

A FUNCTIONAL CLASSIFICATION OF A RANGE OF SOUTHERN AFRICAN SAVANNA TYPES

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DECLARATION

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

J. Karter

24th day of DECEMBER 1993

ABSTRACT

The prediction that savanna communities with similar conditions of plant available moisture (PAM) and available nutrients (AN) have similar structural and functional features was tested for a range of southern African savanna types. This prediction forms the basis of an hypothesis that savannas can be classified functionally on the basis of PAM and AN. Nineteen South African savanna types were sampled over a rainfall gradient of 369 to 690 mm pa and on different geological parent materials. Ecologically meaningful indices of PAM and AN were derived using climate and soil physical and chemical data. The floristic, structural and functional characteristics of the woody plant and herbaceous components of the savanna communities were ordinated and classified in relation to the PAM and AN gradients. The functional classifications were assessed in the plane of PAM and AN.

Plant available moisture was indexed as the mean number of growth days per annum derived from a water balance modelling approach. This index reflected the duration of the growing season in days and was suitably detailed for use at the community level. The AN indices ranged in complexity from a measure of the availability of individual nutrients in the soil to an index based on the results of a bioassay experiment. The usefulness of the AN indices was assessed on a number of criteria and the soil A horizon total nitrogen content in mg/kg was chosen as a suitable AN index.

The species composition of the woody plant and graminoid communities was primarily related to the PAM gradient with AN having a significant but secondary effect. There was overall a high degree of similarity between woody plant and graminoid floristic types. The distribution of members of the woody plant families, Mimosoideae, Caesalpinoideae and Combretaceae were primarily related to the AN gradient. The higher taxonomic classifications of the graminoid communities, based on subfamilies and tribes, were primarily related to PAM.

Structural trends of the woody plant and herbaceous communities were related to the PAM gradient but not to soil fertility. There were a range of structural types for similar conditions of PAM and AN.

The functional trends of the woody plants were primarily related to the AN gradient with PAM having a secondary but significant effect while the graminoid community functional trends were primarily related to PAM with AN having a secondary but significant effect. The woody plant and graminoid communities were not grouped into functional types in the same way.

It was evident from this study that these South African savanna types were related floristically, structurally and functionally to either or both of PAM and AN, which are hypothesised to be the primary determinants of savanna structure and function. Although communities with similar conditions of PAM and AN were not consistently functionally similar, the functional classifications of both the woody plant and graminoid communities mapped well onto the PAM-AN plane. This indicated that the PAM-AN plane does have potential for use as an overall framework for the classification of savannas on a functional basis.

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1.0 INTRODUCTION

1.1 THE STUDY IN PERSPECTIVE

The southern African savanna biome, as delimited by Rutherford and Westfall (1986), is estimated to cover 46.2 percent of the land surface of the subcontinent. Savannas in this region are an important agronomic, pastoral and eco-tourism resource. Increasingly intense use of savannas by an expanding human population is resulting in adverse changes to the soil and vegetation which are affecting the capacity of these systems to support humans and other organisms. The current trend of degradation in savannas in southern Africa, (and around the world), and the consequences of global climatic change provide extreme challenges for the management of savanna areas protected for conservation purposes or used for commercial or subsistence farming.

There are two issues of major concern in savanna management (Frost, Menaut, Walker, Medina, Solbrig and Swift 1986). The first is the alteration of the ecological structure of savanna communities, involving changes in species composition and in the relative abundance of and relationships between species. The second concern is a change in the way savannas function, especially the decline in productivity that results from changes in the availability of water and nutrients. Efficient management of the savanna resource and the determination of responses of savanna vegetation to increased utilization and global climatic change requires an understanding of the mechanisms or factors that control the structure and function of these systems (Frost *et al* 1986). An understanding of the mechanisms which underlie the differences between savanna types is needed (Walker 1985).

The results of research on savanna structure and function in different parts of the world have been synthesised as part of a collaborative international research effort termed the programme on Responses of Savannas to Stress and Disturbance (RSSD). The aim of the RSSD programme is to develop a predictive understanding of the ways in which savannas respond to natural and man-made stresses and disturbances (Frost *et al* 1986).

A key hypothesis of the RSSD research effort is that soil moisture regime, nutrient status, herbivory and fire are the major determinants of savanna structure and function (Frost *et al* 1986). These four determinants are not ascribed equal status in their influence on savannas, and water and nutrient supply are considered to be of primary importance (Frost *et al* 1986). For the purposes of the RSSD programme, these primary determinants have been termed plant available moisture (PAM) and available nutrients (AN) respectively. Various suggestions as to how to characterize PAM and AN have been proposed within the RSSD forum (Frost *et al* 1986, Walker and Menaut 1988).

One of the objectives of the RSSD programme is to develop a framework for comparing and explaining the structural and functional similarities and differences between savannas around the world. The lack of such a framework has hindered attempts to relate research findings from one savanna to another because of the large sub- and intercontinental variations in savanna types (Frost *et al* 1986). Because PAM and AN are considered to be the primary determinants of savanna structure and function on all continents, the PAM-AN concept has been proposed as the most suitable framework for comparison of the world's savannas (Frost *et al* 1986). A classification approach has been proposed as the best way of summarising the structural and functional characteristics of the various savanna types. A structural-functional classification will enable the comparison of savannas that are floristically different but structurally and functionally similar. This is especially important for intercontinental comparisons.

A structural-functional classification that is predictable on the basis of PAM and AN will not only enable inter-site comparisons on a sub- and intercontinental basis, but will also be a means of predicting the functional response of the vegetation at a given site to a given perturbation that affects moisture or nutrients or both. This latter possibility has potential for aiding research on the impacts of herbivory and fire at a fine scale, and for predicting the implications of global climatic change. The results of such research will be potentially important for management purposes.

The aim of this study is, therefore, to test the prediction that savanna communities with similar conditions of plant available moisture (PAM) and available nutrients (AN) have

similar structural and functional features (Frost *et al* 1986). If this prediction is found to hold, it has important implications for the development of predictive models of savanna structure and function based on the development of a functional classification of savannas that is predictable on the basis of PAM and AN.

1.1.1 STUDY OBJECTIVES

The objectives of this study are:

- 1. To develop ecologically meaningful indices of PAM and AN using climatic data and soil physical and chemical data.**
- 2. To classify the sampled savanna types floristically, structurally and functionally and to compare these classifications to one another and to relate them to PAM and AN.**
- 3. To relate the findings of this study to current hypotheses about PAM and AN related floristic, structural and functional trends in savannas.**

1.1.2 FOCUS AND SCALE OF THIS STUDY

An aim of the RSSD programme is to use the functional approach and the PAM-AN framework to develop models for the prediction of savanna dynamics. This study represents a first step towards achieving that aim and consequently is only concerned with the determination of pattern of savanna structure and function in relation to PAM and AN. No consideration is given to the dynamics of savanna floristic, structural or functional types in relation to changes in PAM and AN (e.g. Walker & Noy-Meir 1982).

No single classification can conveniently cover all scales of resolution for which a predictive understanding of savanna change needs to be developed. Consequently, approaches are needed at global, continental, regional, community, patch and plant scales (Solbrig 1990). This study is aimed at developing a structural-functional classification of savannas at the community scale. The community level of resolution is an important scale for the

management of savanna vegetation.

1.1.3 THESIS STRUCTURE

The remainder of chapter 1 presents a review of the determinants of savanna structure and function and the structural-functional classification approach.

Chapter 2 covers the research approach with a description of the study sites and details of the materials and methods.

Chapters 3 and 4 deal with the development of ecologically meaningful indices of PAM and AN respectively. These two chapters address study objective 1.

Chapter 5 deals with the floristic classification of vegetation in relation to the indices of PAM and AN developed in the two preceding chapters.

Chapter 6 deals with the structural trends and classification of the vegetation in relation to PAM and AN.

Chapter 7 deals with the functional trends and classification of the vegetation in relation to PAM and AN.

Chapter 8 provides a general discussion of the results of the study including the comparison of the floristic and functional approaches and implications for future research.

Chapters 5, 6, 7 address study objectives 2 and 3.

1.2 SAVANNA STRUCTURE AND FUNCTION

1.2.1 DEFINITION OF TERMS

The definition of savanna used in this study refers to vegetation with a continuous herbaceous

stratum composed mainly of C4 grasses and forbs, and a discontinuous woody plant layer with a range of densities and heights. The co-existence of woody plants and grasses is a unique feature of savanna vegetation. This definition encompasses a wide range of savanna types from predominantly grassland with few scattered shrubs to closed woodland. In this study savanna types will be used synonymously with savanna communities.

Savanna structure is defined as the spatial arrangement, both horizontally and vertically of the plant biomass in a community. Structural features include density, mean height and canopy cover.

Savanna function refers to the way in which plants are adapted to and respond to environmental factors. Functional features are those features of the plant that are apparent environmental adaptations such as phenology, leaf size, succulence and fire tolerance.

1.2.2 DETERMINANTS OF SAVANNA STRUCTURE AND FUNCTION

As mentioned in section 1.1, four major determinants of savanna structure and function have been proposed (Frost *et al* 1986). This hypothesis has been drawn from syntheses of the ecology of tropical savannas such as Huntley and Walker (1982) and Tothill and Mott (1985). Soil water regime, nutrient status, herbivory and fire are considered to be the major determinants of savanna structure and function on all continents. Human activity is considered a fifth determinant of savanna structure and function but will not be considered in this study.

As stated in section 1.1, the four determinants are not ascribed equal status. Plant available moisture (PAM) and available nutrients (AN), the primary determinants, are considered to have a constraining effect on herbivory and fire, the secondary determinants. These, in turn, are considered to indirectly modify the primary determinants. Although individual determinants have been identified and prioritised, they do not influence savanna structure and function independently and have a correlative and interactive effect (Frost *et al* 1986). Also, the status of the four determinants may be different in different savannas, for example water limitation is considered to be the most important determinant in dry savannas while nutrient

limitation and the occurrence of fire are more important in moist savannas (Walker 1985). This effect is evident in the general model of savanna structure and function proposed by Walker (1987). Models with the same basic elements were constructed for a range of savanna types, the distinguishing feature between them being the difference in significance and relative importance of each element in each model.

The main emphasis in this review will be placed on the primary determinants since these form the focus of this study. These determinants are extensively discussed and reviewed in syntheses of savanna ecology such as Huntley and Walker (1982) and Tothill and Mott (1985) and summarised by Frost *et al* (1986).

1.2.2.1 Primary determinants

1.2.2.1 (a) Plant Available Moisture (PAM)

This section deals briefly with the factors that determine and modify PAM and with some of the apparent effects that PAM has on savanna structure and function. For the purposes of this study it is assumed that each savanna type can be characterised by an average condition of PAM that influences the structure and function of the vegetation.

Plant available water is determined primarily by rainfall. Soil properties such as texture, structure, profile depth and stoniness influence the permeability and water retention of the soil and consequently modify the amount of rainfall that enters the soil and the way in which it is distributed in the soil profile. Temperature also has a modifying effect on PAM through its effect on evapotranspiration and evaporation. The modifying effects of these factors are dealt with in detail in chapter 3 on the development of PAM indices.

Cole (1982) attributes the height and spacing of savanna vegetation to the influence of PAM. The wide range of structural types of savannas eg grassy shrubland to closed woodland is attributed to PAM since the availability of soil water and its distribution in the soil profile is thought to influence the relative amounts of trees and grasses (Walter 1971). An increasing dominance of trees with increasing moisture availability has been hypothesised.

