediate values (10, 25, 50 and 75% of current woodiness). The major hydrological and production variables were accumulated for each simulation, and are presented in Figure 52 on page 174.

5.2.5.1 Water balance

The water balance estimates indicate that evaporation from the soil surface is consistently the major avenue of non-transpirational water loss to the system, having a magnitude similar to the total transpirational loss, and being only weakly dependent on the nature of the vegetation cover. It is highest on sites with a fine textured soil and lower on sandier soils. The amount of moisture that leaves the system by transpiration is fairly constant regardless of the plant type responsible. The general decrease in runoff with decreasing tree density (increasing grass cover) is nearly balanced by increased interception and deep drainage losses, all of which are relatively small. The major hydrological effect of bush clearing is to switch the transpirational pathway from woody plants to grasses. The proportion transpired by each type is not a linear function of the woody plant density, due to

1. the uneven distribution of moisture over time and depth, and the unequal ability of trees and grass to utilise moisture at different depths and times,

2. the increase in grass leaf area which follows a reduction in woody plant density, and

3. the increase in transpiration rate per unit leaf area due to increased soil moisture following clearing.

The dependence of grass transpiration (and therefore grass production) on tree density could be inversely convex or concave (or even sigmoid) depending on the relative strength of these conflicting factors. In all simulated cases the relationship was inversely concave. This is because of the strongly asymmetrical niche overlap between trees and grasses (Table 5.3).

5.2.5.2 The water-use niche

The symmetrical and asymmetrical overlap overlap coefficients for the forty year simulations are given in Table 5.3. They differ in that for the symmetrical measure the total resource used by each species is normalised to one. Therefore overlap is less than or equal to one, and is equal for both species. The asymmetrical measure expresses the overlap relative to the total resource use by each species individually. Therefore the values will differ between species, and may exceed one.

Niche overlap is high on all sites, to the extent that overlap rather than separation could be said to be the characteristic feature of the tree-grass interaction in semi-arid savannas. Separation occurs on the time and depth axes to approximately the same degree. Depth is relatively more important on sites of low water holding capacity (Combretum) and less important where the water holding capacity is high. The total symetrical overlap is in all cases slightly less than the product of the overlap measured on each axis independently. The axes are therefore not independent but have a slight positive interaction (synergism). A mechanism for this could be, for instance, residual water at depth allowing trees to flush earlier than grasses do.

The grass water-use niche is entirely included in the tree water-use niche, both in the time and depth axes. Trees therefore have a stronger competitive influence on grasses than grasses have on trees. Part of the moisture made available by tree removal is used by the remaining trees;

Table 5.3 Niche overlap between trees and grasses, simulated for a 40 year period and measured by Levin's asymetrical index and Pianka's canonical index for each axis individually and in combination. The depth x time productis the theoretical combination value if the axes are independent.

Site	Asymmetric Grass	Asymmetric Trees	Canonical
"Combretum"			
Depth	0.9501	0.8739	0.8330
Time	1.2843	0.7713	0.8908
Depth and time	0.8563	0.7685	0.7278
Depth x time			0.7420
"Mopane"			
Depth	1.8392	0.5789	0.8817
Time	2.9535	0.3773	0.8945
Depth and time	1.8918	0.4375	0.7799
Depth x time			0.7887
"Acacia"			
Depth	7.1603	0.1506	0.9024
Time	7.4759	0.1570	0.9203
Depth and time	6.409	0.1448	0.8177
Depth x time			0.8305

therefore in the general case the relationship between grass yield and woody biomass is always less than a linear interpolation between its minimum and maximum points (i.e. is inversely concave). Compare the predicted relationships with those observed by Donaldson & Kelk (1970), Walker *et al* (1972) and Beale (1973) and with the relationship between grass tuft density to tree basal area determined in chapter 4. The asymmetric overlap coefficients reflect the degree to which the trees are able to use the water made available by partial clearing, therefore the degree of curvature is directly related to the degree of niche overlap. It is highest on the Acacia site and lowest on the Combretum site.

5.2.5.3 Herbaceous production

The increase in mean annual grass production following a reduction in woody biomass is greater than the increase in interannual variability, resulting in decreasing coefficients of variation. Therefore the correlation coefficients of the relationship between annual rainfall and grass production increase with increasing degrees of clearing, contrary to what has been observed in field trials (Dye & Spear 1982). The simulations suggest that bush cleared sites have a higher relative constancy of primary production, but a lower absolute constancy. Thus under fixed herbivore stocking, the higher-producing cleared sites are more likely to fulfil the forage requirements of the herbivores than an uncleared site at the same stocking rate, resulting in a greater constancy of secondary production. If however the stocking rate is allowed to rise in response to the increased mean grass production, both the absolute and relative constancy of secondary production will decrease below that of the uncleared site due to the amplifying effects of time lags in the link between primary and secondary production, and the increased runoff, evaporation and deep drainage losses when grass cover is low. The variability is highest on fine-textured sites, due both to the tendency of these sites to be more xeric than sandy sites, and to the amplifying effects of a high WUE'. The absolute minimum grass production is only weakly related to the woody plant biomass.

Dye and Spear (1982) found that the slopes of the grass production-annual rainfall regressions for cleared plots were nearly parallel to those for wooded plots in three out of four sites (Figure 6 on page 39). The relationships between annual rainfall and grass yield from the forty-year simulations illustrate the effect of increasing WUE_g in a progression from the Combretum to the Acacia sites, but the slopes of the wooded plots are always less than those of the pure grassland plots within a site. Parallel slopes imply a nearly constant annual water use by trees, regardless of water supply. The tree transpiration function in this model is strongly dependent on soil moisture level, although the field data for some species (notably *Colophospermum mopane*) indicates a relatively fixed transpiration rate above a minimum soil moisture level. The model did

not allow for this type of moisture uptake pattern. The evidence suggests that slopes approaching parallel may not be a general case, but are promoted by the following circumstances:

1. insensitivity of E_t to soil moisture level above wilting point;

2. low niche overlap;

3. storm distributions during high rainfall years which favour grasses above trees (i.e. an increase in number of storms rather than mean depth, and an even distribution through the year rather than a highly concentrated wet season).

6.0 THE USE OF FIRE TO CONTROL TREE RECRUITMENT

Exclusion of fire is the most commonly cited cause of bush encroachment, and regular burning the most frequently suggested remedy. Fire however can be regarded as a competitor with herbivores for grass. Burning and grazing may therefore be conflicting objectives. The model described in this chapter explores conditions under which fire can usefully be applied as a bush control measure.

Since fire has a minimal effect on undamaged mature trees (Trapnell 1959, Strang 1974, Frost 1985), to be effective in controlling the density of woody plants it must be sufficiently frequent and intense for fire mortality to balance tree seedling recruitment. Attainment of this minimum fire regime is dependent on the rate of grass fuel accumulation, which is controlled by rainfall, woody plant density, herbivory and decay. A simple model of the interaction of these factors, using published relationships, is applied to determine the conditions under which woody plant recruitment is limited by fire.

6.1 FIRE MODEL

To halt woody plant recruitment fire must occur at least once with an intensity (I) sufficient to kill saplings during their period of susceptibility (n years). Thus

Fuel accumulated in n years $\geq$ Fuel required to kill n-year old saplings

Trollope & Potgieter (1985) have related fire intensity ($kJ.s^{-1}.m^{-1}$) to the grass fuel load G ($kg.ha^{-1}$). Using their linear equation and ignoring the terms relating to the effect of wind and moisture (which account for

only 3% of the variance of their data) by assuming that burns occur under ideal conditions,

$$I=f+gG \quad ...6.1$$

where f and g are constants with values of -230 and 1.3317, respectively, for experimental burns in the Kruger National Park. The accumulation of fuel necessary to allow a burn of given intensity is

$$G^{*}=(I-f)/g \quad ...6.2$$

Accumulation of fuel depends on the annual above-ground dry matter production of the herbaceous layer G_1 minus the losses due to herbivory H_1 and decay D_1. The contribution to the fuel load by woody plant litter is ignored.

Rutherford (1980) has reviewed several published relationships between annual precipitation and annual grass production for semi-arid regions (300-700 mm p.a.) and has noted the wide discrepancies between their predicted yields. Within this rainfall range a linear model seems as appropriate as any other. Thus

$$G_1=r+sP_1 \quad ...6.3$$

where P_1 is the annual precipitation (mm) and r and s are constants. The value of r ranges between -20 and -100, the smaller values being associated with sites with high evaporation from the soil surface or high runoff. The value of s lies between 2 and 5, the higher values occurring on more fertile sites (Rutherford 1980). For the purposes of this model the values are those attributed to the three study sites, which represent a range of soil conditions (Figure 40 on page 126).

Herbivory is considered to be constant per animal unit stocking rate. Lamprey (1983) gives a forage requirement of 3100 kgDM.year^{-1} per Tropical Livestock Unit (1 TLU=a beast weighing 250 kg). Loss of standing crop between seasons due to decay is considered to be constant per unit standing crop. Here it is expressed as the proportion of the

standing crop which is carried over to the next season in the absence of grazing (d). Values for d are not easily found. Grunow, Groeneveld & du Toit (1980) calculated a mean weekly transfer rate of 6.3 $g.m^{-2}.week^{-1}$ for dead standing crop to litter on a mean standing crop of 153 $g.m^{-2}$, which yields a very low d on an annual basis. A mean value of d=0.4 is used.

The minimum conditions for the maintenance of a treeless grassland by burning are

$$(r*sP_I - H_I)d \geq (1-f)/g \qquad .6.4$$

This inequality is presented in the form of a nomogram in Figure 53 on page 183. The minimum combination of fire frequency and intensity required for zero recruitment is biologically determined, and the annual rainfall is climatically determined. The only variables under the control of the land manager are the stocking rate and the woody plant density. To use the nomogram, select the appropriate minimum fire regime (combination of intensity and frequency) from the bottom lefthand graph, and the appropriate annual grass production (combination of site fertility and annual rainfall) from the top righthand graph. Project these values onto the top lefthand graph. If they intersect below the current stocking rate line then bush control by burning is not feasible, if above, then it is feasible.

The precise relationship between the intensity and frequency of fires which will cause complete sapling mortality is not known, and probably depends on the species, time of year and physiological status of the plant. There are many references in the literature (for example, Frost 1984 and Sweet 1985) to a "hot" fire (>1500-2000 $kJ.s^{-1}.m^{-1}$) being necessary to cause complete top-kill. Under favourable conditions a tree sapling could grow out of the herbaceous layer and above the effective flame height (1-2 m) in three years. Sweet (1985) suggests that burning once every seven years would be needed to suppress sapling growth in eastern Botswana.