As in other vegetation types, the availability of soil water is important for the uptake of nutrients from the soil (Bate, Furniss and Pendle 1982) and for the physiological functioning of the plants (Goldstein and Sarmiento 1987). The influence of PAM on plant physiology accounts for the observed trends between the soil water balance and primary productivity (Tinley 1982, Frost *et al* 1986). Plant available moisture is hypothesised to limit the primary productivity of savanna vegetation (Bate *et al* 1982). For both woody plants and grasses, growth and maintenance of photosynthetic material depends on PAM.

The seasonality of PAM has an important influence on the way in which savannas function and the patterns of growth and reproduction of both the major growth forms are dependant on the availability of soil water. Both the woody plant and graminoid components of the vegetation have adaptations that enable them to cope with seasonal changes in the availability of soil water (Medina 1982, Tinley 1982, Frost *et al* 1986 and Goldstein and Sarmiento 1987). These include phenological adaptations, seed dormancy, vegetative dormancy and resurrection, physiological plasticity and leaf size. The variable seasonal availability of PAM also influences savanna dynamics, for example, by affecting the outcome of competition between the two major growth forms (Walker 1987).

Southern African savannas have been divided into two groups on the basis of PAM. This distinction between moist and dry savannas is fundamental for current savanna theory (Huntley 1982, Walker 1985, Frost *et al* 1986).

The effects of PAM on vegetation composition, structure and function are dealt with in detail in chapters 5, 6 and 7 respectively.

1.2.2.1 (b) Available Nutrients (AN)

This section deals briefly with the factors that determine and modify AN and with some of the apparent effects that AN has on savanna structure and function. For the purposes of this study it is assumed that each savanna type can be characterised by an average condition of AN that influences the structure and function of the vegetation.

Nutrient availability is determined by the size of the nutrient pool, the rate of nutrient turnover, plant demand and the ionic movement of nutrients in the soil (Bell 1982, Scholes 1987). The size of the nutrient pool is determined by the geology of the parent material and by the rate at which soil is formed by weathering (Frost *et al* 1986, Scholes 1987). Low AN or dystrophic soils are formed from the weathering of acidic parent materials such as granite, and from sediments and redistributed sands. These soils have a low reserve of weatherable minerals, a low effective cation exchange capacity and small amounts of exchangeable bases. High AN or eutrophic soils are formed from basic igneous rocks. These soils have a high reserve of weatherable minerals, a high effective cation exchange capacity and a large amount of exchangeable bases (Frost *et al* 1986).

Leaching and the relocation of soils and nutrients in the landscape will also influence nutrient availability (Frost *et al* 1986). This phenomenon is clearly illustrated along catenal sequences (Ben Shahar 1990). Soil texture plays an important determining role in AN status of the soil since it determines the ability of the soil to retain nutrients against leaching. The type of clay and the clay content of the soil are important.

Soil organic matter (SOM) dynamics also influence AN. In dry savannas, there are low amounts of SOM. Microbial activity is limited by the availability of water and there is an intermittent nutrient release. In moist savannas there is a high input of organic matter to the soil. There is a high potential for mineralization because of the availability of moisture but the litter is low in nitrogen and high in lignin and phenolics and this limits the microbial activity. These soils have a slow release of nutrients and a consequential low stock of AN (Frost *et al* 1986). Earthworm activity and root turnover also influence the amount and turnover of SOM and hence nutrient availability.

Issues relating to the availability of nutrients will be dealt with in more detail in chapter 4 on the development of nutrient indices.

The availability of nutrients has an important influence on the quantity and quality of plant production. Nutrient availability is an important determinant of plant production, especially the availability of nitrogen and phosphorus. Low AN will limit production where water is

not limiting in moist savannas. It is hypothesised that for the same amount of PAM, there should be higher plant production on eutrophic than on dystrophic soils (Frost *et al* 1986).

AN influences the quality of vegetation by influencing the balance between protein and soluble carbohydrate production (Bell 1982). In this way AN influences the palatability of the vegetation of both woody plants and grasses (Bell 1982, Walker 1985). There are seasonal change in plant quality due to increasing nutrient constraints as the growing season progresses. Plant quality will be high during the growing season and low during the dry season (Frost *et al* 1986). Sclerophyllous vegetation is characteristic of low AN soils in Australia and South America (Walker 1985).

Resource availability determines the extent and type of plant defences (Coley, Bryant and Chapin 1985). Structural defences (thorns and spines) are prevalent where AN is high while chemical defences (secondary compounds) occur where AN is low (Bell 1982, Huntley 1982, Walker 1985).

The moist / arid savanna distinction can equally be regarded as a dystrophic / eutrophic distinction (Scholes 1991). As for the distinction based on PAM, this difference is fundamental for current savanna theory (Huntley 1982, Walker 1985, Frost *et al* 1986).

Plant species create positive feedbacks to nutrient cycling, affecting nutrient cycling directly via uptake, use and loss of nutrients, and indirectly by influencing microbial activity and herbivory (Hobbie 1992). Although AN is considered to be a determinant of vegetation structure and function, vegetation plays an important role in the temporal and spatial distribution of nutrients in savanna soils (Frost *et al* 1986). Trees, for example, influence the status and distribution of nutrients in savanna soil by moving nutrients against the direction of leaching by concentrating nutrients from a wide area (Kellman 1979, Bate & Gunton 1982, Frost *et al* 1986).

The effects of AN on vegetation composition, structure and function are dealt with in detail in chapters 5, 6 and 7 respectively.

1.2.2.1 (c) The PAM-AN plane

One of the RSSD objectives is to develop the optimal characterisation of PAM and AN for comparing savannas in terms of their structure and the way they function. The framework that has been proposed for this is the PAM-AN plane. There is much debate as to how the PAM and AN axes of the plane should be formulated and several suggestions have been made (Frost *et al* 1986, Solbrig, Medina and Mott 1988). The development of PAM and AN indices is discussed in detail in chapters 3 and 4 respectively.

1.2.2.2 Secondary determinants

1.2.2.2 (a) Herbivory

Herbivory has both a direct and an indirect effect on vegetation structure and function. The direct effect is by the damage to and reduction of plant biomass while the indirect effect is via a modification of PAM and AN (Cumming 1982, Breman & de Wit 1983, Tolsma, Ernst & Verwey 1987). Hatton & Smart (1984), for example, recorded a build up of SOM and a release of major nutrients into the soil in areas protected from herbivory for a number of years. Savanna vegetation has co-evolved with browsers and grazers and all plants have adaptations for the survival of herbivory.

Grazing pressure will influence the structure and species composition of the graminoid layer. If there is too little grazing, grasses become moribund. Overgrazing leads to mortality of palatable species and less palatable species become dominant (O'Connor and Pickett 1992). Overgrazing can also lead to woody seedling establishment and bush encroachment. Although browsers can distort tree structure and retard growth rates, defoliation by herbivores can also stimulate plant growth, depending on the intensity and frequency of defoliation (Cumming 1982). Thus, herbivory has an important influence on primary productivity (Cumming 1982).

Large herbivores influence soils by trampling and digging and by reducing plant and litter cover (Cumming 1982). Large herbivore activity will influence soil moisture and nutrients

which will influence vegetation structure and function.

1.2.2.2 (b) Fire

As for herbivory, fire has both a direct and an indirect effect on savanna vegetation. The direct effect is via the loss of plant biomass while the indirect effect occurs through changes in PAM and AN.

Fire frequency, intensity and type and the season of burn are all important for savanna structure and function. Fire influences the tree to grass ratio since it destroys young trees and shrubs and stunts mature plants and the withdrawal of fire leads to bush encroached veld (Trollope 1982). Fire is important for maintaining bush in a suitable state for browsers in terms of height, density and condition (Trollope 1982). The importance of fire as a structural determinant declines with increasing aridity (Scholes 1987). Frequent but low intensity burning can lead to increased tree density due to the weakening of the grass sward (Scholes 1987).

Savanna plants have evolved with fire as an environmental pressure and hence have strategies for fire avoidance and tolerance. The ability to coppice, a thick bark and leaf loss prior to burning are examples of the way in which woody plants are adapted to survive fire. The position of the perennating organ in grasses is an important fire avoidance mechanism (Trollope 1982).

Fire has an important effect on AN by reducing the amount of SOM and total nitrogen in the upper soil layer, and by reducing the amount of litter (Singh 1993). Increased exposure of the soil leads to erosion and the loss of fertile top soil. Fire can also lead to the rapid mineralisation of organic matter and the acceleration of nutrient cycling and increased concentrations of available nutrients such as inorganic P (Coutinho 1982, Brown & Mitchell 1986). The exposure of the soil surface as a result of fire leads to a reduction in PAM because of an increase in runoff, a decrease in infiltration rate and an increase in evapotranspiration.

1.3 A STRUCTURAL-FUNCTIONAL CLASSIFICATION APPROACH

This section deals with a structural-functional approach to the classification of vegetation. The rationale for developing such an approach is presented, together with a brief outline of the history of the approach and a review of studies where it has been used. The use of the term structural-functional classification implies a classification based on either structural features or functional features or a combination of these.

1.3.1 HISTORY OF THE APPROACH

The use of the structural-functional approach is not new. The first classifications of vegetation, developed in classical works on plant geography during the early 19th Century, were based on the physiognomy or structure of vegetation (Whittaker 1973). Development of this approach in the early 20th century led to other classification systems such as the life-form concept based on the position of the perennating organ (Raunkiaer 1934) and the structural system proposed by Dansereau (1951). Knight and Loucks (1969) list a number of studies pre 1968 where features such as leaf size, plant height, root form, vegetative reproduction and method of seed dispersal were used. Other alternative classifications to that of classical taxonomy have been formulated. Mueller-Dombois & Ellenberg (1967) extended Raunkiaer's system to include factors such as plant size and leaf type, size and shape. Grime (1974) proposed a classification based on plant life history strategies and defined three primary strategies that coincide with particular habitat conditions. Noble and Slatyer (1980) formulated a model based on plant vital attributes that is designed to predict dynamics during succession of disturbed environments.

Knight and Loucks (1969), Werger and Sprangers (1982), Floret, Galan, Le Floch, Orshan and Romane (1987) and Montalvo, Casado, Levassor and Pineda (1991) provide useful reviews on the history and use of the structural-functional approach.

1.3.2 BASIS OF THE APPROACH

The basis of the structural-functional approach is that plants under a given set of

circumstances have certain physiological or morphological characteristics in common and can be grouped on the basis of these (Grubb 1985). Organisms exhibit sets of co-adapted traits that are predictably related to their ecology and recurrent patterns of plant specialisation form the basis for a functional description of vegetation (Grime 1985). If individual structural and functional features are understood to be the result of adaptive processes to environmental factors then a structural-functional classification must be ecologically meaningful (Werger and Sprangers 1982). Recognition that a species must make some trade-offs in coping with environmental stresses and that physiological and morphological constraints will lead to certain groups of trade-offs being made is central to the idea that functional groups can be defined Botkin (1975) (as cited in Noble 1988).

In order to develop a useful structural and functional description of vegetation, plant characteristics that vary predictably in relation to environmental variables need to be identified (Grime 1985). Attributes should be easily measured on a large number of plants and the ecological significance of the variation of the particular attributes needs to be established (Grime 1985). There should be a direct physiological basis for the selection of diagnostic criteria that reflect measurable attributes of the environment (Gillison 1970). A functional classification will need to be open ended but hierarchical and purpose specific (Noble 1988).

1.3.3 RATIONALE FOR USING THE APPROACH

The structural-functional approach to characterising vegetation is considered by several authors to have certain advantages over the floristic approach. It is considered less laborious and does not require a detailed floristic knowledge of the vegetation (Werger & Sprangers 1982). Consequently relatively inexperienced observers can be trained to recognise and record physiognomic features (Moll, Campbell & Probyn 1976). The structural approach is considered more generally applicable than the floristic one thus increasing the comparability of its results. The results of the floristic approach are sensitive to chorological patterns of species distribution so that the comparability of results is somewhat more restricted (Werger & Sprangers 1982). Because of the emphasis on the plant adaptations to the environment new information can be communicated without knowledge of species

composition (Knight 1965). The structural-functional approach enables the investigation of the ecology of the community directly rather than indirectly through plant names (Knight and Loucks 1969). It enables the comparison of vegetation in geographically separate areas that is structurally and functionally similar but floristically different. A large number of species can be grouped into a lesser number of common and easily measurable structural-functional types. The structural approach can be used for describing large geographic zones of vegetation, similar in appearance but with different floras (eg Fosberg 1961, Moll *et al* 1976 and Box 1981), and for examining small scale or local environmental gradients (eg Knight 1965, Webb, Tracey, Williams & Lance 1970, Bredenkamp & Theron 1985).

The structural-functional approach is useful in vegetation such as fynbos which is floristically diverse and where large parts of the flora have had little or no taxonomic treatment (Linder & Campbell 1979). The method of structural analysis is rapid and is considered to show promise in complex tropical vegetation for which floristic data are not available (Webb Tracey & Williams 1976).

Classification of vegetation on the basis of species composition has become the standard way of describing vegetation. There are, however, problems associated with the use of a purely floristic approach. The species is a taxonomic abstraction without necessarily any inherent ecological meaning. Often little is known about the species that enables ecological interpretation (Knight and Loucks 1969, Gillison 1970). The high species diversity found in most ecosystems hinders ecological comparisons between vegetation types and limits attempts to predict vegetation dynamics (Noble 1988). Floristic differences between vegetation types may mask structural and functional similarities that would enable inter-site comparisons irrespective of species composition. More than a floristic approach is needed if a classification as a basis for causal analysis, effective conservation and informed management is desired (Grime 1985). A structural-functional classification approach is considered suitable for these purposes.

1.3.4 REVIEW OF STUDIES

The rest of this section contains a review of studies post 1968 where a structural-functional

approach has been employed. A common feature of these studies is that the vegetation was grouped by ordination and/or classification on the basis of a number of structural and functional characteristics. The resultant structural-functional groups were related to environmental variables. This is similar to the approach that has been taken in this study.

These studies have been conducted in different vegetation types and at different spatial scales.

1.3.4.1 Mediterranean vegetation

Cowling and Campbell (1980) used structural features of growth form, leaf size, leaf duration and spinescence to determine whether convergence of plant community structure has occurred between the Cape mediterranean region and the mediterranean regions of California and Chile. Structural variation was sampled along climatic gradients on each continent. Variation in structural features was also found in relation to soil nutrient content. They concluded that under similar climatic constraints the structure of genetically distinct plant communities need not necessarily converge but suggested that the non-convergence was related to differences in soil nutrient conditions between the areas under comparison. Convergence in vegetation structure between floristically distinct vegetation along similar climatic gradients in Chile and California has been demonstrated (Parsons and Moldenke (1975) cited in Cowling and Campbell (1980).

Cowling and Campbell (1983) used structural features to test the hypothesis that there would be less structural variation along fynbos than non-fynbos coenoclines because the overriding influence of low levels of soil nutrients would be manifest in a great deal of structural convergence in fynbos. The results indicated that there was structural variation in relation to soil nutrient and climatic conditions. Fynbos structure was interpreted largely as a response to low levels of soil nutrients while non-fynbos structure was explained in terms of variations in soil moisture and climate. This was a comparison of vegetation types of disparate biogeographical affinities but found under similar climatic conditions. The authors used physiognomic-structural features that were easily observed or measured characters to which some functional or adaptive significance could be attributed eg leaf texture, leaf size, spinescence, growth forms.

Floret, Galan, Le Floc'h, Orshan and Romane (1987) considered the use of growth forms in a descriptive and a functional way in *Quercus ilex* coppice in southern France. They found that location of renewal buds was a good integrating indicator of plant adaptations to the environment and that renewal bud location and leaf consistency appear to vary significantly along a gradient of increasing environmental constraints, especially climatic ones. Five groups of characters such as those describing the above-ground parts of the plant, those describing the photosynthetic organs, those concerning the underground parts of the plant, those related to longevity and seasonality and those related to the plant's mode of regeneration and multiplication were used. Two environmental factors were shown to be important namely bedrock and soil types and the number of dry months.

Montalvo *et al* (1991) compared species composition and morphological and functional traits in Mediterranean grasslands along an altitudinal gradient. They used 60 morphological and functional traits. Pattern in morpho-functional traits along the altitudinal gradient coincided with the pattern on the basis of floristic composition and hence 'styles of adaptation' of ecological systems were recognised. They hypothesised that plant species composition and traits were mainly determined by physical factors.

1.3.4.2 Prairie vegetation

Knight (1965) compared stands of Wisconsin prairie vegetation along a moisture gradient on the basis of plant structure and function. Characters such as method of vegetative propagation, phenology, height, leaf form, leaf size and root system structure were used. Many of these characters showed a trend along the moisture gradient. Knight (1965) developed a structural-functional index for characterising vegetation that was designed to indicate the relative importance of plant features characteristic of dry prairie.

1.3.4.3 Forest vegetation

Knight and Loucks (1969) studied the structural and functional features of the trees, shrubs and herbs in the upland forest communities of Wisconsin to determine their potential for describing relationships between the vegetation and the environment. The authors used 29

tree structural-functional features. The results indicated that the upland forest communities could be described and studied on the basis of these features. Certain adjacent stands of forest vegetation were similar structurally and functionally but were different floristically indicating that a difference in floristic composition did not necessarily mean a difference in structural-functional characteristics.

Werger and Sprangers (1982) compared floristic and structural-physiognomic classifications of a dry semi-evergreen forest and thicket vegetation of south-eastern India. They found the classifications to be very similar in their main groupings which were interpreted as ecologically meaningful. They concluded that the use of structural-physiognomic criteria allows a detailed and ecologically significant classification of vegetation.

Webb *et al* (1976) classified tropical forest vegetation on a physiognomic-structural basis. They found that the structural classification of the simple forests was not useful but that classification of the complex forests produced meaningful site-groupings. These authors suggest that a structural-physiognomic approach could be useful in tropical forest vegetation where many species are as yet unnamed but a classification is needed for use in resource management and utilization. Classification of the sites recovered broad environmental information. Structural classifications in complex forests were correlated with altitude, moisture availability, soil texture and aeration and mineral nutrients.

1.3.4.4 Arid rangeland vegetation

Friedel, Bastin and Griffin (1988) used a multivariate procedure for reducing a large number of species in arid Australian rangelands into a smaller number of functional groups for the purposes of management in response to climate, grazing and fire. This approach reduced 107 species into 6 groups on the basis of 25 attributes. Species were divided into functional groups on the basis of vital attributes and functional groups were used to classify the monitoring sites into condition states. These authors suggest that until autecology is well documented, it would be wise to collect field data at the species level. Future data collection at the functional level would mean increased speed and efficiency and a reduced data requirement. They concluded that functional groups are important for ease of interpretation

of complex vegetation change for managers and pastoralists and suggested that attributes should be selected according to their relevance for management.

Milton (1990) used structural and functional attributes to investigate the incidence of animal-associated adaptations in plants in arid shrublands. Features of morphology, dispersal and phenology in relation to local variation in soil moisture and nutrient status were considered.

1.3.4.5 Semi-arid woodland vegetation

Leishman and Westoby (1992) did a multivariate analysis of 43 traits of semi-arid woodlands in western New South Wales in Australia. They used vegetative, life-history, phenological and seed-biology characters. The purpose of this study was to determine if there was an objective basis for grouping plants by these traits. The classification reduced 300 species into 5 groups on the basis of 43 traits. The 5 groups correspond to major growth-form groupings.

Other, recent studies such as Box 1987, Danin & Orshan 1990, Floret, Galan, Le Floc'h, Orshan and Romane 1990 and Halloy 1990 are cited in Montalvo *et al* (1991).

1.3.5 COMPARISON OF CLASSIFICATIONS

Many floristic analyses have been supplemented by profile diagrams and physiognomic-structural data (Moll, *et al* 1976) but only during the last 20 years have structural-functional and floristic analyses been compared on a statistical basis (Knight & Loucks 1969, Webb *et al* 1970, Werger & Sprangers 1982).

1.3.6 APPROACHES TO STRUCTURAL-FUNCTIONAL CLASSIFICATION

There are two approaches to the structural-functional classification of vegetation. The *a priori* approach uses fixed classes defined by a few subjectively selected criteria. The vegetation is classified into a preconceived range of structural-functional forms. The *a posteriori* approach involves the classification of the vegetation based on a large number of

attributes. Classes and groups are synthesised out of empirical data and items are grouped on the basis of their similarity. Linder and Campbell (1979) compared these approaches in fynbos vegetation and concluded that the *a posteriori* approach was preferable. This classification can be easily added to and provides a general purpose, information rich classification with a high predictive power. The *a priori* approach was found to be restrictive and prone to misclassification.

1.3.7 THE STRUCTURAL-FUNCTIONAL APPROACH IN SAVANNAS

Several *a priori* structural classification systems have been developed for African savanna vegetation (eg Pratt, Greenway and Gwynne 1966, Coetzee & Gertenbach 1971, Edwards 1983, Bredenkamp & Theron 1985, Grunblatt, Ottichilo & Sinange 1989).

Many studies in savannas (eg Gertenbach 1983, Fraser, van Rooyen & Verster 1987, Belsky & Amundson 1990, O'Connor 1992) have used a floristic and structural approach in order to explain vegetation - environment relationships.

The savanna vegetation of southern Africa has as yet not been classified on an *a posteriori* structural-functional basis. Existing classifications of savannas are predominantly floristic and do not provide much information about function. Research towards formulating a general structural-functional classification of these savannas is needed (Frost *et al* 1986).

2.0 MATERIALS AND METHODS

2.1 STUDY SITES

Study sites were chosen to represent the aridity and fertility gradients present in South African savannas. Sampling regions in the savanna biome were chosen on the basis of mean annual rainfall to provide a gradient of plant available moisture (Fig. 2.1). Within each rainfall region, two or more sites on different soils were sampled to provide available nutrient gradients. As far as possible, both nutrient rich and nutrient poor soils were sampled in each rainfall region (Table 2.1). All the sites were located in conservation areas to eliminate the direct effects of anthropogenic activities, such as wood harvesting and cattle grazing, on the vegetation. The vegetation at all sites had both a woody plant and a herbaceous component, but with varying structure and composition. A total of nineteen sites were sampled. Throughout this document, sites are referenced by the numbers shown in Table 2.1.

2.2 COLLECTION OF SOIL DATA

2.2.1 SOIL PROFILES

A single soil pit at each site was excavated to a depth of between 1000 and 1300 mm or to the bottom of the profile if shallower. Each soil profile was described and soils were classified to form (Macvicar, Loxton, Lambrechts, Loux, de Villiers, Verster, Merryweather and van Rooyen & Harmse 1977). Soil samples were taken from each of the horizons identified in each profile.