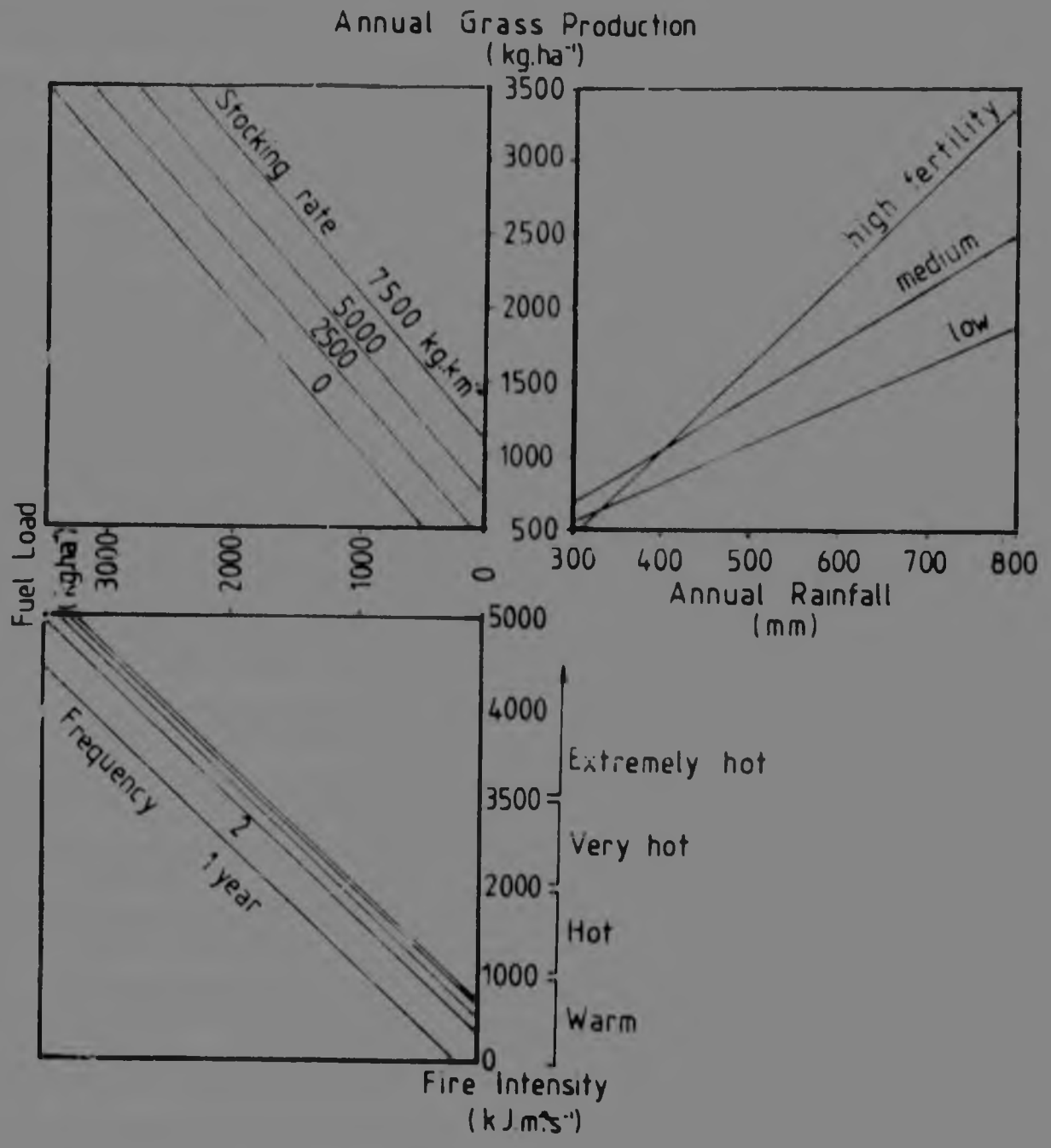

Figure 53. Nomogram relating fire regime, annual rainfall and herbivory: see text for explanation.

If it is assumed that a hot fire is required once every five years for adequate recruitment control, then the diagrams illustrate that fire is a

feasible mechanism for the maintenance of open grasslands even at the lower rainfall limit of semi-arid savannas (350 mm). Such control can occur even at reasonable levels of herbivory (2500 $kg.km^{-1}$).

6.1.1 THE INFLUENCE OF PARTIAL ENCROACHMENT

Where the system already has a considerable woody biomass, the annual grass production is depressed. Several studies have quantified the effect of increasing woody biomass (as tree density or basal area) on herbaceous layer production (Donaldson & Kelk (1970); Walker, Moore & Robertson (1972) and Beale (1973)). In most cases the form of the relationship is inverse and concave. At low tree densities a small increase in woody biomass can cause a dramatic reduction in grass yield. Equations of several forms can be fitted to the data. Beale suggests as an average over several years on two Australian sites dominated by *Acacia anuera*

$$G_i = a * bt^W \quad \ldots 6.5$$

where W is the basal area of woody plants in m^2/ha and a, b and t are constants with values of 0 363 , 104.86 and 0.546 respectively

The interaction of the woody biomass term and the rainfall term can take various forms. The data provided by the above authors are insufficient to determine which fits best Ten years of data from totally bush cleared and uncleared sites in Zimbabwe, presented by Dye & Spear (1982), reveal that on three out of four sites increased rainfall resulted in a similar absolute grass yield increase on cleared and uncleared sites. Thus there is no interaction between the woody biomass and rainfall terms. Since when W=0

$$r * sP_i = a * b \quad \ldots 6.6$$

Then at any other value of W

$$G_i = (r * sP_i) - ((a * b) - (a * bt^W))$$

which simplifies to

$$G_I=(r*sP_i-b-bt^W \quad ...6.7$$

At the fourth site in the Dye & Spear (1982) study the slope of the relationship between grass yield and annual rainfall was higher on cleared than uncleared plots. This interactive effect between woody biomass and rainfall is equivalent to assuming that woody plants are able to increase their water use as water availability increases, and could be modelled by

$$G_I=(r*sP_I)(a*bt^W/(a*b)) \qquad 6.8$$

Partial encroachment by trees dramatically reduces the availability of fire as a mechanism for preventing further encroachment. This is particularly true if the interactive model (equation 6.8) applies. Furthermore, the non-linearity of the relationship between grass yield and woody biomass and the decreasing fire susceptibility of trees with age introduce an element of hysteresis into the system. A run of dry years may allow encroachment, but a run of equivalently wet years will not allow the situation to be reversed

6.1.2 THE EFFECT OF RAINFALL VARIABILITY

Annual precipitation varies considerably, especially in the semi-arid range. Thus a safety margin must be built into the threshold for the use of fire for bush control to allow for the chance coincidence of a run of unfavourable years

The distribution of rainfall totals tends towards normality as the period of accumulation increases (Green 1969b). Assuming independence between annual rainfall totals (work on rainfall periodicity suggests that this may be an optimistic assumption) the probability of receiving less than a given depth of rainfall in n successive years is described by a χ^2 distribution with n-1 degrees of freedom.

$$\chi^2_{\alpha,n-1}=(1/\sigma^2)\sigma(P_i-P)^2 \quad ...6.9$$

where σ^2 is the variance of the annual rainfall depths and P is the mean annual rainfall. Using this equation it is possible to calculate the safety margin to be subtracted from the mean annual precipitation for a given risk (α) of exceeding the threshold as a result of climatic fluctuation. Within the semi-arid rainfall range the coefficient of variation of annual rainfall (σ/P) is about 30% (Green 1969b).

6.1.3 THE INFLUENCE OF MANAGEMENT PRACTICE

One of the few tools which a pasture manager has to allow the effects of climatic variation to be absorbed is the ability to alter the stocking rate by adding, removing or redistributing animals. In practice this ability is constrained by many factors, but a manager with a flexible stocking policy is more likely to have success with bush control by burning than one with a fixed stocking rate policy. However, even a manager with total control over stocking rate cannot achieve the level of bush control which he would have with no grazing. Grazing and fire are incompatible in the sense that they use the same resource. Stocking rate must be reduced from the short-term optimum to allow burning to maintain the long-term productivity of the herbaceous layer.

If it is assumed that a free-range animal has the same grass consumption per head as a paddocked animal, then the type of grazing management has little effect on the outcome of this model. However, if animals select for certain areas or the grass production or bush encroachment susceptibility is not homogeneous then division of the area into homogeneous camps may be necessary to allow an even degree of bush control.

The use of browsing herbivores in conjunction with burning appears to be more effective than the use of either alone. The browsers keep the woody plants within range of the flames, and the fire maintains the browse in a condition attractive to browsers. This synergistic effect is difficult to incorporate into the model due to the lack of quantitative data. The effect would be to increase the number of years for which the sapling is susceptible to fire, or in other words to decrease the required burning frequency. The model should be considered conservative in the presence of browsers.

7.0 COPPICE REGROWTH FOLLOWING CLEARING

Regrowth of woody plants following bush clearing can occur by the establishment of new individuals by seed, or by the regrowth of existing individuals, damaged but not eradicated by the clearing operation. The latter process is potentially much more rapid than the former (Strang 1969b). Not a single example of establishment from seed was observed over th ration of this study in the three hectares of cleared grasslands, but coppice regrowth was conspicuous despite poisoning of the felled stumps.

Given that an artificial grassland derived from savanna is ultimately unstable unless the conditions for a fire-subclimax or hydromorphic grassland can be met, the rate at which it tends back to woodland becomes very important. If it is slow, then the economic benefits to be gained from bush clearing may justify the cost of repeated clearing.

Strang (1974) measured the woody plant density, basal area and height on a large number of clearings of known age in *Brachystegia spiciformis/Julbernardia globiflora* woodland in Zimbabwe. He found that in the absence of fire the regrowth of the woody basal area (B, $m^2.ha^{-1}$) on cleared (but not cultivated) land could be modelled by

$$B=-3.4+0.5(t)+0.0043(t)^2$$

where t is the age of the clearing in years. The rate of regrowth was rapid during the first twenty years and then levelled off. Full recovery took about fifty years. Tree density increased to a maximum at about twenty years and decreased thereafter. Recovery was much slower if the fields had been cultivated (in other words if the below-ground portion of the trees had been killed). Regular fires did not alter the rate of recovery of the woody plant density, but did suppress the basal area and height.

Taush and Teuller (1977) applied a dendrochronographic technique to the study and simulation of post-clearing succession of Pinyon-Juniper woodlands in Nevada. They predicted a return to pre-clearing basal area in about 20 years. These species both exhibit unambiguous annual growth rings, unlike most of the woody plants of southern Africa (Lilly 1977, Kromhout 1977).

7.1 COPPICE: A MODEL OF COPPICE REGROWTH

7.1.1 PROCEDURE

Ring structures were discernable in one of the major woody plants investigated in this study, *Colophospermum mopane*. Polished cross-sections of coppice stems from clearings with a known history revealed narrow bands of boundary parenchyma which were associated with growth periods. They are obscured in mature stems in which secondary lignification has occurred. The ring counts agreed very well with the known ages of the clearings (up to seven years), provided that the exceptionally wide outermost ring was attributed to the 1983/4 and 1984/5 seasons in combination. Winter rainfall in July 1984 rendered these seasons continuous, with little leaf fall in *C mopane*.

Ring diameters were measured to the nearest 0.05mm on 76 coppice stems. The stem cross-sectional area increment between successive rings was a linear function of the cross-sectional area enclosed by the smaller ring. The slopes of these relationships were related to the seasonal (July-June) rainfall of the years to which they were attributed (Figure 54 on page 190).

The leaf dry mass per unit area of stem cross section was determined by harvesting and stripping the leaves from fifteen stems. It was found

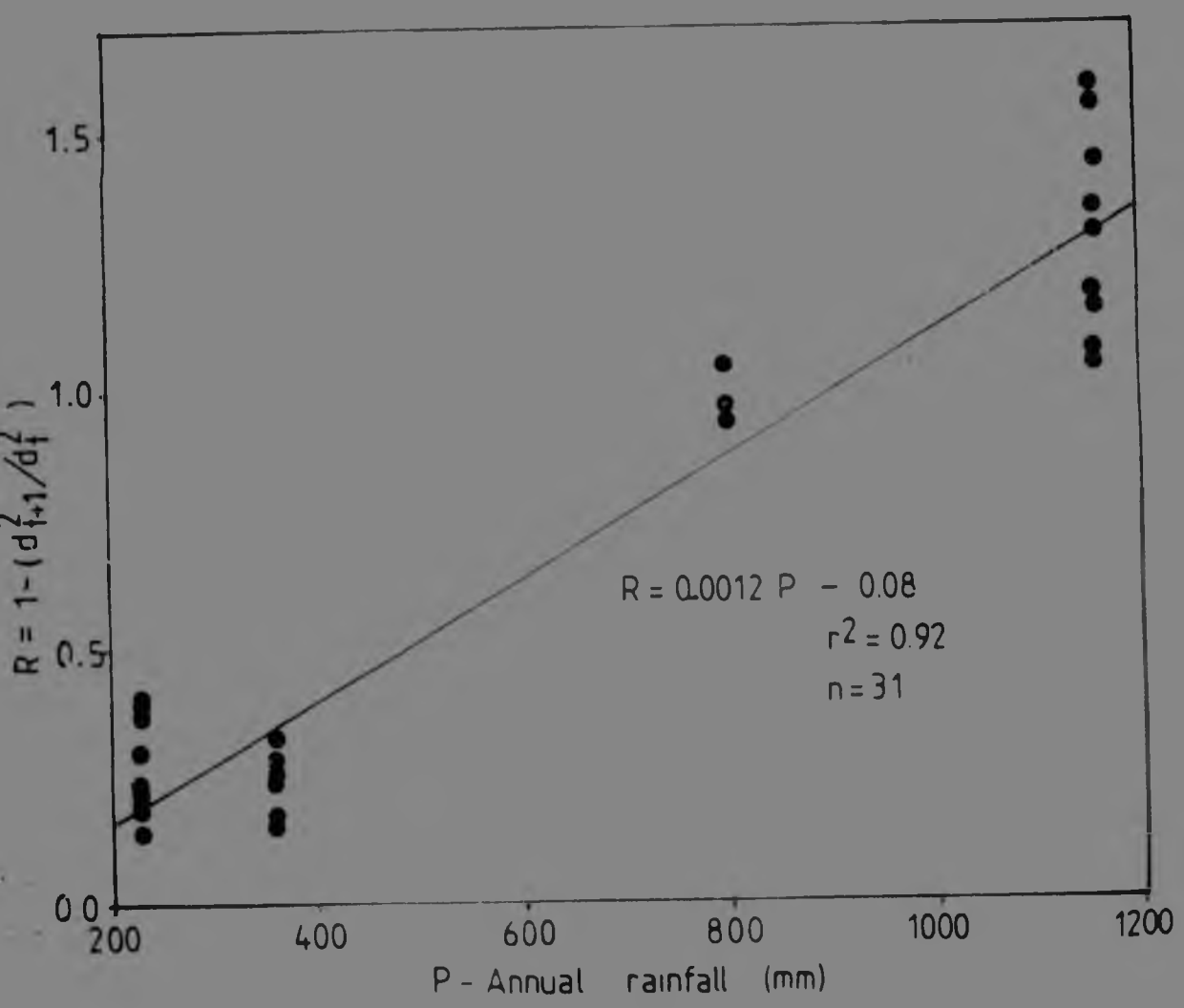

Figure 54 Relationship seasonal rainfall (P) and relative stem growth (R).

to be considerably higher on coppice stems than mature stems (Figure 55 on page 191) and varied between a wet year and a drought year, probably because of premature leaf fall in the latter.

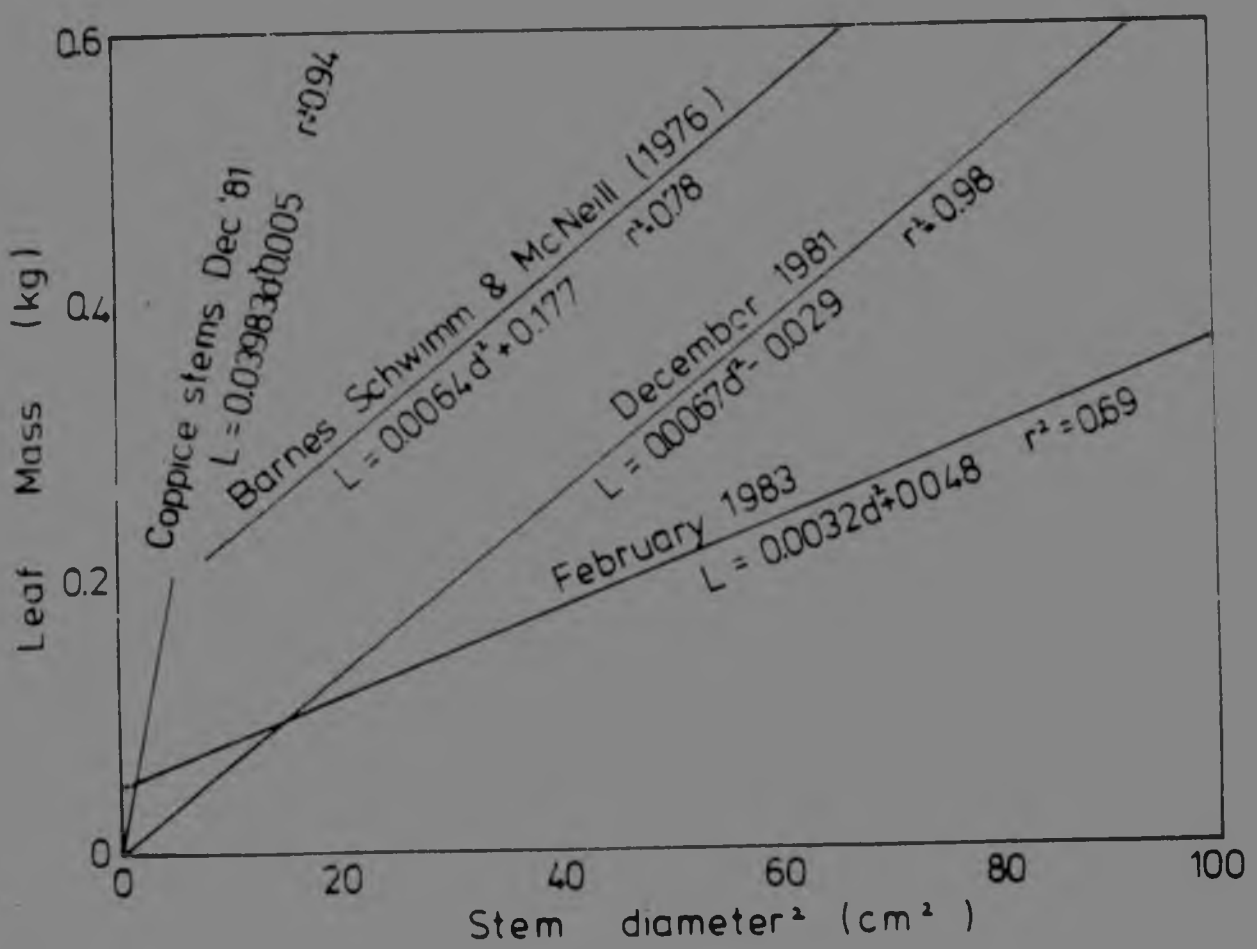

Figure 55. Dependence of leaf mass on stem cross diameter squared: *C. mopane*

The density and basal area of coppice stems per hectare was estimated on several clearings of known history (Table 7.1) by counting and measuring every stem within eight replicate 5x50m belt transects.

These data allowed a simple model of coppice regrowth to be formulated. During the regrowth period studied the basal area increment followed an exponential pattern, which can be described by

Table 7.1 Coppice regrowth of *Colophospermum mopane* following clearing. Estimates from counting and measuring all stems in 6 2.5x50m belt transects in each plot. Standard errors in parentheses.

Site	Method of clearing	Age (yrs)	Number of plants (ha^{-1})	Number of stems (ha^{-1})	Basal area ($m^2.ha^{-1}$)	Mean stem diameter (mm)
Mg	Brushcutter	1.3	475	3396	0.14	6.5
M0	Bulldozer	4.4	600	6980	1.52	14.5
M0	Bulldozer	7.5	2120 (458)	7933 (1168)	3.45 (0.36)	21.1
MVp	Brushcutter	5.9	1360 (240)	6987 (938)	1.60 (0.19)	16.1
Ms	Bulldozer	8.2	2820 (144)	12800 (836)	3.89 (0.10)	18.3
Mg	Pre clearing	0	872	2002	6.40	

$$B_t = B_0 e^{rt} \quad \ldots 7.1$$

where B_t is the basal area at time t after clearing, B_0 is the post-clearing basal area (about 0.35 $m^2.ha^{-1}$), and r is the instantaneous growth rate (0.29). The fit is imperfect in the first three years (which is why B_0 is actually equivalent to the year two basal area). This is thought to be due to the simultaneous processes of stem number increment and stem diameter growth.

If growth continues at this rate, then complete recovery of basal area would occur in eleven years The equivalent annual growth proportion (R) is 1.34. It is obvious that there must be some finite limit to the regrowth, imposed by resource competition between the plants. The simplest model to express this pattern is the logistic equation.

An area of regrowth was considered to have a fixed number (S) of equal-aged stems, the growth of which are dependent on the moisture available to each. Thus for year t the mean stem diameter squared (d^2_t) is

$$d^2_t = d^2_{t-1} R \quad \ldots 7.2$$

where R, the growth increment, is a function of moisture availability. Moisture availability is controlled by the annual rainfall (P) and the total stem basal area (B_t) in relation to the maximum stem basal area of a mature stand (K). Therefore, assuming that the relative growth rate is at a maximum when there is no intraspecific competition (B=0) and is zero when B=K,

(ie, using a logistic equation)

$$R = 1 + [(aP + c)((K - B_t)/K)] \quad \ldots 7.3$$

Constants a and c are the slope and y-intercept of Figure 54 on page 190 and

$$B_t = S d^2_t \pi/4 \quad \ldots 7.4$$

The leaf mass per hectare is given by

$$L_n = S(bd^2_t + e) \quad \ldots 7.5$$

where b and e are the slope and intercept of Figure 55 on page 191. The model was run using an initial stem density of 1000 ha^{-1}, an initial stem cross section of 1.0 cm^2, a maximum total basal area (K) of 10.0 $m^2.ha^{-1}$ and a mean annual rainfall of 500 mm. At this rainfall level, the maximum annual increment (R) is 1.52, as compared to the R value for the exponential model of 1 34. However, by year eight the R value for the logistic model has decreased to 1.26, while that for the exponential model is unchanged

The predictions of the two models are compared to field data in Figure 56 on page 194.

It could be argued that total leaf area would be a better parameter on which to base the competition model. Modelling on this basis produced virtually identical results, not surprisingly, since leaf area and basal area

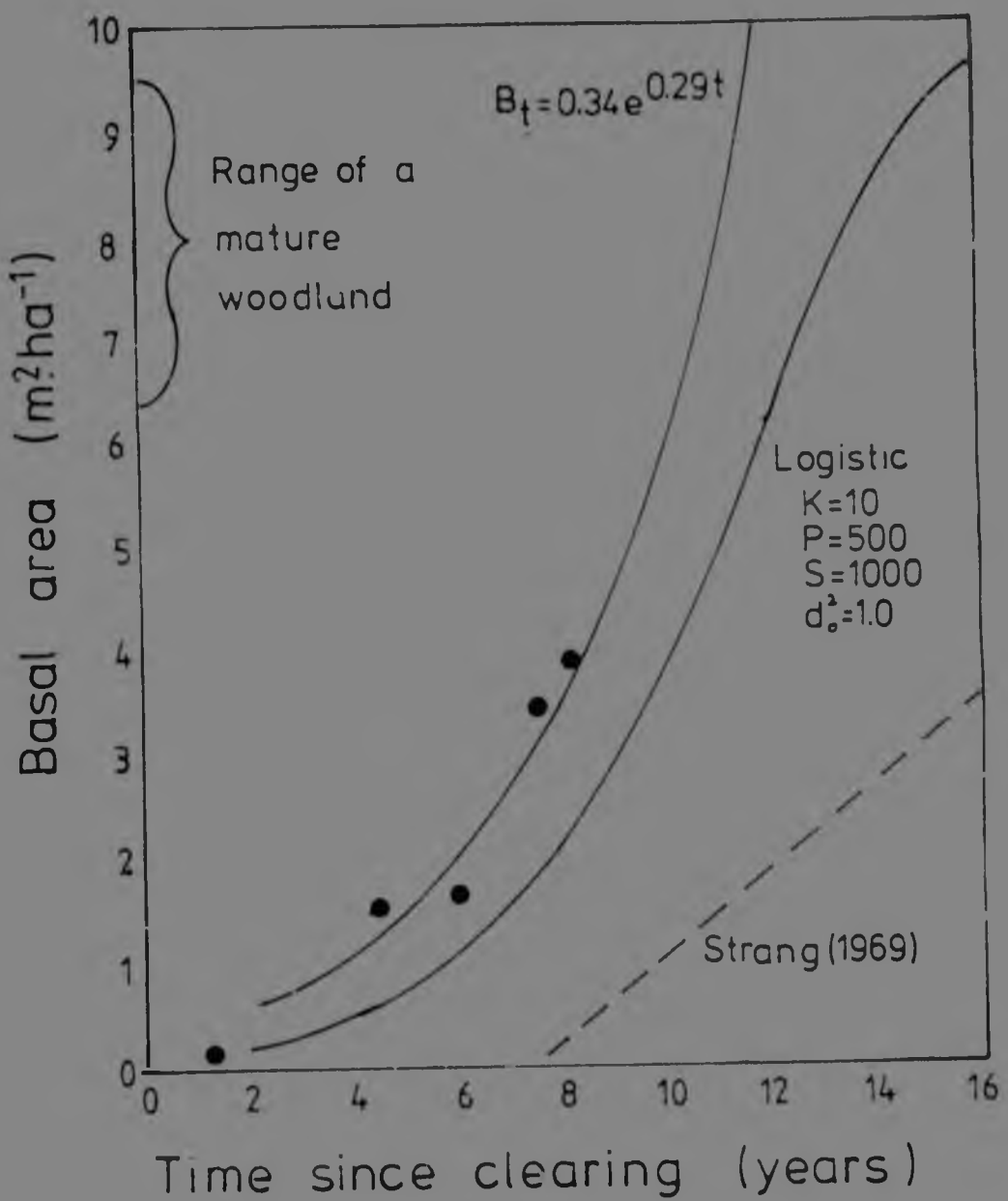

Figure 56. Two models of coppice regrowth in *Colophospermum mopane*. ●=basal area of clearings of known age.

are closely correlated. The relationship between basal area and leaf area changes with age, however, and this necessitates further assumptions regarding the nature of the transition.