2.2.2 SURFACE SOIL SAMPLES

Ten surface soil cores were collected at each site, nine located randomly and one located near the soil pit. A 50 x 300 mm stainless steel sampling tube was used, which was hammered

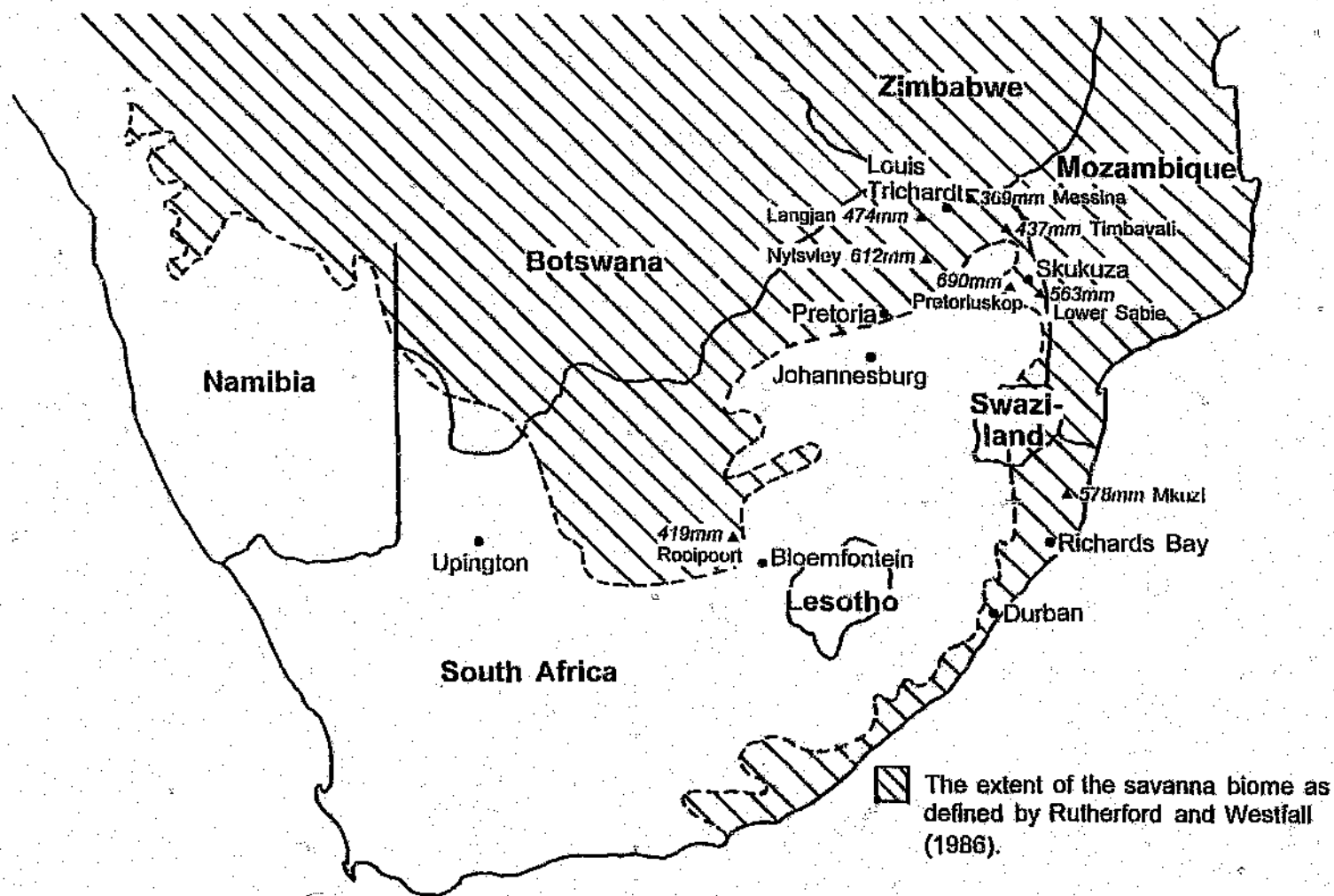


Figure 2.1 The location and mean annual rainfall of sampling regions (▲) within the savanna biome of South Africa. Mean annual rainfall figures were extracted from Weather Bureau (1988) records.

Table 2.1 The geology and dominant woody species of each of the sites sampled in each sampling region. (Nomenclature for dicotyledons follows Gibbs-Russell *et al.* (1987).)

Location	Site	Geology	Vegetation
Mkuzi Game Reserve	1	Quaternary sands	<i>Combretum molle</i> , <i>Acacia burkei</i>
	2	Basalts	<i>A. nigrescens</i> , <i>A. nilotica</i>
	3	Alluvium	<i>A. xanthophloea</i>
	4	Lebombo rhyolite	<i>C. apiculatum</i>
	5	Marine sandstone	<i>A. tortilis</i> , <i>A. nilotica</i>
Nylsvley Nature Reserve	6	Waterburg sandstone	<i>Burkea africana</i> , <i>Terminalia sericea</i>
	7	Felsite	<i>C. apiculatum</i> , <i>C. molle</i>
	8	Waterburg sandstone (old settlement site)	<i>A. tortilis</i> , <i>A. nilotica</i>
Rooipoort Game Farm	9	Kalahari sands	<i>A. mellifera</i> , <i>A. erioloba</i>
	10	Mudstone	<i>Tarchonanthus camphoratus</i> , <i>Rhus undulata</i>
	11	Andesite	<i>A. mellifera</i> , <i>Grewia flava</i>
Langjan Nature Reserve	12	Karoo basalts	<i>Grewia</i> spp., <i>T. pruniodes</i>
	13	Kalahari sands	<i>C. apiculatum</i> , <i>G. flavescens</i>
Messina Agricultural Research Station	14	Quartzite gneiss	<i>Colophospermum mopane</i>
Lower Sabie	15	Sabie River basalts	<i>Albizia harveyi</i> , <i>Dichrostachys cinerea</i>
Timbavati Nature Reserve	16	Timbavati gabbro	<i>A. nigrescens</i> , <i>Grewia</i> spp.
	17	Granite gneiss uplands	<i>T. sericea</i> , <i>Sclerocarya birrea</i>
Pretoriuskop	18	Granite gneiss midlands	<i>T. sericea</i> , <i>D. cinerea</i>
	19	Granite gneiss uplands	<i>C. collinum</i> , <i>C. zeyheri</i>

into the soil. The cores ranged in depth from 130 to 250 mm. Soil samples were placed in paper bags and air dried.

2.2.3 SOIL PHYSICAL AND CHEMICAL PROPERTIES

Soils were screened through a 2 mm mesh sieve and dried to constant mass at 65°C. Soils from each site were bulked prior to analysis to reduce the sample variation and consequently the number of samples analysed per site. A-horizon soils were comprised of three to six profile samples (collected from the soil pit at each site) plus five surface cores. B-horizon soils were comprised of three to six profile samples (collected from the soil pit at each site). Two subsamples of each bulked soil type were analysed in each case to check for consistency of results.

Bulk density was calculated from the mass and known volume of each of the surface soil cores. The soil core volume was calculated from the dimensions of the hole from which the core was removed. All natural inorganic particles greater than 2 mm were weighed to determine the percentage stone content of each soil. The values of all soil variables expressed on a mass basis were corrected for stoniness using the percentage stone content of each soil. Particle size distribution was determined using the Bouyoucos method (Black 1965).

All subsamples were analysed for pH (in 1M KCl), extractable cations (Ca, K, Mg) (1M Ammonium acetate) and extractable acidity using standard methods (Anderson and Ingram 1987) and resin extractable phosphorus (Murphy and Riley 1962, Sibbensen 1978). Only the A-horizon subsamples were analysed for total nitrogen, nitrogen mineralization rate (Keeney 1982, Dorich and Nelson 1983) and percentage organic carbon (Nelson and Sommers 1975) since the major pools and dynamics of these elements occur in the upper soil layer.

The methods of analysis of these soil data are presented in chapter 4 where the development of available nutrient indices is discussed.

2.3 COLLECTION OF CLIMATE DATA

The climate data for each sampling region were summarised in climate diagrams after Walter and Leith (1969). The water balance at each site was modelled. The modelling procedure is presented in chapter 3 where the development of plant available moisture indices is discussed.

2.3.1 ESTABLISHING THE WATER BALANCE MODEL PARAMETERS

2.3.1.1 Geographical data

Altitude (m) and latitude and longitude (degrees and minutes) was determined for each site.

2.3.1.2 Climate data

Mean monthly rainfall (mm) and mean monthly maximum and minimum temperature (°C) data were extracted from Weather Bureau (1988) records. These data were collected from the weather station with the most complete records that was closest to the sites in each sampling region (Appendix 1 a). Fifty year sequences of daily rainfall (mm) were generated using the rainfall simulation model of Zucchini and Adamson (1984). The weather stations from which records were used in the simulations and the approximate distance and direction of these stations from each site are listed in Appendix 1 b and c.

Daily potential evapotranspiration (PET) was estimated from latitude and mean maximum and minimum temperature using Linacre's equation (Linacre 1977).

2.3.1.3 Soil data

The number of horizons and the depth (mm) of each was recorded at each site. Bulk density, percentage organic carbon and stone content was measured for the A-horizon and estimated for lower horizons based on the soil profile descriptions.

The soil water content at field capacity (~ 0.02 MPa), wilting point (~ 1.5 MPa) and air dry (~ 10 MPa) was estimated for each horizon using a curve fitting procedure, based on empirical relationships published by Hutson (pers. comm.). One of the variables required for the estimation of soil water content was the saturated hydraulic conductivity in the vadose zone. This was measured *in situ* at each site (Amoozegar 1988, submitted). An estimate of the hydraulic conductivity of the bottom boundary of the profile was required. This estimate ranged from 0 mm/day for an impermeable bottom boundary, such as bedrock, to 500 mm/day for a totally permeable bottom boundary, such as deep sand.

2.4 COLLECTION OF VEGETATION DATA

2.4.1 WOODY VEGETATION

2.4.1.1 Field sampling

Prior to sampling, the woody vegetation at all sites except Rooipoort sites 10 and 11, where only shrub vegetation occurred, was stratified into two height classes, (tall and short). The decision to stratify was based on the range in height of the woody vegetation at each site. Cut-off heights between tall and short classes ranged from 1.5 m to 2.5 m. The woody vegetation was sampled by measuring the distance from a 100 stratified points to the nearest plant, and from that plant to its nearest neighbour (two-distance data). Points were located using transects x m long and y m apart with x and y values varying according to the horizontal structure of the vegetation, such that no woody individual was measured twice.

A total of 240 woody individuals were measured at each site, (120 points and 2 plants per point for unstratified vegetation and 60 points with 2 tall and 2 short plants per point for stratified vegetation). The area over which woody plants were measured at each site was used to delimit the bounds of the site and all other vegetation data and soil data were collected within these bounds.

The species, basal circumference (cm), height (m) and canopy dimensions (m) (long and

short axes) of each nearest plant and nearest neighbour were recorded. Life history features were noted.