Regrowth as modelled above is essentially a vegetative process, and as such the rate should be strongly dependent on the initial plant density. To test the effect of clearing mortality on the subsequent rate of regrowth, the logistic model was run with different initial stem densities. There must also be some small (probably not constant) rate of invasion by seedlings. Since no seedling recruitment was ever observed during this study, it is difficult to assign a value to this rate. Counts of *C. mopane* plants in a twenty-year old abandoned field where regrowth was presumably all by seedlings, indicated a mean annual input of four stems.ha^{-1}. This field was not entirely surrounded by *C. mopane* propagule sources, so the value is probably conservative. The logistic model was run with the initial stem density at zero, but with this rate of seedling recruitment. The results of these simulations are presented in Figure 57 on page 196.

7.1.2 DISCUSSION

The exponential growth model, while providing the best fit to the regrowth period for which data is available, is likely to underestimate the period required for complete recovery, since it does not allow for intraspecific competition. The logistic growth model, furnished with independently collected data on stem growth rates and densities, shows an approximately two-year lag behind the field data and exponential model over the first eight years. It is believed that this is because it only considers the growth of existing stems, and not the increase in the number of stems which also occurs during the first few years (Table 7.1). Inclusion of this mode of growth would require an age-structured model and considerably more data than was available. It is likely that the number of stems per hectare will decline again as the thicket approaches its terminal density.

Another factor contributing to the lag could be the assumption that the thicket will have the same ultimate basal area (K) as the woodland from which it was derived. It is possible that the thicket, due to its multi-

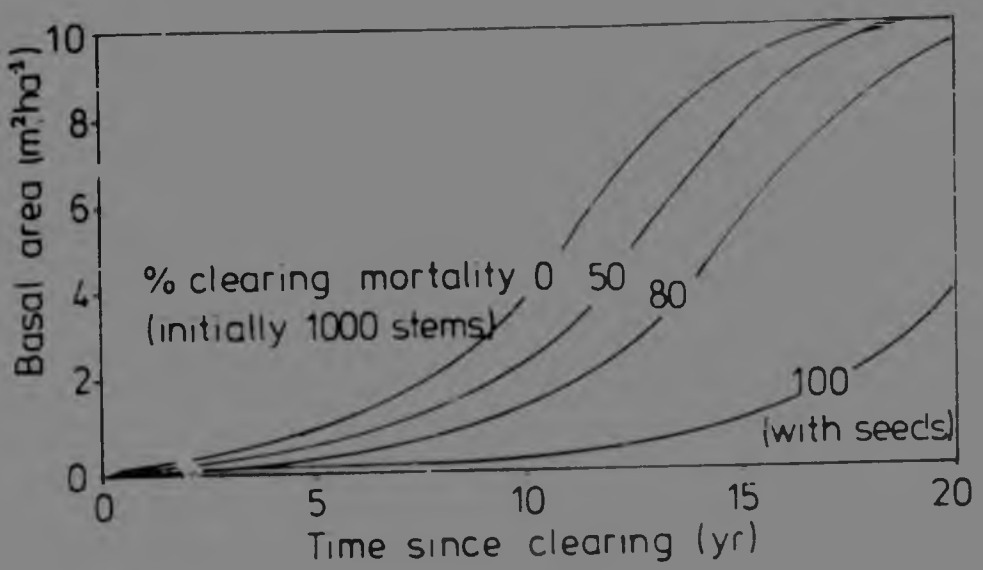

Figure 57. Simulated coppice regrowth with different levels of clearing mortality.

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stemmed, even-aged structure, could have a higher basal area than the woodland.

Reduction in the initial stem density, usually brought about by poisoning the stumps at the time of clearing, serves to retard the regrowth rate. A 50% clearing mortality increases the time to 80% basal area recovery by two years; 80% mortality increases it four years. This "diminishing returns" effect is due to more rapid growth when fewer stems are left. Complete mortality at clearing can have a pronounced effect if the recruitment from seeds is low. Once plants become established, however, the regrowth rate is rapid. On the basis of the crude estimates of re-seeding rate made in the model, recovery to 80% basal area by seeding alone would require twenty-five years.

If 80% regrowth of a *Colophospermum mopane* woodland is assumed to require fifteen years, then the rate of aboveground woody biomass accumulation must be in the region of 1000 $kg.ha^{-1}.yr^{-1}$, or 5% of the peak woody biomass.

8.0 DISCUSSION

Chapters three, four and five develop the main themes of this study: hydrology, productivity and resource partitioning in semi-arid savannas. Chapters six and seven touch on the role of fire and regrowth following clearing. Each of those chapters include discussions of their subject matter. The aim of this chapter is to show the linkages between those individual aspects of savannas. Savanna structure and function will be the main vehicle of synthesis, with the emphasis on the functional changes which result from a structural alteration.

8.1 COMPETITION AND COEXISTENCE IN SAVANNAS

8.1.1 WATER USE STRATEGIES

It is clear that the success or failure of a plant group in a variable environment such as a semi-arid savanna cannot be summarised in anything as simple as a single competition coefficient. Fitness is the product of a large number of interactions which can only be expressed in terms of a life history strategy. Every strategy has a cost associated with it. The price of a conservative water strategy is a limited ability to make use of water when it is freely available, and the price of opportunism is a high level of risk. The array of possible strategic variants is infinite, but in savannas natural selection has delineated two broad patterns which seem very nearly balanced in the long term: the grass pattern and the woody-plant pattern. These generalised strategies differ in many respects, including growth form, lifespan, and response to herbivory and fire. Their respective water use strategies are only one component, albeit an important one, of a total life history.

The findings of this study with regard to the water use niche are as follows.

1. A large degree of niche overlap exists between trees and grasses in semi-arid savannas.

2. The overlap is asymmetrically biased in favour of woody plants (the grass water use niche is completely included in that of woody plants).

3. The overlap is greatest on heavy textured soils.

4. What separation there is is approximately equally due to phenological separation and rooting depth separation, with depth separation slightly more important on sands and time separation more important on clays.

5. The phenological and depth separations act synergistically to permit a greater separation than their product would suggest.

There are three axes to the water use niche: the soil depth at which the water is extracted; the time of the year, wetting cycle or day when water extraction occurs; and the water potential at which extraction occurs. The first axis was emphasised by Walter (1971) in his model of competition in savannas and the second by Westoby (1980) in a model of arid range dynamics. The third was not explicitly treated in either, but is implicit in the Westoby concept. Phenological separation has traditionally been emphasised by South American savanna ecologists (Sarmiento, Goldstein & Meinzer 1985) while separation in root depth has been emphasised in Africa . Modelling of a competitive system of trees and grass (chapter 5) suggests that the first two axes are nearly independent and account for similar degrees of niche separation between trees and grasses. On highly permeable soils with a low water capacity rooting depth separation is relatively more important, while the time axis is dominant on clayey soils. These two axes are correlated to a small degree, since the presence of water at depth permits deep-rooted plants to transpire for longer.

Therefore the overall overlap is reduced by the interaction of the axes more than if they had acted completely independently.

The third axis of possible separation (soil water potential) was investigated in the study, but insufficient data were available to allow it to be included in the model. It is not independent of the phenology axis, since the declining soil water potential is correlated with time since the last rainfall event. Separation clearly exists between plants with an opportunistic water strategy (broadly, grasses) and a conservative strategy (woody plants). The significance of this separation is not in the production achieved at low water potentials (very little moisture remains in the soil at low potentials) but in the head start which a physiologically active plant has over a dormant plant at the onset of the next wetting cycle. The water potential axis therefore interacts synergistically with the phenology axis.

The onset of water stress occurred earlier in grasses than in trees in this study. The plant available water content of the soil is a function of both the wilting-point potential of the species concerned, and the total rooting volume (depth, in the case of a community). Trees have a greater rooting depth, but little is known about the wilting point of savanna plants. For short-term wilting, root density (greater in grasses) and tissue storage capacity (greater in trees) also play a role.

Within the woody plant group, two sub-groups were apparent. The "water spenders", represented by *G. bicolor* and *Acacia nigrescens* had high transpiration rates per unit leaf mass, but these rates were strongly dependent on soil moisture availability. "Water savers", such as *Colophospermum mopane*, *Combretum apiculatum* and *Sclerocarya birrea* had lower initial rates, but sustained them at lower water potentials.

The measure of success of a resource strategy is not the absolute quantity of the resource obtained, but the resultant increase in production; in other words, the product of the rate of use and the use efficiency. The WUE data in this study are incomplete, but it appears that woody plants are able to sustain (or even increase) their WUE under water stress while the one grass measured (*Panicum maximum*) could not.

The WUE of woody plants and grasses appears to be fairly similar despite the different photosynthetic pathways that they employ.

Viewed over the duration of a plant lifespan it is not possible to say that grasses are superior competitors for water than trees, or *vice versa*, since each has advantages under certain circumstances. In a variable and unpredictable environment it is the differences between strategies which permit coexistence, not the precise balancing of competitive abilities.

Woody plants may have some access to extremely deep water sources, but the fact that the overwhelming majority of them are deciduous and show signs of water stress during intraseasonal droughts, indicates that this access is limited. It may make the difference between survival and death during a prolonged drought such as that of 1982/3, when little direct tree mo tality but extensive grass mortality was observed, but probably has little impact on productivity since the amount of water available from this source is small. The moisture which woody plants use for growth comes mostly from the same soil horizons as the moisture used by grasses: predominantly the topsoil. This is reflected by the distribution of woody roots. There are exceptions to this rule: some individuals of deciduous species a.d all individuals of some species (such as *Lonchocárpus capassa*) remained green and continued to transpire at a rapid rate throughout the winter and the dry summer of 1982/3, when there was no moisture in the soil profile. These individuals were rare, and apparently had access to deep water sources. The dominance of grass roots in the top 100mm of soil is of some advantage, since this layer wets even after small storms, but it also dries out rapidly due to evaporation.

The asymmetry of water use niche overlap means that trees exert a strong competitive effect on grasses, but grasses only a weak effect on trees. This is in agreement with the experimental findings of Knoop (1982).

8.1.2 IMPLICATIONS FOR CURRENT MODELS

The Walter hypothesis (Walter 1971) proposes a dynamic competitive equilibrium between woody plants and grasses, based on niche differentiation in rooting depth. There is no direct evidence that such an equilibrium actually exists. The apparent stability of the woody/grass mixture over large areas and long periods of time has not been tested. Over the period of historical record, which unfortunately coincides with a period of great disturbance, there have been considerable changes in savanna structure.

The main evidence for the Walter hypothesis lies in the interpretation of natural gradients of woodyness in savannas. Where more water would be expected to penetrate to the subsoil (i.e. sandy soils and moister climates) woody plants are believed to be relatively more dominant. These trends have not been quantified or tested in a systematic fashion. In this study, the generalisation held for the sandy and clayey extremes, but failed to account for the high woody plant biomasss and density at a site of intermediate texture. Furthermore there are many factors other than the penetration of moisture to the subsoil which are covariant to these gradients and could play a role in their maintenance: the intensity and frequency of herbivory and fires, the soil nutrient status and the duration of soil moisture are examples.

In the absence of fire, there is a tendency for the woody plant density to increase (Trapnell 1959). Similarly a trend towards greater woody density and biomass has been recorded in heavily grazed areas, (Kennan 1969b), but a spontaneous reversion to lower woody biomass has not been reported when grazing pressure has been reduced. It can easily be demonstrated that trees have a competitive effect on grasses (the "bush clearing response", as shown in this study and many others), but the reverse effect has not been shown to be sufficiently intense to prevent the growth of mature trees. This is partly due to the asymmetry in niche overlap between trees and grasses, and partly due to the large differences in spatial scale and lifespan which exist between the two growth forms. Only when trees and grasses operate at a similar time-and-space

scale, i.e. when the tree is a newly established seedling, can a convincing case be made for an effective competitive influence of grass on trees.

The Walter hypothesis has two necessary postulates: trees have a higher proportion of their roots in deeper soil layers (originally stated as exclusive access to the deeper layers); and grasses are superior competitors for water in the surface layers. This study and others (Strang 1969a, Knoop 1982) have shown that the differences in rooting depth between grasses and trees are relative rather than absolute, and the effective niche separation achieved may be marginal, especially in soils with a high water holding capacity. The rooting patterns of both growth forms reflect the fact that moisture in semi-arid savannas is most frequently located in the surface soil.

The greater competitive ability of grasses, necessary for their persistence in the Walter model, has not been unequivocally demonstrated. The pattern of water use and photosynthesis changes as the soil dries out. For competitive exclusion to take place, superior competitiveness must result in increased production which must then lead to an even greater share of the limited resources in the next period of competition. In savannas, however, the biomass accumulation by grasses over the course of one growing season does little to enhance its growth in the next season. Trees, on the other hand, do show incremental growth over a period of many seasons. The whole concept of steady competition is inappropriate in a situation of fluctuating resource levels, especially when one competitor has a markedly longer lifespan than the other.

The arid rangeland model of Westoby (1980), while not specifically a model of savanna structure and function, does have relevance in this context. It makes allowance for asymmetrical competition, the influence of differential herbivory and the interaction of the abiotic and biotic components of the system. It emphasises niche separation in time, which has been shown in this study to be at least as important as niche separation due to rooting depth, and more so in more xeric situations. The Westoby model lacks, however, the simplicity and predictive power of the Walter hypothesis, and is therefore less amenable to testing.

The postulates of the Walter hypothesis are not absolutely wrong, but they are certainly incomplete. The omission of phenological separation between trees and grasses is a major fault. The hypothesis that trees and grasses are in competitive equilibrium mediated by rooting depth separation is unsupported by evidence and is rendered unlikely by the great scale differences between the two growth forms.

It is much more probable that the tree-grass combination which constitutes a semi-arid savanna is an inherently unstable mixture which tends towards increasing woodyness until "intra-specific" (actually intra-growth form) competition between trees limits further tree growth and recruitment. There is evidence for competitive interactions between savanna trees at high densities (*Colophospermum mopane* in this study, *Acacia* spp. in Smith and Walker, 1983, Penridge & Walker, 1986). A limited grass cover may persist at these terminal woody densities, since under a stochastic rainfall regime there will always be growth opportunities for grass plants to exploit. Due to the longevity of trees, this hypothetical "woody plant carrying capacity" would reflect long-term mean environmental conditions. The grasses are able to respond to shorter-term fluctuations about this mean. The woody plant biomass in most savannas is considerably below this upper limit, due to the following factors.

1. There is episodic mortality of mature trees for reasons other than competition from grasses. Factors such as the interaction of fires and ringbarking scars (R.I.Yeaton, Department of Botany, University of Venda: personal communication) drought (van Wyk, Bosch & Kruger 1969) and elephant feeding (Scholes 1985) have been shown to cause significant mortality in savanna trees.

2. Tree recruitment is slowed (and may even be arrested) by the intense competition between grasses and tree seedlings, at which stage their water-use niches are almost totally overlapping and they are at a similar spatial scale. There is a strong controlling effect of fire on tree recruitment. Fire intensity is in turn positively correlated with grass biomass (see chapter six). The effect of browsing on tree

growth is also strongest during the sapling phase, when the foliage is within reach of most browsers.

In summary, savanna structure is mostly determined by the interaction of tree life-history strategies with a variable, largely abiotic environment. Inter-growth form competition plays a role in limiting the productivity of the herbaceous component and the rate (but not direction) of structural change. Competition between woody plants controls woody plant growth and recruitment at high densities, and therefore defines the upper limit to woody biomass. The explanation for the current density of woody plants in a savanna community should therefore be sought in its history of regenerative opportunities, rather than in a climatic and edaphic equilibrium between trees and grasses.

The dynamic equilibrium approach is a reasonable approximation to production dynamics of broad functional groups at a time scale larger than that of an individual storm but less than the lifetime of a woody plant, in other words, at the annual scale. The distribution of annual primary production amongst the two main plant groups in semi-arid savannas is in good agreement with the proportion of the total transpiration each contributes. The assumption that water is the single overriding limiting factor in semi-arid savannas is therefore a useful approximation at this scale as long as inter site differences in WUE are taken into account. Over shorter time periods its usefulness breaks down.

Competition and coexistence of growth forms in semi-arid savannas bear only a distant relationship to one another. This is because they deal with different parameters and operate at very different scales. Competition is a short-duration, localised process which influences productivity. The unit of coexistence, on the other hand, is persistence. The processes involved are recruitment and mortality, which operate at the population level, at large scales and over long periods of time

8.2 THE ECOLOGICAL CONSEQUENCES OF BUSH CLEARING

Some indication of time scale is necessary when discussing the possible ecological consequences of bush clearing. Three broad time categories have been used in this discussion. They have been chosen to be appropriate to the major processes occurring in savannas.

1. **Short-term** corresponds to the lifespan of a single grass tiller, that is, in the order of a year.

2. **Medium-term** corresponds to the lifespan of a woody plant, that is, in the order of a few decades.

3. **Long-term** corresponds to several woody-plant generations, that is, in the order of a century or more.

8.2.1 CONSEQUENCES ON SYSTEM STABILITY

The term "stability" has been so broadly and loosely applied in ecology that it has come to be synonymous with "system dynamics". Stability concepts can be classified into two groups, the interrelationship of which is at present unclear.

1. **Equilibrium-centred concepts** deal with the behaviour of systems in the vicinity of an equilibrium point. Such systems are likely to be relatively closed; in other words they vary in response to their own internal dynamics rather than in response to external abiotic fluctuations. If they exist at all in Nature, they have one or more stable points, each surrounded by a domain of attraction. The stability concepts which fall into this group describe the location of the points and the behaviour of the system when displaced an arbitrarily small distance away from them. The central concept of this group is stability (May 1973, 1977); that is, the ability of the system to return

to its former state once the disturbance has been removed. Such stability can be local or global.

2. **Boundary-oriented concepts** do not necessarily assume that an equilibrium combination exists, but describe the behaviour of the system near the limits of its integrity. The system is carried there under the influence of driving force not under the control of the system itself, i.e. external to it. Such concepts must be qualified stating what the nature of the perturbing force is, and which system variables are under consideration. The central concept of this group is resilience (Holling 1973), the relative ability of the system to persist in the presence of disturbance. It also includes concepts such as resistance, which is a measure of how difficult it is to bring about a change in the system variables, and constancy, a measure of the fluctuation of the system variables over time.

A consideration of the first group of concepts follows, while the second group is dealt with in the detailed discussion of the effect of bush clearing on each system component.

8.2.1.1 Equilibria in semi-arid savannas

The evidence for and against equilibrium-based models of savanna dynamics is presented in the first section of this chapter, and a modified model is presented. If the disequilibrium concept of savanna dynamics is correct, then it is pointless aiming for a "natural" woody plant density solely on the basis of the soil texture and rainfall of the area. The historical woody plant density would be more closely related to the historical fire regime; which may in turn relate to the soil fertility and rainfall through the rate of fuel accumulation. Furthermore, no amount of grazing reduction would lead to a spontaneous reversal of bush encroachment; at least not within the lifetime of the land manager.

to its former state once the disturbance has been removed. Such stability can be local or global.

2. **Boundary-oriented concepts** do not necessarily assume that an equilibrium combination exists, but describe the behaviour of the system near the limits of its integrity. The system is carried there under the influence of driving force not under the control of the system itself, i.e. external to it. Such concepts must be qualified stating what the nature of the perturbing force is, and which system variables are under consideration. The central concept of this group is resilience (Holling 1973), the relative ability of the system to persist in the presence of disturbance. It also includes concepts such as resistance, which is a measure of how difficult it is to bring about a change in the system variables, and constancy, a measure of the fluctuation of the system variables over time.

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Derived grasslands are likely to be unstable. The relative rarity of non-hydromorphic tropical grasslands implies that such grasslands are not globally stable. A case can be made for the metastability of grasslands derived from savannas if the intensity of the grass-tree seedling interaction is sufficiently strong and continuous to prevent tree recruitment. An interruption due to drought or heavy grazing would however permit establishment of trees and this would facilitate future tree establishment due to their supressive effect on grass production and presence as a propagule source. Given the extreme variability of rainfall and grazing in semi-arid savannas, it is unlikely that even the most diligent management of a derived grassland could prevent reversion to a savanna with time. The best that could reasonably be expected would be to retard the rate of re-encroachment by the judicious manipulation of burning and grazing regimes. It is essential to ensure that the mortality of woody plants at the time of clearing is high, otherwise the control exerted by grasses on tree establishment is circumvented. Tree regrowth can be indefinitely postponed by repeated reclearing or mowing.

The contention by Tinley (1979) that woody plants invaded seeplines in the lowveld during the drought period of the mid-sixties implies that hydromorphic grasslands are also not globally stable. A necessary corollary to this argument is that the invasive trees dried the seeplines out to the point where they were insufficiently saturated to exclude trees when good rains returned. While this study has no direct evidence on this point, the similarity of transpiration rates between trees and grasses and the stronger drying in grasslands than savannas indicate that the notion of the trees "pumping the seepline dry" is erroneous. The persistence of trees in the seepline is probably because once established they have considerable tolerance to episodic saturation. The seeplines are so narrow that it is possible that a portion of the tree root system is outside the saturated zone. The protracted saturation needed to cause tree death is probably a fairly rare event. In this case hydromorphic grasslands are globally stable, but the return times following woody plant invasion may be very long.

One bush clearing option is to concentrate on the smaller woody plants and bushes, leaving a few mature trees to create a pleasant park-like

landscape, retain the benefits of the subcanopy habitat and woody-plant litter and suppress the establishment of tree seedlings. Apart from the fact that if sufficient large trees are retained to significantly retard seedling establishment their effect on grass production will be considerable (Walker *et al* 1973, Kelly, Schwimm & Barnes 1978)), this vegetation structure is in the long term unstable, for obvious reasons. It is suggested that size-neutral clearing would satisfy all but the first of these objectives equally well.

8.2.2 THE HYDROLOGICAL CYCLE

The savanna hydrological cycle consists of a number of fluxes (rainfall, evaporation, transpiration etc.) into and out of one major pool, soil moisture. The first section that follows discusses the changes in the fluxes, and the second section discusses the consequences to the soil moisture pool.

8.2.2.1 Alterations to the water budget

The hydrological characteristics of the semi-arid savannas observed in this study are as follows.

1. A stochastic and seasonal water supply results in a series of periods of soil moisture availability of varying depth and duration.

2. A high rate of evaporation from the soil surface consumes 30-40% of the annual water budget (about the same amount as transpiration).

3. Drainage to ground water is relatively small on a long-term basis, but the inter-annual variability in the absolute amount is high.

4. Interception losses (5-10%) are low in comparison to forests or grasslands;

5. There are two main hydrological sub-habitats, one beneath the canopy of woody plants and one between them.

6. Runoff losses are low (<5%) but sensitive to small changes in the state of the system.

All but the last are characteristics of semi-arid savanna hydrology in general; some savannas exhibit much higher rates of runoff than these.

Interception

Interception losses increase following bush clearing due to the increase in interceptive area resulting from the increased grass standing crop. The grass canopy has a more uniform spatial distribution, a higher leaf area per unit biomass and a higher biomass than the tree leaf area it replaces. The increase is greatest on highly fertile sites (up to 50%) and least on sandy sites with a high initial tree biomass.

The absolute values, however remain small. The estimates from this project are crude (5-13%) but in line with national estimates (11%, Whitmore 1971). The upper limit of 15% suggested by de Villiers (1976) would appear to be exaggerated. Extrapolations from the canopy storage volume underestimate interception losses, indicating that evaporation during the course of the storm is an important component. Interception losses partially reduce losses by evapotranspiration, but probably not to a large degree (McNaughton 1981). Since interception losses are strongly linked to grass canopy cover, they will be reduced by high rates of herbivory.

The main ecological significance of interception in savannas is its strong controlling influence on erosion rates throug the reduction in the kinetic energy of the raindrops In this respect a grass cover is superior to a tree cover of equal leaf area in this regard because it is less patchy and closer to the soil surface.

Stemflow

The hydrological significance of stemflow is mainly as a correction factor to interception losses when the latter is estimated with an array of rainguages below the canopy. On densely wooded sites, such as the Mopane site it can total 3% of the incoming precipitation, while interception by trees totals about 5%. It can therefore represent a significant source of estimation error.

The ecological significance of stemflow is as a mechanism for the local concentration of water and nutrients. Stemflow is collected over the entire area of the canopy, but infiltrates into the soil in the immediate vicinity of the stem, which may therefore receive a moisture supply well above average. Deeper moisture penetration beneath plants has been observed in other savannas (Pressland 1973). Stemflow and leaf drip both contain more dissolved nutrients than rainfall, due to their picking up leachates and dust from the canopy surface (Alcock & Mouton 1985). Stemflow at the beginning of a storm is the colour of strong tea. Stemflow is sufficiently large to be an important contributing factor to the maintenance of the sub-canopy habitat. Stemflow from woody plants is obviously lost when the plants are cleared. Stemflow also occurs in grasses, but at a much smaller spatial scale and therefore without the nutrient and moisture concentrating effects of stemflow from trees

Runoff

Runoff is in general initially increased by bush clearing due to the disturbance of the soil and herbaceous layer incurred by the bush clearing operation, and to the loss of tree canopy cover. Within one or two seasons however (herbivory and rainfall permitting) the grass cover of the clearing exceeds the combined grass and tree cover of the original savanna, and runoff decreases. A possible exception may occur on shallow soils with a low water holding capacity, which may become saturated during the early part of the season when total grass transpiration is low. Subsequent rainstorms will result in runoff.