2.4.1.2 Floristic features

Appendix 4 contains a list of all the species that were sampled in this study. A list of the species at each site is contained in Appendix 2 a-s. Nomenclature for dicotyledons follows Gibbs-Russell, Welman, Retief, Immelman, Germishuizen, Pienaar, van Wyk & Nicholas (1987). The woody plant families (following Gibbs-Russell *et al* 1987) that occurred at the sites are listed in Appendix 3. The woody plant species at each site were grouped into families (Appendix 2 a-s).

2.4.1.3 Structural features

A conditioned distance method (Cox 1976) was used to estimate woody plant density (number of plants per hectare) using the two-distance data. This method provided a robust estimator minimally biased over a range of distribution patterns from regular through random to clumped. Mean woody density per species and per site was estimated (Appendix 2 a-s).

Woody basal area per species and per site (m^2/ha) was estimated from the mean area per individual multiplied by the density of that species (Appendix 2 a-s). Equivalent basal areas of multi-stemmed species were calculated from the number and size of stems per individual.

Mean plant height (m) per species and per site was estimated from field measurements. Mean maximum height at each site was also determined (Appendix 2 a-s).

Percentage canopy cover (c) was estimated from measurements of the major (a) and minor (b) canopy axes using the equation $c = ab(\pi/4)$ where $\pi = 3.14$ (Appendix 2 a-s).

The vertical distribution of woody biomass at each site was stratified into browse height classes based on the heights at which common browsers feed. The classes were 0 to 0.5 m (duiker), 0.5 to 1.5 m (impala), 1.5 to 2.0 m (kudu), 2.0 to 6.0 m (giraffe) and > 6.0 m

too tall for browsing. The browse volume (m^3) in each browse height class per species and per site was calculated using height and percentage canopy cover data, assuming the plant to be cylindrical (Appendix 2 a-s).

2.4.1.4 Functional features

Functional data were mainly collected from a review of the literature but also from field observations and discussions with experienced persons. The functional features chosen (Table 2.2) were based on those used in other studies with a functional approach (e.g. Knight and Loucks 1969, Werger and Sprangers 1982), and on features currently considered important in savannas (e.g. Huntley 1982, Frost *et al* 1986). It was not possible to obtain information on every variable for every species and consequently a subset of the functional features with the most complete data sets were used. Leaf duration, leaf type, leaf size, spinescence, and an estimate of palatability (Table 2.2 a-e) were assessed in relation to plant available moisture and available nutrient gradients.

Information on leaf duration (Table 2.2 a) was obtained from sources such as Coates Palgrave (1977) and van Wyk (1988).

Leaf type (Table 2.2 b) (simple or compound) was recorded in the field.

The average range in leaf size (Table 2.2 c) of each species was determined from sources such as Coates Palgrave (1977) and van Wyk (1988). These average values were used to assign each species to one of five leaf size categories, based on those given in Gillison (1970) (Table 2.2).

The occurrence and type of spinescence (thorns or spines) was noted in the field. The degree of spinescence of each species was estimated using a prickliness rating devised by Cooper and Owen-Smith (1986) based on a combination of the sharpness and robustness of the prickles (Table 2.2 d).

Table 2.2 Woody plant functional attributes. The numbers indicate the numerical code for each attribute class. The attributes of each species are listed in Appendix 4.

(a) Leaf duration (leaf dura)	(b) Leaf Type	(c) Leaf Size	(d) Spinescence (Spin) (Type)
0 unknown	1 compound	1 leptophyll <25 mm ²	1 unarmed t thorns
1 deciduous	2 simple	2 nanophyll 26-225 mm ²	2 very low s spines
2 semi deciduous	3 3 or 5 foliate	3 microphyll 226-2025 mm ²	3 low
3 evergreen		4 notophyll 2026-4500 mm ²	4 intermediate
		5 mesophyll >4501 mm ²	5 high
			6 very high
(e) Palatability (Pala)	(f) Growth Rate (Grow rate)	(g) Cold & Frost (Cold)	(h) Fire
0 unknown	0 unknown	0 unknown	0 unknown
1 palatable	1 fast	1 resistant	1 resistant
2 partially palatable	2 intermediate	2 sensitive	2 sensitive
3 unpalatable	3 slow	3 intermediate	3 intermediate
(i) Drought (Drou)	(j) Reproduction (Repr)	(k) Parts eaten (plus leaves)	(l) Fruit Type
0 unknown	0 unknown	0 unknown	0 unknown
1 resistant	1 from seed	1 fruit or pod	1 dehiscent pod
2 sensitive	2 not from seed	2 flower	2 indehiscent pod
3 intermediate	3 from shoot	3 root	3 fleshy
	4 not from shoot	4 gum	4 capsule
	5 coppice	5 bark	5 winged
		6 litter	6 other

A rough estimate of palatability of each species was made. The species were classed as palatable, partially palatable (if recorded eaten in some areas and not in others) and unpalatable (if recorded rarely or never eaten) (Table 2.2 e). The palatability estimates were based on data from a number of sources e.g. Dunham (1980 a & b), Pellew (1984) and Owen-Smith & Cooper (1987).

The functional features scored for each woody species are presented in Appendix 4.

2.4.2 HERBACEOUS VEGETATION

2.4.2.1 Field sampling

The herbaceous layer was sampled using the same two-distance method described for woody plants but within a smaller area. A total of 240 grass and 240 forb individuals were measured at each site. The site was subjectively quartered and 30 points were sampled in each quadrant with 2 grass and 2 forb individuals, (nearest plant and nearest neighbour of each), measured at each point. Both under and between canopy areas were sampled, and this distinction was recorded for each point.

Grass species, tuft basal circumference (cm), tuft height (m), and inflorescence height (m) and forb species and plant height (m) were recorded. Life history features were noted.

2.4.2.2 Grass floristic features

Appendix 6 contains a list of all the species that were sampled in this study. A list of the species at each site is contained in Appendix 5 a-s. Nomenclature for monocotyledons follows Gibbs-Russell, Reid, van Rooyen & Smook (1985). The grass species represented three different subfamilies (Table 2.3 n) and five different tribes (Table 2.3 o) (following Gibbs-Russell, Watson, Koekemoer, Smook, Barker, Anderson & Dallwitz 1990). The subfamily and tribe to which each species belongs is indicated in Appendix 6.

2.4.2.3 Grass structural features

Grass density (number of plants per hectare) per species and per site was estimated as for the woody vegetation (Appendix 5 a-s).

Grass basal area ($\text{m}^2/100\text{m}^2$) per species and per site was estimated from basal circumference measurements (Appendix 5 a-s).

Mean plant height (m) per species and per site and mean maximum height (m) per site were

Table 2.3 Graminoid functional attributes. The numbers indicate the numerical code for each attribute class. The attributes of each species are listed in Appendix 6.

(a) Phenology (phen)	(b) Physiology (phys)	(c) Growth Form (gfor)	(d) Reproduction (repr)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Annual	1 C3	1 Tufted	1 Obligately vegetative
2 Biennial	2 C4 NADP-ME (Malate)	2 Stoloniferous	2 Vegetative & sexual
3 Perennial	3 C4 NAD-ME PEK-CK (Aspartate)	3 Rhizomatous	3 Obligate sexual
4 Facultatively perennial		4 All forms	
		5 Tufted - stoloniferous	
		6 Tufted - rhizomatous	
		7 Stoloniferous - rhizomatous	
(e) Seed size (size)	(f) Seed number (no.)	(g) Seed dispersal (disp)	(h) Grazing response (graz)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Small	1 Many	1 Awned	1 Decreaser
2 Medium	2 Average	2 Not awned	2 Increaser I
3 Large	3 Few	3 Barbed	3 Increaser II
		4 Plumed	4 None of above
(i) Summer Palatability		(j) Winter Palatability (wint)	(k) Successional status (succ)
Early (earl)	Late (late)		
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Unpalatable	1 Unpalatable	1 Unpalatable	1 Early-successional
2 Low	2 Low	2 Low	2 Mid-successional
3 Intermediate	3 Intermediate	3 Intermediate	3 Late-successional
4 High	4 High	4 High	4 Anywhere
(l) Fire response (fires)	(m) Fuel production potential (fuel)	(n) Subfamily (sfam)	(o) Tribe (trib)
0 Unknown	0 Unknown	0 Unknown	0 Unknown
1 Increaser	1 one (low)	1 Arundinoideae	1 Aristidaee
2 Decreaser	2 two	2 Chloridoideae	2 Pappophoreae
3 Unchanged	3 three	3 Panicoideae	3 Chlorideae
4 Unchanged or increaser	4 four		4 Paniceae
	5 five		5 Arundinelleae
	6 six		6 Andropogonacae
	7 seven		
	8 eight		
	9 nine (high)		

estimated from field measurements (Appendix 5 a-s). Because of prevailing drought conditions in the far Northern Transvaal at the time of sampling, (February 1989), a true reflection of sward height could not be obtained. Thus Langjan sites 12 and 13 and Messina site 14 were excluded from data analyses and interpretation that involved plant height.

A grass volume index (m^3/ha) was calculated for each species and each site (except sites 12, 13 and 14), as the product of basal area and height data (Appendix 5 a-s).

2.4.2.4 Grass functional features

Grass functional data were collected from a review of the literature, from field observations and discussions with field staff. The functional features were chosen on the same basis as for the woody vegetation. In comparison with woody vegetation, there was a large amount of literature available on grass functional features and of those chosen only fire response was excluded from the analyses owing to paucity of data (Table 2.3). A lack of data on the response of grasses to fire is mentioned by several of the contributing authors in Booysen and Tainton (1984).

Grazing response (Table 2.3 h) refers to the way in which species respond to herbivory. Decreaser species tend to decrease in abundance when the veld is under or over utilised. Increaser I species tend to increase when the veld is under utilised. Increaser II species tend to increase when the veld is overutilised.

Seed dispersal (Table 2.3 g) refers to the structure of the seed coat of a species that relates to its method of dispersal. The class 'non-awned' refers to seeds that do not have any dispersal structures.

Because grass palatability (Table 2.3 i & j) is known to vary seasonally, the palatability of each species during the early growing season, late growing season and in winter was estimated.

Successional status (Table 2.3 k) refers to the habitat condition under which the species are

commonly found. Early successional species were considered to be those common to disturbed habitats and late successional species common to undisturbed habitats.

The estimate of the fuel production potential (Table 2.3 m) for each species was based on that derived by Trollope, Potgieter & Zambatis (1989) for key grass species in the Kruger National Park.

The grass functional data were collected from a number of sources including Chippindall (1955), Tainton, Bransby & Booysen (1976), Ellis, Vogel and Fuls (1980) and Gibbs Russell *et al* (1990).

The functional features scored for each grass species are presented in Appendix 6.

2.4.2.5 Forbs

The forbs at each site were considered as a single functional group. No consideration was given to forb species composition or to the functional features of individual species. The reasons for this were time constraints on the identification of forb species and the paucity of forb functional in the literature.

Forb density (plants per hectare) at each site was estimated in the same way as grass density (Appendix 7).

Mean forb height (m) and mean maximum height (m) were estimated from field measurements (Appendix 7).

2.4.3 END OF SEASON SAMPLING

Because vegetation was sampled throughout the growing season, changes in floristic and structural characteristics of the herbaceous layer were anticipated as a consequence of seasonal growth. In order to assess these seasonal effects, the herbaceous vegetation at Mkuzi sites 1, 2 and 3, sampled at the beginning of the growing season (October and November 1988), were resampled at the end of the growing season (May 1989) (Appendix

8 a-d). Only the herbaceous vegetation was resampled since the woody vegetation was expected to show no significant change over one season.