On the sites investigated runoff contributed only 2-5 % of the annual water loss from the system, which is comparable to the national estimate of 6 % (Whitmore 1971). Its major ecological significance is therefore not as a pathway of moisture loss, but as an agent and index of soil erosion. Since runoff rate and erosion by raindrop impact are both exponential functions of the percentage of bare earth (Morgan 1979), they are highly sensitive to changes in grass cover. Thus a change from 2 to 4% of the annual budget as runoff represents more than a doubling in erosive potential.

The reduced runoff on bush cleared sites is dependent on a non-disruptive method of bush clearing and the subsequent maintenance of a good grass cover. Gifford (1973) reported increased runoff and sediment yield following chaining. Under very high levels of herbivory, the uncleared savanna will yield less runoff than the clearing, since a large portion of the savanna plant cover consists of parts unavailable to herbivores. The sensitivity of runoff to a disturbance by herbivory is therefore increased by clearing. Since erosion is in the short term irreversible, the resilience of all variables influenced by topsoil depth (which includes herbaceous productivity, the size of the nutrient pool, the water holding capacity and the infiltration rate) to a grazing disturbance is reduced. This is especially true of soils with a high erodibility (steep slopes), low permeability (deflocculated clays) and soils prone to forming clay caps. Bush clearing on such sites should be undertaken with great care, if at all.

Deep drainage

For the purposes of this study all moisture penetrating below 1m was classified as deep drainage. Both trees and grass have some access to this water, however, and so it is not necessarily all lost to the vegetation system. The modelling assumption of a near-infinite water potential gradient at the bottom of the soil column will also lead to overestimates of deep drainage. The granite underlying all the study sites is poorly permeable. Therefore most of what is here called deep drainage will in fact flow laterally down the lithic contact. Deep drainage estimates in this study are indirect, and their absolute values are not reliable. The

study nevertheless showed an increase in the circumstances leading to deep drainage (moisture in the deep soil layers) on all sites and an increase in deep and lateral drainage can be reliably inferred.

Deep drainage is a sporadic event which mainly occurs when the soil water holding capacity is exceeded, since unsaturated flow is very slow. Once the water holding capacity threshold has been exceeded, deep drainage could be relatively large. The mean value averaged over several years as a percentage of the water budget is probably very small (possibly 1%), so small percentage increases can have large absolute consequences.

The significance of deep percolation is not as a pathway of water loss, but as the agent of transport of soluble soil fractions and the recharge of the water table. There are three possible detrimental consequences of an increase in drainage, the mechanisms of which are discussed in detail in later sections.

1. Nutrients are lost by leaching beyond the rooting zone (Dyer 1983).

2. Salinization results from a raising of saline ground water into the rooting zone (Milne & Calton 1944).

3. Sodification of the lower catena is accelerated.

All of the above possibilities are the result of exceeding a threshold. The consequences are therefore relatively sudden, and once the symptoms are manifest, fairly far advanced. In practical management terms, they are irreversible. They represent changes in system state (that is, changes in the nature of the system rather than changes of degree) causable by bush clearing.

"Raising the water table" is sometimes cited in the lay literature as one of the desirable consequences of bush clearing. Water appearing at the soil surface following clearing is much more likely to represent a "perched" water table due to the presence of an impermeable horizon than the true water table, which is tens of meters deep in most semi-arid regions.

Evaporation from the soil surface

This is the major path of "non-productive" water loss in semi-arid savannas. It is inversely related to transpiration and can thus viewed as an invisible competitor with trees and grass for soil moisture.

There is a general slight decrease in evaporation following bush clearing, due to deeper penetration of water into the soil and to the increased grass cover, which reduces the radiant energy reaching the soil surface and increases the canopy diffusive resistance to water vapour. Cumulative evaporation from the soil surface is less on sandy than clayey sites because of deeper moisture penetration and a tendency for the surface layers to dry out and form a barrier to upward moisture fluxes. Clays contain a large amount of water at soil water potentials more negative than plant wilting point. This moisture is unavailable to plants but can be extracted by a dry atmosphere. High and sustained evaporation from the soil surface is the ultimate cause of the xeric nature of clay substrates in arid regions.

The decrease in evaporation which may follow bush clearing is again dependent on the maintenance of a dense grass cover. An overgrazed clearing will have a higher rate of evaporation than a similarly overgrazed savanna, where the trees retain some shading and boundary layer effect.

A reduction in evaporative losses represents one of the most promising ways of increasing the whole-system WUE. Examination of several published relationships between rainfall and primary production (for example, Rosenzweig 1968) show a steepening slope (i.e. increasing WUE') near the upper semi-arid threshold. The cause could be the supression of evaporation by a dense and continuous grass cover The resultant higher water availability would allow the growth of mesic grass species with a high WUE, thus providing a positive feedback. The extremely high grass production at the Acacia site during the wettest year could be an example of this effect. If so it represents a locally stable high productivity state: should the grass cover be reduced to below the level where it suppresses

evaporation, the high productivity mesic species would be lost until a high rainfall year allows their re-establishment.

Transpiration

Total transpiration makes up 40-50% of the annual water budget and is relatively independent of the vegetation structure in the sites studied. It increased slightly with bush clearing on the Mopane site, where evaporation from the soil is particularly high, but in the other sites the decrease in evaporation from the soil surface with clearing is almost exactly balanced by the increases in deep drainage and interception losses.

The major effect of bush clearing on transpiration is to alter the proportions due to trees *versus* grasses. This resource partitioning is an inverse concave function of woody plant leaf biomass and is considered to be the underlying cause of the general form of the grass production/tree biomass curve (Figure 7 on page 40). This form follows from De Wit's analysis of productivity in mixtures of competitors (De Wit 1960, Berendse 1979), where the overlap between competitors is asymmetrical. It is due to a portion of the resources made available by a reduced tree biomass being used by the remaining trees. It is predicted that the curve will be most pronounced when overlap in the water use niche is high and asymmetric in favour of trees and transpiration rates in the tree species are strongly dependent on soil moisture levels (i.e. "water spender" strategies). Consider the situation where the overlap is 100 %. The removal of half of the trees will result in the resources being split one-third to the remaining trees and two-thirds to the grasses (excluding the possibility of increased losses due to runoff, deep drainage or evaporation). With constant WUE, this will result in a 33 % increase in grass production, not the 50 % predicted by linearity. The situation is exaggerated by asymmetry of competition, but only if the remaining trees have the "surplus capacity" to allow them to use the additional resources.

Inversely convex relationships between tree biomass and grass production, such as was reported by Aucamp *et al* (1983) are considered to be exceptional and must arise from some facilitative interaction (ie a

negative competition coefficient at low densities) between trees and grasses, possibly to do with the subcanopy habitat.

8.2.2.2 The duration of plant available water

The moisture status of a savanna can be expressed in several ways. In general the annual rainfall is used as a moisture index, but this has the drawbacks of ignoring site differences in runoff, runon, and evaporation from the soil surface. A daily record of the soil moisture content throughout the profile provides a complete picture of the water status, but some sort of summary statistic is required for comparative purposes. Stresses can be seen as having three components: frequency, intensity and duration. The absence of stress can be viewed similarly.

Grasses and trees observed in this study seemed capable of resuming transpiration and photosynthesis soon after a short period of water stress had been relieved. The frequency of wetting events does not therefore seem to have a strong effect on plant production, although more frequent, lighter rainfalls would increase losses by interception and evaporation from the soil surface, and decrease deep drainage. Measurements of water use efficiency using both infra-red gas analysis and a pot experiment (chapter four) show the WUE to be relatively insensitive to soil water potential above wilting point. The intensity component is therefore also relatively weak. This suggests that the key parameter relating water status to plant production in savannas is the duration of plant available water. Bush clearing significantly increased the duration of plant available water on all sites in all seasons.

8.2.3 PRIMARY PRODUCTION

8.2.3.1 The rainfall dependence of herbaceous production

This study confirms the strong link between soil moisture availability and plant production in semi arid savannas reported in many otner studies. Annual herbaceous production is typically linearly related to annual rainfall over the 300-700mm per annum range in semi-arid savannas, which are therefore by definition water limited. This does not mean, however, that other factors limiting production are not simultaneously or sequentially operative. Since the rainfall-production relation is central to this (or any other) study of production in semi-arid savannas, it bears detailed analysis. The following interpretation of the linear relation is offered as a hypothesis.

The slope of the relation, here dubbed the **fertility factor** since it is higher on more fertile sites, is related to the WUE of the herbaceous layer. WUE is strictly defined as

$$WUE = \text{net } CO_2 \text{ fixed} / H_2O \text{ transpired}$$

Its long-term value is indexed the sward annual WUE

$$WUE' = \text{Aboveground annual herbaceous production}/(\text{annual rainfall} - R')$$

where the year is taken to correspond to the rainfall season and R' is a a correction for water leaving the system other than via the grass sward. WUE' is a function of both the sward species composition and its growth environment, in particular its nutrient status (Low 1976). A fertilised plot will produce more dry matter for the same rainfall than an unfertilised plot (Donaldson, Rootman & Grossman 1984); therefore the WUE' must be a function of soil fertility, as well as being controlled by the photosynthetic and transpirational physiology of the plant. This dual dependence of production on both water and nutrient supply leads to some

confusion in the application of classical limiting-factor theory: which is the most limiting factor? In semi-arid savannas this apparent paradox is easily resolved by postulating an alternation of limitation in time. The supply of moisture is discontinuous, and whereas the the supply of nutrients is relatively continuous, they can only be taken up by plants in the presence of water. Thus the moisture status limits the duration of the productive process, while the nutrient status limits the rate at which it proceeds when activated.

The y-axis intercept of the rainfall-production is controlled by soil physical characteristics, and is here called the **aridity factor**. This is more obvious if it is expressed instead in terms of the x-axis intercept, R'

$$R' = -(\text{y-axis intercept}/WUE)$$

R' is the theoretical minimum rainfall for herbaceous production (in practice the relation is non-linear in the low ranges; see Rutherford 1980) This minimum is higher on fine-textured soils than on coarse. It approximately the sum of evaporation from the soil surface and tree transpiration for situations where runoff and drainage are small. In derived grasslands it may be closely related to the difference between the water held in the soil profile at wilting point and at air-dryness. Assumptions implicit in this approximation are that evaporation from the soil, tree transpiration and the ratio of above- to belowground allocation remain constant over the rainfall range.

8.2.3.2 Herbaceous production

Herbaceous production invariably shows an increase following bush clearing, provided that the disturbance to the soil during clearing is not so severe as to cause compaction or capping. This increase is initially due to enhanced performance by individual tillers and in the short term

to increased tiller number per tuft. In the medium term it is due to a change in tuft density per hectare and a concommitant aiteration in species composition from low productivity (low WUE) xeric species to high productivity (high WUE) mesic species.

Field evidence (Dye & Spear 1982) indicates that the slopes of the regression lines between annual grass production and annual rainfall in cleared and uncleared sites is often nearly parallel (three sites out of four), as would be predicted by the production-rainfall model outlined above. The field evidence from this study is for too short a period to provide convincing support for that observation, but it appears to apply in two sites out of three. The simulation model suggests that the WUE' of the cleared treatment is always higher than that of the uncleared treatment. The difference in slope is most pronounced for both harvest data and simulated data on fine textured soils, whereas in the Dye & Spear (1982) study pronounced slope differences occurred on a shallow sandy soil. It is suggested that large differences in WUE' on cleared *versus* wooded sites could arise where tree transpiration is strongly dependent on soil moisture status (for example, the Acacia site) or where evaporation from the soil is high but can be suppressed by high grass production (the Acacia site in this study, the Tuli sandveld site in Dye & Spear 1982).

The constancy of herbaceous production under a highly variable rainfall regime is an important consideration when assessing the stocking rates of grazing herbivores. The linear rainfall-production model outlined above makes the following predictions.

1. Sites with high fertility will have higher absolute variability but similar relative variability to low fertility sites with the same physical soil characteristics.

2. Sites with a high aridity factor (i.e., fine textures or shallow soils) will have a similar absolute variability but a higher relative variability than soils with a low aridity factor but similar fertility, since the variation occurs relative to a lower production base.

3. Derived grasslands will in general have a higher absolute variability but a lower relative variability than uncleared savannas, due to their considerably higher production base.

4. Since R' is always positive, the relative variability of herbaceous production should be higher than the relative variability of rainfall.