2.5 ANALYSIS OF VEGETATION DATA

The vegetation data were analysed in three ways.

(1) Structural and functional features were related to the gradients of plant available moisture (PAM) and available nutrients (AN) individually using a Pearson's product-moment correlation (SAS 1985).

(2) The relationships between both PAM and AN and the floristic, structural and functional characteristics of the vegetation were analysed using Detrended Correspondence Analysis (DCA) (CANOCO package, ter Braak 1988). CANOCO enables environmental variables to be analysed concurrently with the vegetation data. The major vegetation gradients were extracted by DCA and related to indices of PAM and AN. (The development of these indices is detailed in chapters 3 and 4). Detrending was by second order polynomials and sample scores were mean weighted species scores.

(3) The TWINSpan algorithm (Hill 1979) was used to obtain hierarchical classifications of the floristic, structural and functional data. The ordination was used to evaluate the assignment of sites to groups by TWINSpan, and where warranted, reassignments were made to produce a more meaningful classification of vegetation in terms of environmental relations. Five cut levels were used (0.00, 0.37, 0.92, 1.85, 3.70). All other default options were used.

Species with less than four occurrences were excluded from all the analyses. Rare woody plant and graminoid species are indicated in Appendix 4 and 6 respectively.

The woody plant and herbaceous communities were analysed separately. Unless otherwise stated, percentage basal area (log transformed) was the abundance measure used in the

analyses of both the woody plant and graminoid vegetation.

2.5.1 FLORISTIC CLASSIFICATION

2.5.1.1 Woody Vegetation

Woody plant floristic features were considered at three taxonomic levels. Firstly, species data were ordinated and classified to determine how the sites were floristically related to one another and to PAM and AN. Secondly, the woody plant families were ordinated and classified. Thirdly, following the hypothesis that species of the Mimosoideae occur predominantly in arid and nutrient rich areas and members of the Caesalpinoideae and Combretaceae in moist and nutrient poor areas (Huntley 1982), the sites were ordinated and classified on the basis of the abundance of these three families.

2.5.1.2 Herbaceous vegetation

Graminoid floristics were also considered at three taxonomic levels. Firstly, sites were analysed on the basis of species composition, secondly, on the basis of the tribes at each site and thirdly on the basis of the subfamilies represented at each site.

2.5.2 STRUCTURAL TRENDS AND CLASSIFICATION

2.5.2.1 Woody vegetation

Trends in woody plant structural features (total density, total basal area, % canopy cover, mean height, mean maximum height and total browse volume) at each site were compared with PAM and AN gradients. The values for each structural variable for both the short and tall woody plants at each site were combined for these analyses. The prevalence of these features at each site was plotted on the PAM-AN plane. The structural features of rare species were excluded. Structural features were also compared with soil stone content and profile depth since these are physical properties of the substrate that could influence woody vegetation structure independently of PAM and AN.

Community browse volume distribution profiles were compared and sites were grouped according to similarities in the pattern of vertical distribution of woody biomass. Browse volume distribution data were ordinated and classified and browse volume distribution groups were plotted on the PAM-AN plane.

A sites by standardised structural attributes matrix was ordinated and classified. The sites were also classified using existing structural classification systems of Pratt, Greenway and Gwynne (1966), Bredenkamp and Theron (1985), Edwards (1983) and Grunblatt, Ottichilo and Sinange (1989). These classifications were compared with indices of PAM and AN.

2.5.2.2 Herbaceous vegetation

Grass structural features (density, basal area, volume index, mean height and mean maximum height) and forb structural features (density, basal area, mean height) at each site were compared with PAM and AN gradients. The prevalence of species at each site were also plotted on the PAM-AN plane. Only the structural features of non species were used.

A sites by standardised grass structural attributes matrix was ordinated and classified. The sites were also classified using existing structural classification systems of Pratt, Greenway and Gwynne (1966), Edwards (1983) and Grunblatt, Ottichilo and Sinange (1989). These classifications were compared with indices of PAM and AN.

2.5.2.3 STRUCTURAL RELATIONSHIPS OF THE WOODY PLANT AND HERBACEOUS COMMUNITIES

These structural relationships were investigated using a Pearson's product-moment correlation (SAS 1985). The variation in woody plant to graminoid biomass ratio over the range of sites was compared with the PAM and AN gradients. The relationship between graminoid and forb density and PAM and AN was investigated.

2.5.3 FUNCTIONAL TRENDS AND CLASSIFICATION

2.5.3.1 Woody Vegetation

Leaf duration, leaf type, leaf size, palatability and degree of spinescence were compared with PAM and AN gradients. Where appropriate, these functional features were ordinated and classified individually and the functional trends were plotted on the PAM-AN plane.

Leaf duration, leaf type, leaf size, palatability and degree of spinescence were ordinated and classified together to produce a woody plant functional classification in the plane of PAM and AN.

2.5.3.2 Herbaceous vegetation

Phenology, physiology, growth form, mode of reproduction, fuel production potential, successional status, grazing response and palatability were compared with PAM and AN gradients. Where appropriate, these functional features were ordinated and classified individually and the functional trends were plotted on the PAM-AN plane.

Physiology, growth form, mode of reproduction, fuel production potential, successional status, grazing response, palatability and seed characteristics were ordinated and classified together to produce a graminoid functional classification in the plane of PAM and AN.

2.5.4 HYPOTHESES

The floristic, structural and functional results of this study were compared with current hypotheses of savanna composition, structure and function.

2.5.6 COMPARISONS OF THE CLASSIFICATIONS

The floristic and functional classifications were compared in three ways. Firstly, the floristic groupings derived from the classification of woody plant and graminoid species composition

were compared, secondly, the functional groupings derived from the classification of woody plant and graminoid functional classifications were compared and thirdly, the woody plant and graminoid floristic classifications were compared with the functional classifications.

3.0 PLANT AVAILABLE MOISTURE INDICES

3.1 INTRODUCTION

The aim of this chapter is to present and discuss the development of biologically meaningful climatic indices for describing the availability of water to savanna plants. A biologically meaningful index should be based on the interpretation of climate as it relates to plant growth. For the purposes of this study, plant available moisture (PAM) is defined as water that can be taken up by a plant and used in physiological processes.

It is generally accepted that broad scale vegetation distribution and structure, and basic features of plant form are determined primarily by the general levels and mean seasonal patterns of rainfall and temperature (Walter 1979, Box 1981). On this basis there have been various approaches to classifying or indexing climate in relation to vegetation. These approaches have been designed for use at different spatial scales and vary in the complexity and type of data required.

Plant geographers have related climate maps to vegetation maps in order to describe the relationship between climate and vegetation distribution. Climatic models have been devised for mapping vegetation at the global scale. Two such classic classification systems, based on rainfall and temperature statistics, are those developed by Köppen (1918) (as quoted in Schulze 1947) and by Thornthwaite (1948). Using the Thornthwaite system, for example, all major tropical savannas are classified in the category of medium precipitation, high temperatures and wet summers and dry winters. Belsky (1991) refers to two other global models, viz. one based on rainfall, temperature and evapotranspiration (Holdridge 1947) and the other based on rainfall and temperature (Whittaker 1975). Both of these models were devised to determine the climatic boundaries of the major vegetation types of the world. Both these models characterized tropical savannas as having a low to moderate rainfall and a high mean annual temperature. There have been more recent approaches to describing the relationship between climate and vegetation at the global scale. Box (1981), for example, developed an empirical model which relates the world's geographically most important plant

life forms to eight macroclimatic variables associated with plant energy and water budgets.

Several attempts have been made to describe the relationship between climate and vegetation at the regional scale. Certain bioclimatic systems have been applied to southern African savannas and are reviewed in Schultze and McGee (1978). Other systems include Phillips' bioclimatic units of southern Africa (Phillips 1983) and Rutherford and Westfall's moisture matrix of a summer aridity index and winter concentration of precipitation (Rutherford and Westfall 1986). These bioclimatic systems are useful for defining biomes and for comparing regional climatic differences between biomes but not for within biome comparisons (Huntley 1982). More detailed climatic indices are needed for this purpose.

The interactions of energy and water that determine the effective environment of plants can be described by climatic water balance modelling (Stephenson 1990). One of the widely used approaches to water balance modelling is that of Thornthwaite and Mather (1955). This approach considers monthly precipitation and evaporative demand but does not provide a biologically meaningful index. A water balance model that does provide a biologically meaningful index has been used to define the biomes of southern Africa (Ellery, Scholes and Mentis 1991). The index derived from this model indicates the length of the growing season in days per annum, i.e. the seasonal duration of plant available water. These water balance models are useful for estimating water deficit, storage and excess but do not include the modifying effects of soil properties.

Soil type and plant-water relations reduce the effectiveness of rainfall (Johnson and Tothill 1985). It is necessary, therefore, to include the modifying effects of soil properties for detailed water balance modelling. Loucks (1962) and Waring and Major (1964) modelled available moisture on the basis of soil properties such as water holding capacity, storage and runoff, where available moisture in the entire profile was expressed as a percentage of the storage capacity. Detailed water balance models that have been used in savannas include WATBAL (Keig and McAlpine 1974) and SAVANNA (Scholes 1987).

For the purposes of this study, a water balance model was developed that would provide a biologically meaningful index, detailed enough to use at the local scale. The model described

in this study estimates the length of the growing season in days per annum and is a modification of Ellery *et al* (1991) to include the effects of soil properties. This model includes parameters suggested by Frost *et al* (1986) such as air temperature, rainfall, soil texture and seasonality.

This chapter partly addresses study objective 1. The water balance modelling procedure is presented in section 3.2. Section 3.3 details the climatic characteristics of each of the savanna regions sampled and mean annual rainfall and two indices derived by water balance modelling are compared. The results are discussed in section 3.4.

The methods of data collection for the water balance modelling procedure are detailed in chapter 2, section 2.2 and 2.3. The sites are referred to by number as in Table 2.1.

3.2 WATER BALANCE MODELLING

A water balance model (Fig. 3.1 a,b,c) has been developed for the estimation of the duration of the growing season in days per annum (Gdays) based on daily rainfall sequences and reference evaporation. The duration of the growing season is the mean number of days per annum on which potential evapotranspiration is fully satisfied by available soil water (Ellery *et al* 1991). The mean number of days per annum on which sufficient water is available to permit unrestricted plant growth was considered a biologically meaningful index of water availability. Expressing the concept in terms of days rather than a dimensionless ratio of rainfall to evaporation helps to make its biological meaning more intuitive (Ellery *et al* 1991).