The duration of this study was insufficient to test these predictions with harvest data. All except the last are supported by the data from the long-term simulations. The slight reduction in interannual herbaceous production variability relative to rainfall variability shown by the model may be due to interannual soil moisture carry-over. Since the relative variability of primary production decreases following bush clearing, it is expected that the constancy of secondary production (and therefore stock-farming income) increases provided that the stocking rate is kept well below the ecological carrying capacity.

8.2.3.3 Woody-plant production

Total aboveground woody plant production was not measured during this study, but the measurements of peak leaf biomass give a minimum estimate of leaf production, since the majority of the species involved are deciduous. Rutherford (1978) estimated that aboveground wood production constituted about 3 % of the total aboveground woody biomass in savannas. On this basis, wood production is about 600, 300 and 180 $kg.ha^{-1}.y^{-1}$ in the Mopane, Combretum and Acacia sites in this study. Coppice regrowth data for the Mopane site suggest a woody increment of 1000 $kg.ha^{-1}\ y^{-1}$

Woody plant production obviously ceases following complete bush clearing, with a consequent loss of browse forage and leaf litter.

8.2.3.4 Total production

Total aboveground primary production in the savannas studied was higher than in the grasslands derived from them. This can be seen from the minimum estimate of woody leaf production alone. Once stem and shoot production is included as well, the difference is likely to be considerable. That a savanna therefore makes more efficient use of available moisture than a grassland is axiomatic. Trees are able to make use of early-season rainfall and deep groundwater more efficiently than grasses.

Total leaf production (grass plus trees) usually decreases after clearing since the increase in grass leaf production does not compensate for the loss of tree leaf. The exception occurs on high fertility sites in above-average rainfall years. Despite the reduction in total leaf biomass, the total forage available to ungulate herbivores (now restricted to grazers) increases since a larger portion of the aboveground biomass is within feeding range and is in an edible form. While this is the major advantage and rationale of bush clearing, it has the disadvantage of making the system more vulnerable to overexploitation. The unavailable woody plant tissues in a savanna act as a buffer preventing the rapid consumption of all primary production by herbivores, and therefore increases the resistance of the primary production to high herbivory. Unmanaged populations of wild ungulates whose ability to disperse has been restricted frequently exhibit large population fluctuations. Increasing the available food supply without controlling the herbivore populations is likely to increase the magnitude of these fluctuations and the severity of their consequences (Scholes 1985, Walker, Emslie, Owen-Smith & Scholes in press).

The absolute and relative constancy of total primary production will decrease following clearing. This is because woody plant production is less sensitive to annual rainfall fluctuations than herbaceous production is. There is a certain degree of carry-over of moisture between seasons in the woody-plant tissues and in the very deep soil moisture pools to which trees appear to have exclusive, if limited, access.

8.2.3.5 Herbaceous species composition and forage quality

It is assumed that the quality of herbaceous forage is a function of its species composition rather than chemical variation occurring within a species grown under differing conditions. There is no apparent universal pattern of herbaceous species change following bush clearing. Several factors operate to confuse the issue.

1. Chance fluctuations of climate.

2. The nature and degree of disturbance caused by the clearing operation.

3. The nutrient status of the site.

A conceptual model of herbage quality in relation to soil nutrient and moisture status is proposed in Figure 58 on page 222. Herbage quality, in the most general terms, is the ratio of the nutritional value of the forage (in particular, its protein content) to its content of poorly digestible tissues, broadly called fibre. It is hypothesised that the protein content is a monotonic function of soil nutrient (particularly nitrogen) availability, while fibre production is a U-shaped function of soil moisture availability. The xeric grasses of arid sites tend to be fibrous in order to maintain leaf stiffness at low water potentials. Where water is freely available relative to the nutrient supply, the excess photosynthates are turned into fibre. The axes of the nutrient-moisture plane presented in Figure 58 on page 222 are interpreted in terms of the fertility and aridity factors derived from the rainfall-production model proposed above. High quality herbage is associated with fertile sites and adequate moisture availability. Excessive moisture, however, produces tall and fibrous herbage of poor acceptability to most grazers. Bush clearing results in an increase in water availability on all sites. This will usually improve the herbage quality on nutrient-rich substrates, but have little effect on nutrient-poor substrates. With time the nutrient status of the subcanopy habitats on nutrient poor sandy substrates is likely to decline and thus the overall sward quality will decrease The field data from

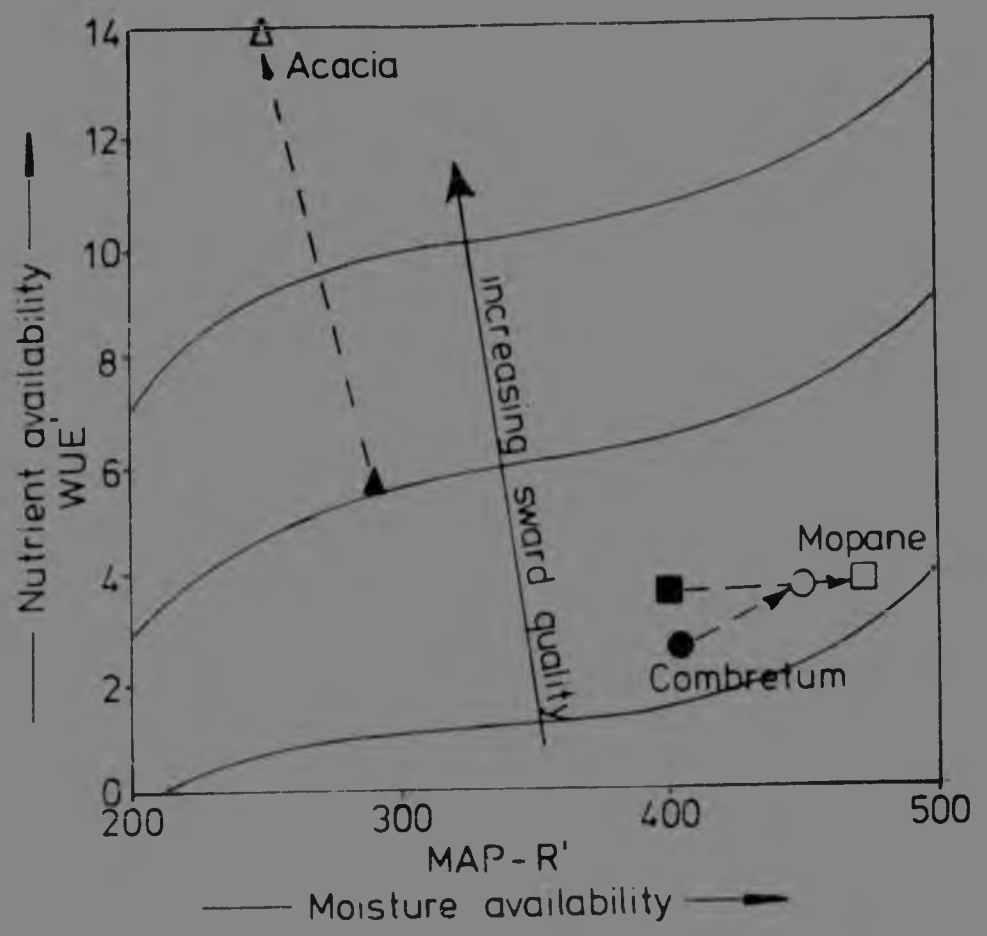

Figure 58. Conceptual model of herbage quality in relation to moisture and nutrient status: preclearing (solid) and postclearing (open) positions of the study sites are indicated.

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this study support the model, but more critical testing is needed to establish its generality.

Once the subcanopy habitat species have been lost, the species composition of sandy cleared areas will be more stable than that of clayey cleared areas, which are subject to greater extremes of moisture supply.

In general, the herbaceous species composition changes resulting from the bush clearing treatment are less than the changes resulting from climatic fluctuations, in the short-term at least.

8.2.4 NUTRIENT CYCLING

8.2.4.1 Nutrient loss through harvest

In nutrient-poor savannas it may be possible for a significant portion of the total system nutrients to be lost by the removal of woody plant tissues at the time of the clearing. Estimates of the nutrient pool stored in the aboveground tissues of woody plants and in the soil are given in Table 8.1. The nutrient concentrations in woody tissues have been derived from the figures published by Ernst (1975), Bate & Gunton (1982) and Frost (1985). The soil values were calculated from the soil analysis results in Table 2.2, assuming the topsoil to be 300mm thick and the subsoil 700mm thick.

Macro-nutrient depletion by wood harvesting seems unlikely in any of the communities studied. The potential for the loss of micronutrients due to wood harvesting is unknown. Of the nutrients analysed, nitrogen has the largest proportion in the woody plant pool. This element can be fixed from atmospheric sources, so depletion is potentially replaceable. Phosphorus is the next most likely element to be depleted, with 1-2% in the woody pool. This is likely to be an overestimate since the Bray-1 extraction measures extractable rather than available phosphorus. A similar proportion of the total phosphorus was lost by the erosion of 20mm of topsoil during the 1982/3 drought.

Table 8.1 Estimated macro-nutrient loss due to the removal of the above-ground woody plant tissues.

	Nutrients ($kg.ha^{-1}$)					
	N	P	K	Na	Mg	Ca
Combretum site						
Soil pool	2155	55	872	1061	1336	4288
Woody plant pool	225	0.6	0.9	0.2	1.7	5.9
% loss	10	1.0	<0.1	<0.1	<0.1	<0.1
Mopane site						
Soil pool	4633	64	829	129	1922	17025
Woody plant pool	433	1.1	1.7	0.4	3.2	11.3
% loss	9	1.8	0.2	0.3	0.2	<0.1
Acacia site						
Soil pool	2600	20	1137	825	3247	12483
Woody plant pool	114	0.3	0.4	0.1	0.9	3.0
% loss	4	1.5	<0.1	<0.1	<0.1	<0.1

8.2.4.2 Nutrient loss through deep leaching

It has been shown that deeper penetration of soil moisture follows bush clearing, leading in turn to downward displacement of soluble ions. At the same time, mean rooting depth decreases. It is therefore inevitable that the soil nutrient pool available to herbaceous plants on a bush-cleared site will be smaller than than that available to a combined tree-grass system. In the short term the nutrient content of the soil profile will probably be little affected since the quantities of water involved are small, and the moister soil conditions could conceivably accelerate primary mineralisation. A downward redistribution of nutrients within the profile is more likely, as has been suggested by Dyer (1983). The rate at which this will occur is unknown, but it is unlikely to be sufficient to cause a decline in herbaceous production in the medium term since production is controlled by the flux rate of nutrients to the roots rather than the absolute quantities of nutrients present in the soil. The following section

will suggest that the nutrient turnover under a derived grassland is likely to be more rapid than under the original savanna.

8.2.4.3 Patterns of nutrient concentration

Woody plants impose patchiness on the nutrient distribution in savannas due to the higher nutrient concentrations in the sub-canopy habitat. In the long term that patchiness will be lost following bush clearing. Two related factors are suggested to be involved in its short-term persistence: the organic matter and clay content of the soil. A considerable portion of the nutrient concentration in the sub-canopy habitat must be present in the slow-decomposing woody-plant litter. The remainder will be on the cation exchange sites, which are mostly contributed by clays in clayey soils, and humified soil organic matter on sandy soils. The presence of clay stabilises the decomposition of organic matter.

It is therefore predicted that the nutrient concentration in the subcanopy habitat will decline fastest in sandy soils, due to simultaneous loss of the soil organic matter nutrient pool and a major portion of the cation exchange capacity. The concentration will persist on clayey sites (such as the Acacia site in this study) as nutrients are gradually transferred from the organic pool to the clay cation exchange capacity. Persistence will be adversely affected by disturbance to the soil during clearing, since this will lead to a mixing of the sub- and between-canopy soil.

8.2.4.4 The rate of nutrient cycling

The rate of nutrient cycling through a derived grassland is likely to be considerably higher than through a savanna. Frost (1985b) has indicated

that the nutrient cycle in savannas consists of a rapid cycle (through grasses) and a slow cycle (through woody plants) operating in parallel. This is because nutrient retention in live and dead woody plant tissues is of longer duration than in grass tissues. In the case of live tissues this is purely a function of longevity and relative biomass. In dead tissues (litter) it is a function of the relative decay rates, which are high for grasses and low for woody plants. If the system is in steady state with regard to biomass, the broadly similar productivity and tissue nutrient concentrations in both imply that the annual nutrient flux through each must be similar. Therefore size of the soil litter pool must be higher in savannas than tropical grasslands. This, and the differences in the quality of litter inputs, could result in a decrease in the cation exchange capacity (a significant proportion of which is contributed by soil organic matter in sandy soils) following clearing. This would lead to increased leaching of nutrients in the medium term.