The model also calculates the mean temperature on the days when water is available. Temperature can act on savannas in two ways, as a regulator of growth rate (growth temperature or wet day temperature) and as a low temperature stress (no-growth temperature or dry day temperature). Wet day temperature is the mean temperature on days when water is available for growth, giving an indication of energy supply. Dry day temperature is the temperature on days when water is not available for growth and hence a measure of cold

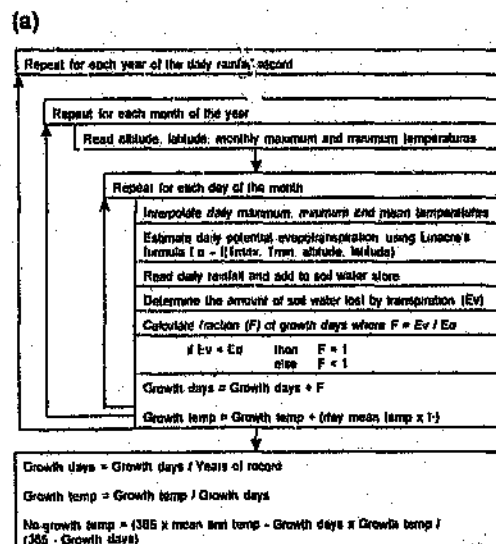
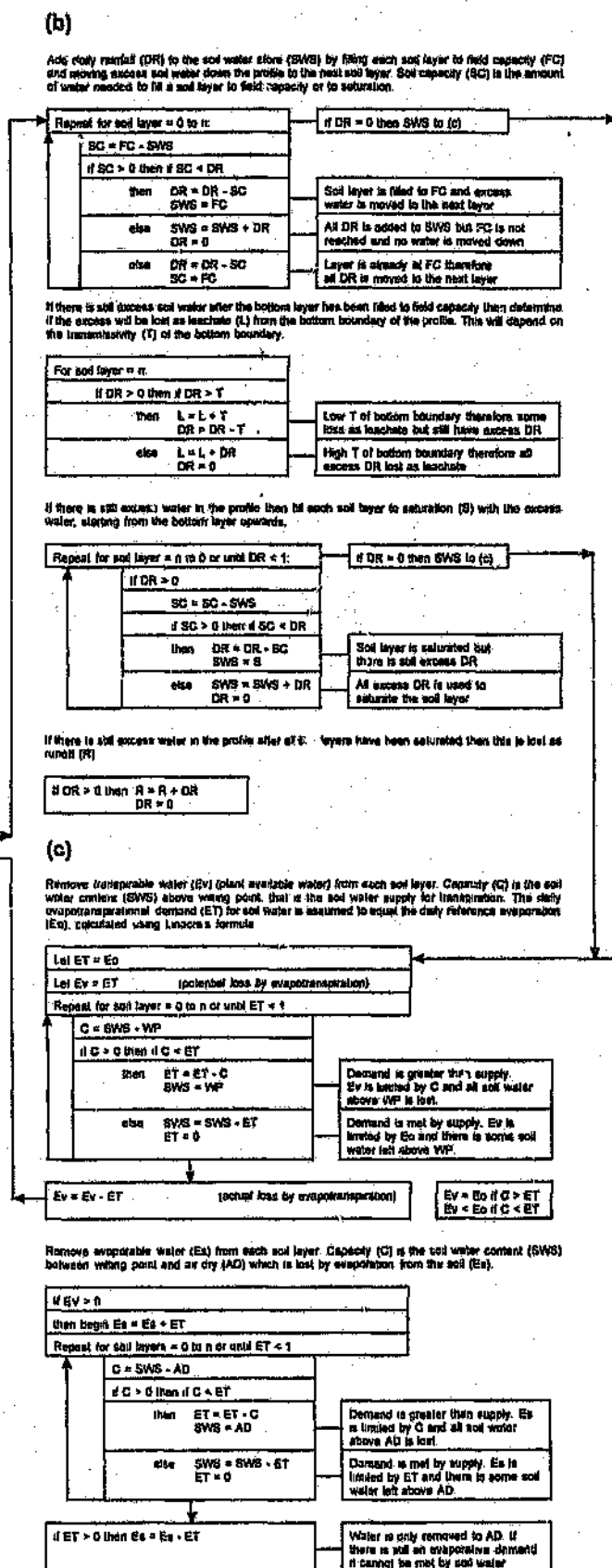


Figure 3.1 Schematic diagram of the water balance model used to generate indices of growth days, growth temperature and no growth temperature (modified from Ellery *et al* 1991). Model input variables are summarised in Table 3.1. Fig. 3.1 (a) illustrates the procedure for the bucket water balance model. Fig. 3.1 (b) and (c) illustrate the additional procedures used for the soil water balance model to include the effects of soil properties on the water balance. Fig. 3.1 (b) shows how daily water is added to the soil water store. Fig. 3.1 (c) shows how water is removed from the soil water store.



stress, mostly during the dry season (Ellery *et al* 1991).

The model can be used in two forms, a simple 'bucket' form and a more complex 'soil' form. The bucket water balance model is useful for broad scale modelling, for example at the biome level (Ellery *et al* 1991). This model does not take the effects of soil properties into account but is useful if detailed soil data are not available. The more complex soil water balance model is designed for modelling at a smaller spatial scale, for example at the landscape or patch scale. The soil water balance model includes soil properties (Table 3.1) which modify the fluxes and pool sizes in the hydrological system. The inclusion of soil information in the model facilitates a more detailed estimation of what happens to soil moisture in terms of evapotranspiration, leakage, runoff and storage (Fig. 3.2).

Table 3.1 Data required for the soil water balance model. Input variables 1 to 8 are required for the bucket water balance model. Model input variables are discussed in chapter 2, section 2.3.

1.	Site description
2.	Number of years of data from Weather Bureau records (for information only)
3.	Station latitude (and longitude, for information only)
4.	Station altitude
5.	Mean monthly rainfall (mm) (for information only)
6.	Mean monthly maximum temperature
7.	Mean monthly minimum temperature
8.	Daily precipitation in tenths of a mm (output from Genrain (Zucchini & Adamson 1984))
9.	Number of soil horizons and saturated hydraulic conductivity of bottom boundary
10.	Depth, bulk density, stone content and organic carbon for each horizon
11.	Field capacity (-0.02 MPa), wilting point (-1.5 MPa) and air dry (-10 MPa) water content per horizon
12.	Initial water content (volumetric proportion) for each horizon

The model output includes monthly and annual estimates of relative humidity, potential evapotranspiration (PET) and number of growth days. Mean monthly and annual rainfall is calculated from the simulated daily rainfall data for comparison with the Weather Bureau

records of mean monthly and annual rainfall. The model also provides mean annual estimates of transpiration, evaporation, runoff, leaching and storage and estimates of annual wet day temperature and dry day temperature.

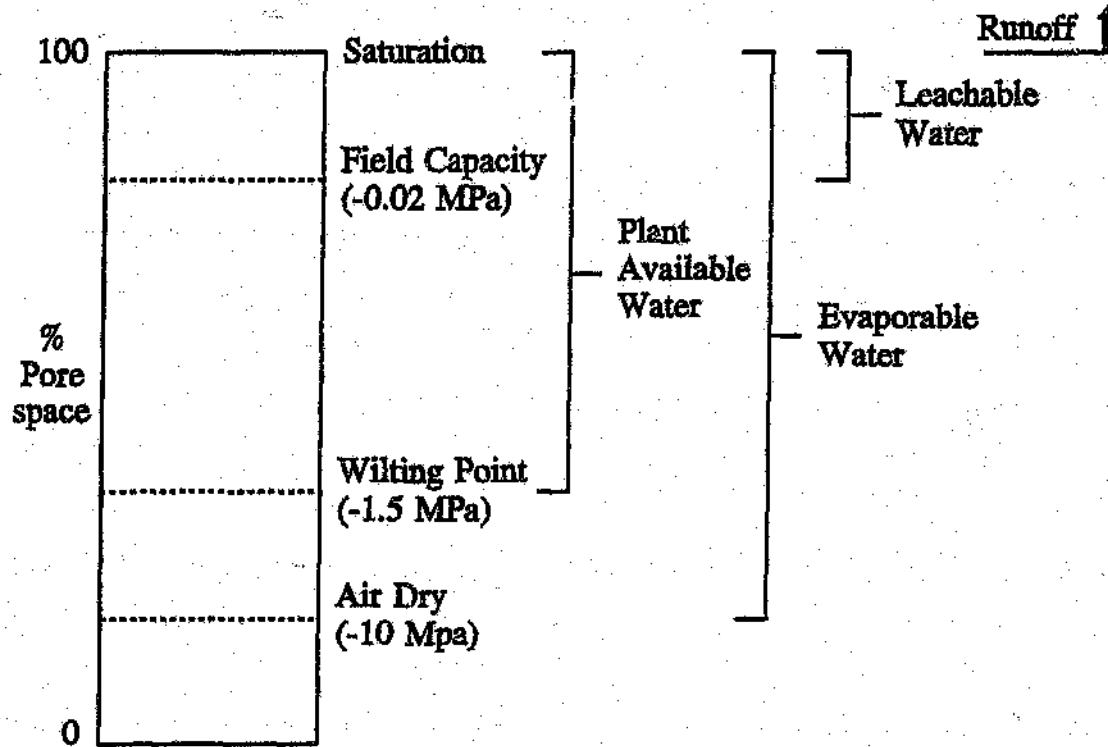


Figure 3.2 Schematic diagram showing the ways in which water at different water potentials is removed from a layer of soil.

3.3 RESULTS

3.3.1 CLIMATIC CHARACTERISTICS

All the areas sampled fell into Köppen's arid zone steppe climatic group (hot, dry steppe with a winter dry period) and Thornthwaite's semi-arid warm steppe climatic group (Schulze 1947).

There was a unimodal seasonality of both rainfall and temperature in all the savannas sampled with wet, warm to hot conditions alternating with dry, warm to cool conditions (Fig. 3.3). The duration of the rainy season, estimated as the number of months during which mean monthly rainfall exceeded 50 mm, ranged from three to six months (Fig. 3.3).

According to Huntley's definition of savanna climates (Huntley 1982) all the areas sampled, except Pretoriuskop, were semi-arid, with rainfall < 650 mm pa and seven or more dry months. Walter (1971) used a rainfall threshold of 600 mm/ann. to distinguish between semi-arid and humid savannas and on this basis, the Nylsvley and Pretoriuskop areas would be considered to be humid. Johnson & Tothill (1985) emphasise the relative lengths of the wet and dry seasons for distinguishing humid (dry period of 2.5 to 5 months) and arid (dry period of 5 to 7.5 months) savannas. On this basis, all the savannas sampled in this study would be considered to be arid.

The seasonal variation in temperature was similar for all the areas sampled (Fig. 3.3). Similarities in growth temperature and no-growth temperature were also evident (Table 3.2). Mid-winter frosts occur at Nylsvley (Frost 1987) and at Rooipoort (Berry, M. pers. comm.) but are uncommon in the other savanna areas sampled (Venter and Gertenbach 1986, Goodman, P.S. pers. comm.). The regular occurrence of frost may be linked to the higher altitude of Rooipoort (1198 m) and Nylsvley (1080 m) in comparison with the other areas (Fig. 3.3) (Huntley 1982, Walker 1985).

The estimated reference evaporation was higher than the mean rainfall for all months, indicating a year round monthly water deficit (Table 3.2).

3.3.2 PLANT AVAILABLE MOISTURE INDICES

Three PAM gradients were derived (Fig. 3.4). The first consisted of mean annual rainfall figures calculated from daily rainfall data. The second gradient consisted of the Gdays index derived by the bucket water balance model, and the third gradient consisted of the Gdays index derived by the soil water balance model. These PAM gradients were compared and their suitability as indices of PAM considered.