The increased nutrient turnover rate would help to counterbalance the decreased available nutrient pool, at the expense of a decrease in the long-term stability of nutrient supply. De Angelis (1980) argues that more rapid cycling confers resilience on the system. This claim must be weighed against the increased resistance to change that the savanna has as a consequence of the nutrients held in the woody tissues.

8.2.5 PEDOGENIC CONSEQUENCES

8.2.5.1 Erosion

The erodibility of a soil is strongly influenced by the vegetation cover which it bears (Morgan 1979). The percentage ground cover and the mean canopy height are the controlling parameters for erosion by rain. The percentage ground cover increases and the mean canopy height decreases following non-disruptive clearing, leading to a decreased erodibility. If

the grass canopy is reduced by fire or grazing, however, the erodability may increase above that of the uncleared savanna. Given the fluctuating grass production typical of savannas, there is a high risk of episodes of heavy grazing unless herbivore numbers are controlled at a level considerably below the ecological carrying capacity. While erosion is a normal feature of any area, repeated severe erosion events will eventually lead to decreased primary production.

Similar arguments hold for wind erosion (which is not a problem in the study area, due to the particular nature of the climate and soils), except in this case the greater surface roughness imparted by the trees is important in erosion control. In areas prone to wind erosion the maximum dimension of the clearing in the direction of the prevailing wind should not exceed ten times the height of the trees in the surrounding uncleared savanna in order that they may function effectively as a windbreak.

The greater risk of erosion is one of the main potentially deletarious consequences of bush clearing in the short and medium term. For this reason sites with a high erosion risk should not be cleared. This includes steep slopes, duplex soils and riparian fringes.

8.2.5.2 Sodification

The typical catenary sequence which occurs in the study area (Figure 12 on page 51) is widespread in semi-arid areas on granitic substrates all over Africa. The development of a catena is the consequence of the downslope movement of moisture through the soil profile. To the extent that bush clearing increases this movement, it will accelerate the process towards its end point, which is sodicity in the bottomland soils. It is not known how quickly this end point will be reached, but since sodicity is present or incipient in the bottomlands of many Lowveld catenas already, the upslope extension of sodic patches may become apparent in the medium to long term. Sodicity is not in itself a major problem, although the accompanying shift in woody vegetation

to thicket-forming *Colophospermum mopane* and *Euclea* spp. may be undesirable. The major problem is the greatly increased risk of erosion on the duplex sodic soils, with consequent loss of herbaceous productivity. Sodicity can be ameliorated by the incorporation of gypsum, but this is not likely to be practical or affordable on an extensive basis. Clearing on duplex soils increases the risk of topsoil erosion and a consequent loss of productivity. Sodicity will only be promoted by clearing on upland soils. Bottomland soils, unless already sodic, are suitable for clearing.

8.2.5.3 Salinisation

The ground water in arid regions is frequently saline, and if it is raised into the rooting zone may cause plant mortality. The symptoms are leaf necrosis in mature trees commencing with those growing in the bottomlands, followed by their death some years later. The increased deep drainage brought about by bush clearing could cause a rise in the water table such that it is within the rooting zone in bottomland areas. Salinisation has been observed following bush clearing in Australia and East Africa (Milne & Calton 1944).

The groundwater in the study area is known to be very saline in places. The deaths of *Spirostachys africana* in recent years in the lowveld, and the discolored leaves on large specimens of *Colophospermum mopane* growing in the valley bottoms (which became very prominent during the drought) may be evidence that salinization is a potential problem.

9.0 BUSH CLEARING AS A MANAGEMENT TECHNIQUE

A number of factors indicate that bush clearing is likely to become a widely-applied technique of savanna management in Africa, as it is in the wooded rangelands of Australia and North America. The increasing demand for meat products and the rising value of savanna lands will in time make bush clearing more attractive economically than it is at present. Furthermore, large areas of savanna with a high rural population are undergoing *de facto* bush clearing as a result of the demand for fuel wood and building materials.

In a practical sense there is only a limited set of management actions available to the manager of semi-arid savannas. These consist broadly of controlling the herbivore stocking rate (through such strategems as fencing, water provision, culling and introductions), the fire regime (by controlled burning) and the woody plant density (by bush clearing). The two primary determinants of production in semi-arid savannas, moisture and nutrient supply, are effectively beyond the direct control of the manager. Even if irrigation was economically feasible, there is insufficient water in semi-arid regions to permit its use on a widespread scale. Runoff is a minor component of the water budget in the savannas studied here, leaving little scope for improved surface-water management. The fertilisation of extensive rangelands is currently not economically justified.

Bush clearing simultaneously raises the moisture and short-term nutrient availability to herbaceous vegetation. The major economic product of semi-arid savannas is meat from domestic cattle, which make little use of browse as a food source. Therefore an increase in herbaceous production at the expense of browse will lead to an increase in meat production in grazer-dominated systems. There is no evidence that bush clearing increases the overall system primary productivity; the data from this study show a decrease in aboveground production following clearing. It has been suggested (Ward & Cleghorn 1964, Trollope 1982b) that secondary

production could be maximised in a savanna system by using a combination of browsers and grazers. A large proportion of woody plant production is however unavailable to browsers due to structural, chemical and phenological factors. Furthermore problems with the management and marketing of browsers indicate that cattle will remain the mainstay of agricultural activity in semi-arid savannas for the foreseeable future. Enhanced herbaceous production will therefore be the most practical option for future increases in meat production in such areas.

There is apparent concensus among range scientists that recent increases in woody plant biomass ("bush encroachment") are a major factor threatening the meat production industry. The evidence that bush encroachment has in fact had an impact on meat production, and that the cause of bush encroachment is bad range management is largely circumstantial since the changes in herbivory and burning regimes concommitant with the establishment of the industry make the determination of cause-and-effect relationships difficult. It has been suggested (Pienaar 1980) that bush clearing to redress bush encroachment should be subsidised as an action in defence of a nationally important industry. It should be borne in mind that bush encroachment is a symptom of underlying changes in savanna function, and unless these are corrected the problem of bush encroachment will persist.

Considerable areas of savanna lands (especially in the region where this study took place) are primarily used for tourism, hunting and recreation rather than meat production. Although the presence of wild animals is the key factor in determining the value of land for this purpose the economic arguments for or against bush clearing tend to break down in this case. The conservation ethic is strong in such areas and ecological justifications for bush clearing are sometimes appropriate. In general, however, bush clearing is undertaken to increase the aesthetic appeal of the landscape, improve game-viewing and increase the habitat for preferred game species. Bush clearing increases game sightings mainly by improving visibility, but also by increasing the populations of grazing species.

9.1.1 ADVANTAGES OF BUSH CLEARING

1. The productivity of the herbaceous layer increases by 200 to 2000 kg $ha^{-1}.yr^{-1}$, which commonly represents a large proportional increase. Consequently the productivity of grazing ungulates also increases, but by a lesser proportion. This lack of proportionality is mostly attributed to the fraction of primary production which is not consumed by herbivores. Where primary production is strongly seasonal but consumption is essentially continuous some wastage due to decay is inevitable A decline in forage quality could also be responsible for disappointing secondary production increases following clearing

2. Visibility and accessibility increase.

3. Structural diversity of habitats is introduced.

9.1.2 DISADVANTAGES OF BUSH CLEARING

Bush clearing, if well planned, carefully executed and correctly managed after clearing need have no seriously detrimental ecological consequences in the medium and long term. Poor siting, inept clearing and mismanagement after clearing can however have serious consequences. The following disadvantages apply even to a well executed clearing.

1. Total system productivity decreases.

2. The browse resource is lost and the sub-canopy habitat may be lost.

3. The vulnerability of the system to overexploitation is increased. For instance although erosion rates may on average decrease on cleared land, the risk of extreme erosion events is increased. The increased vulnerability is due to the high proportion of the biomass which is

potentially consumable, the greater absolute variability in primary production and the short generation time of grasses relative to trees.

4. The herbaceous layer species composition may change. This change is usually smaller in magnitude than the changes which occur between wet and dry years and may result in a sward of higher or lower quality than the uncleared savanna.

9.2 SITE LOCATION

9.2.1 FACTORS TO BE CONSIDERED

Sites vary greatly in their response to bush clearing. The inherent fertility of the site, the texture of the soil, the erosion risk and the pre-clearing woody biomass are important factors in selecting a site which will provide the most advantageous response at the least economic and ecological cost.

1. In general, fertile sites will show a greater increase in herbaceous product per unit of bush clearing effort than infertile sites.

2. Sites on heavy textured soils will show a greater response because they are more xeric than sandier sites receiving the same rainfall, the niche overlap between trees and grasses is higher and a high grass biomass can increase the system water use efficiency on the cleared site through suppression of evaporation from the soil surface.

3. The non-linearity of the relationship between woody biomass and herbaceous production means that the herbaceous production increase per unit of woody biomass removed is greater at low than high initial woody biomass levels.

In the context of Klaserie these factors are highly correlated. Clearing on the clayey, eutrophic, sparsely wooded bottomland soils is more rewarding than clearing on the sandy, dystrophic, densely wooded upland soils. Furthermore, in this study sward quality declined on the upland soils after clearing, but improved on the bottomlands. The *Acacia* species dominant on the bottomlands are not prone to resprout after clearing, which greatly reduces the effort required to keep the grassland treeless.

If maximisation of herbaceous production is not the primary objective of bush clearing then the optimal cost : benefit ratio is not an appropriate criterion for site selection. For instance if the improvement of game viewing is the primary objective, then sites with a high woody plant density (such as the *Colophospermum mopane* site in this study) may receive priority.

9.2.2 HYDROMORPHIC GRASSLANDS

Narrow hydromorphic grasslands (seeplines) can frequently be observed in mid-catenal positions in the lowveld. There is evidence (Tinley 1982) that these grasslands have been invaded by woody plants in the last forty years. The possibility of re-establishing a hydromorphic grassland makes these seeplines attractive sites for bush clearing. Olbrich (1984) has shown that the width of the seepline is strongly controlled by the annual rainfall and the length of the catchment slope. In Klaserie the slopes are short and the rainfall is low, so the seeplines are only a few meters wide. Clearing beyond the expected width of the seepline will not result in an additional area of hydromorphic grassland.

The upper boundary of the seepline is marked by a fringe of *Terminalia sericea*. Clearing should begin below this fringe. Invasive woody species are usually the species found in the bottomlands. Clearing of the fringe or the upland vegetation above it will probably increase the amount of water available for the maintenance of the seepline and may result in a

perched water table becoming apparent at the soil surface, but is not recommended for the following reasons.

1. The sandy, dystrophic upland soils are not themselves suitable for clearing.

2. The conditions of hydromorphicity and sodicity are closely related, since they belong to the same pedogenic sequence. Increased catenal water movement will increase the width of the seepline but will probably also accelerate sodification. It is not known over what time period the consequences of accelerated sodification will become apparent, but given the marginally sodic nature of many of the bottomland soils, a few decades may suffice. Toxic salinisation of the bottomlands was observed within years of upland clearing in one case in East Africa (Milne & Calton 1944).

9.2.3 SITES TO BE AVOIDED

The greatest long-term danger of bush clearing is the increased risk of erosion. Sites with a high erosion potential should therefore be avoided. This includes steep slopes, riparian fringes and strongly duplex soils (which in the Lowveld are usually sodic as well).

9.3 PATTERNS OF CLEARING

9.3.1 DEGREE AND EXTENT OF CLEARING

It is usually desirable not to clear all of the woody plants. The remainder provide a browse resource and shelter for animals. Partial clearing can be achieved in two ways: the selective removal of individuals over the entire area; or complete clearing in patches. In general the latter approach is preferable for the following reasons.

1. The non-linearity in the woody biomass-herbaceous production relation means that the best cost : benefit ratio is obtained by complete clearing.

2. A complete clearing is easier to maintain in a treeless state than a partial clearing. Regrowth is easily monitored and can be curbed by the use of fire. Sources of seeds and woody suckers are restricted to the periphery of the clearing.

3. A diverse habitat is produced which meets the requirements of a diversity of wildlife.

The patch size and shape is usually dictated by topography and vegetation. It should be large enough to be functionally different to the uncleared area. For instance, its radius should exceed the rooting radius of the surrounding trees, which can be up to seven times the crown radius (Rutherford 1982). The total extent of clearing is limited by economic factors, the availability of suitable sites and the need to leave an adequate browse reserve.

Author Scholes R J
Name of thesis Response of three semi-arid Savannas on contrasting soils to the removal of the woody component 1987

PUBLISHER:
University of the Witwatersrand, Johannesburg
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