3.3.2.1 Gradients based on mean annual rainfall and the bucket water balance model index

A comparison of the mean annual rainfall and bucket PAM gradients illustrates the modifying

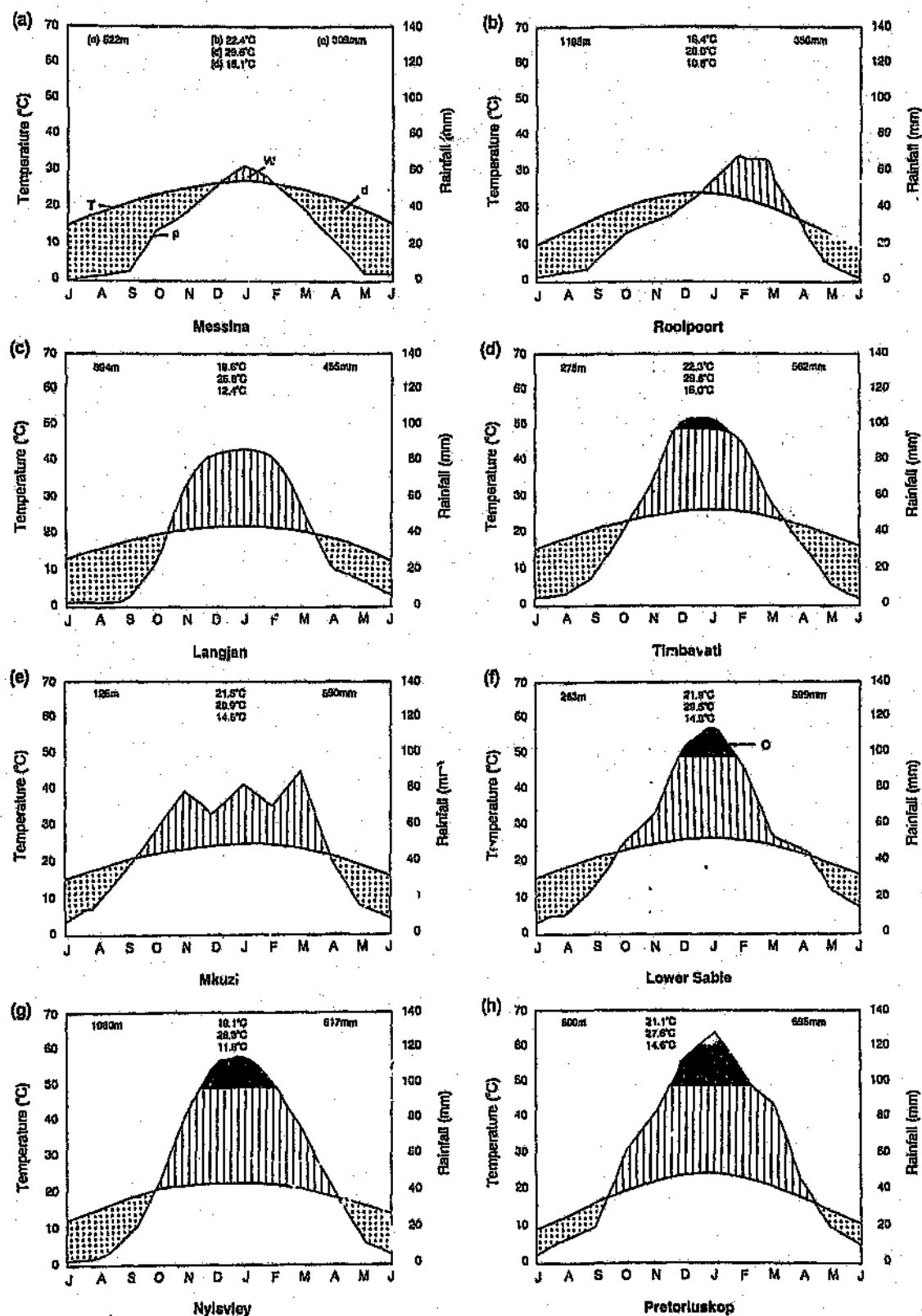


Figure 3.3 Climate diagrams for each of the savanna areas sampled, drawn after Walter & Leith (1960). T = mean monthly temperature in °C; p = mean monthly precipitation in mm (from 50 year simulated rainfall sequences); w = wet season; d = dry season; o = mean monthly rainfall > 100 mm. (a) = altitude; (b) = mean annual temperature; (c) = mean maximum temperature; (d) = mean minimum temperature; (e) = mean annual rainfall.

Table 3.2 Growth temperature, no-growth temperature and reference evaporation (E_0 , the amount of water that would evaporate from a large body of water) for each of the rainfall areas sampled.

Location	Mean annual rainfall (mm)	Estimated annual reference evaporation (mm)	Growth temp. (°C)	No-growth temp (°C)
Messina	308	2519	25.3	22.1
Rooipoort	355	2625	25.0	21.8
Langjan	455	2332	24.3	21.5
Timbavati	562	2424	23.5	21.4
Mkuzi	590	2285	22.8	20.6
Lower Sabie	598	2446	22.4	19.2
Nylsvley	617	2393	21.6	18.5
Pretoriuskop	695	2216	21.3	18.1

effect of the energy budget on the availability of water to plants. The bucket index includes the effects of altitude, latitude and temperature (as PET) which all modify the effectiveness of rainfall, thus reflecting more realistically the amount of rainfall available to plants.

Similarities and differences in PAM between the savanna areas were more evident on the bucket gradient than shown by the distribution based on rainfall alone (Fig. 3.4).

The order of savanna areas along the two gradients was different (Fig. 3.4). Although Messina had a lower mean annual rainfall (supply of water) than Rooipoort it also had a lower PET (demand for water) (Table 3.2). Therefore, in terms of supply and demand, (bucket index), Messina had a greater availability of water and was relatively less arid than Rooipoort (Fig. 3.4). There was also a change in the order of the Mkuzi, Lower Sabie and Nylsvley areas along the bucket gradient (Fig. 3.4). Although Mkuzi received the lowest mean annual rainfall of these three areas, it also had the lowest PET (Table 3.2), thus having the greatest number of Gdays of the three areas (Fig. 3.4). Lower Sabie had the highest PET of the three areas (Table 3.2). Pretoriuskop, the area with the greatest number of Gdays,

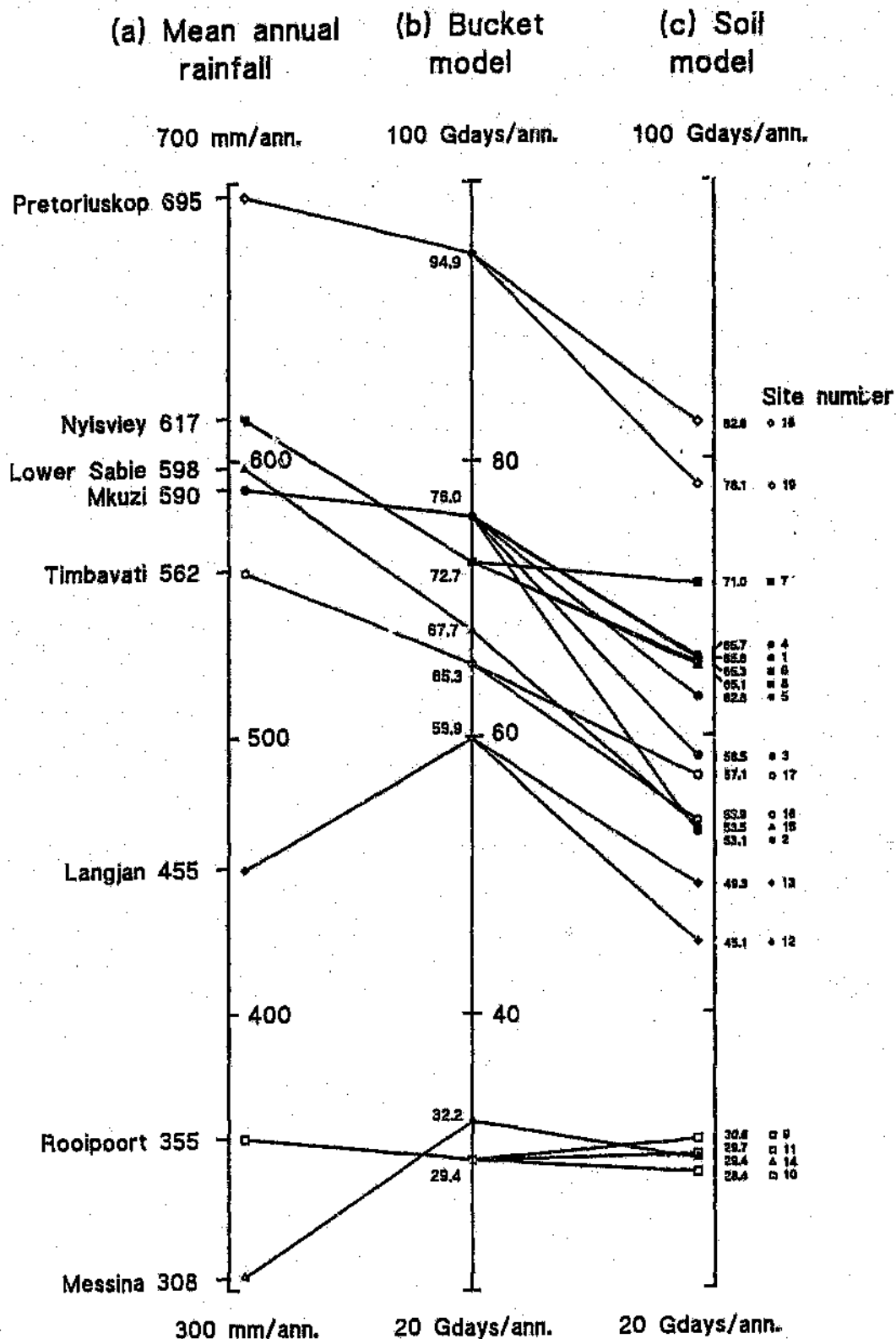


Figure 3.4 A comparison of the PAM gradients derived from (a) mean annual rainfall (mm/ann.), (b) the bucket water balance model (Gdays) and (c) the soil water balance model (Gdays). The 8 symbols on gradients (a) and (b) correspond with the 8 savanna areas sampled. The symbols on gradient (c) show which sites come from which areas. Site numbers are as in Table 2.1.

had the highest rainfall and the lowest PET of all areas sampled.

3.3.2.2 Gradients based on the bucket and soil water balance model indices

For all sites except Rooipoort 9 and 11, the soil model Gdays value was lower than the bucket model Gdays value (Fig. 3.4). This indicated that there was less water available to plants at each site than indexed for each area without consideration of the soil. Also, the range of Gdays was lower for the soil model than for the bucket model (Fig. 3.4). These results indicate the modifying effects of soil properties on the supply and demand components of the water balance.

The order of sites along the soil model gradient indicated that, because of the modifying effects of soil properties, sites in different areas could have similar amounts of PAM even though they had different water and energy budgets. This is especially obvious for Likuzi 1 and 4 and Nylsvley 6 and 8 and also for Timbavati 16 and 17 and Lower Sabie 15.

Within each rainfall region there was a trend in G days and soil texture (Fig. 3.5 a) supporting the hypothesis that for the same rainfall and energy budgets, a clayier soil is more xeric than a sandier soil (Scholes 1987). This was evident even though the fine textured soils had a higher water holding capacity than the coarse textured soils (Fig. 3.5 b). Evaporation from the soil surface on the clayey soils was higher than on the sandy soils (Fig. 3.5 c) indicating that there was less water available for plant growth and more water lost by evaporation on clay than on sandy soils in each area.

3.4 DISCUSSION

3.4.1 CLIMATIC CHARACTERISTICS

The similarities in temperature between the savanna areas suggests that the effect of temperature on vegetation is likely to be most marked via the energy budget of the water balance, rather than via a direct effect of temperature on species composition and plant

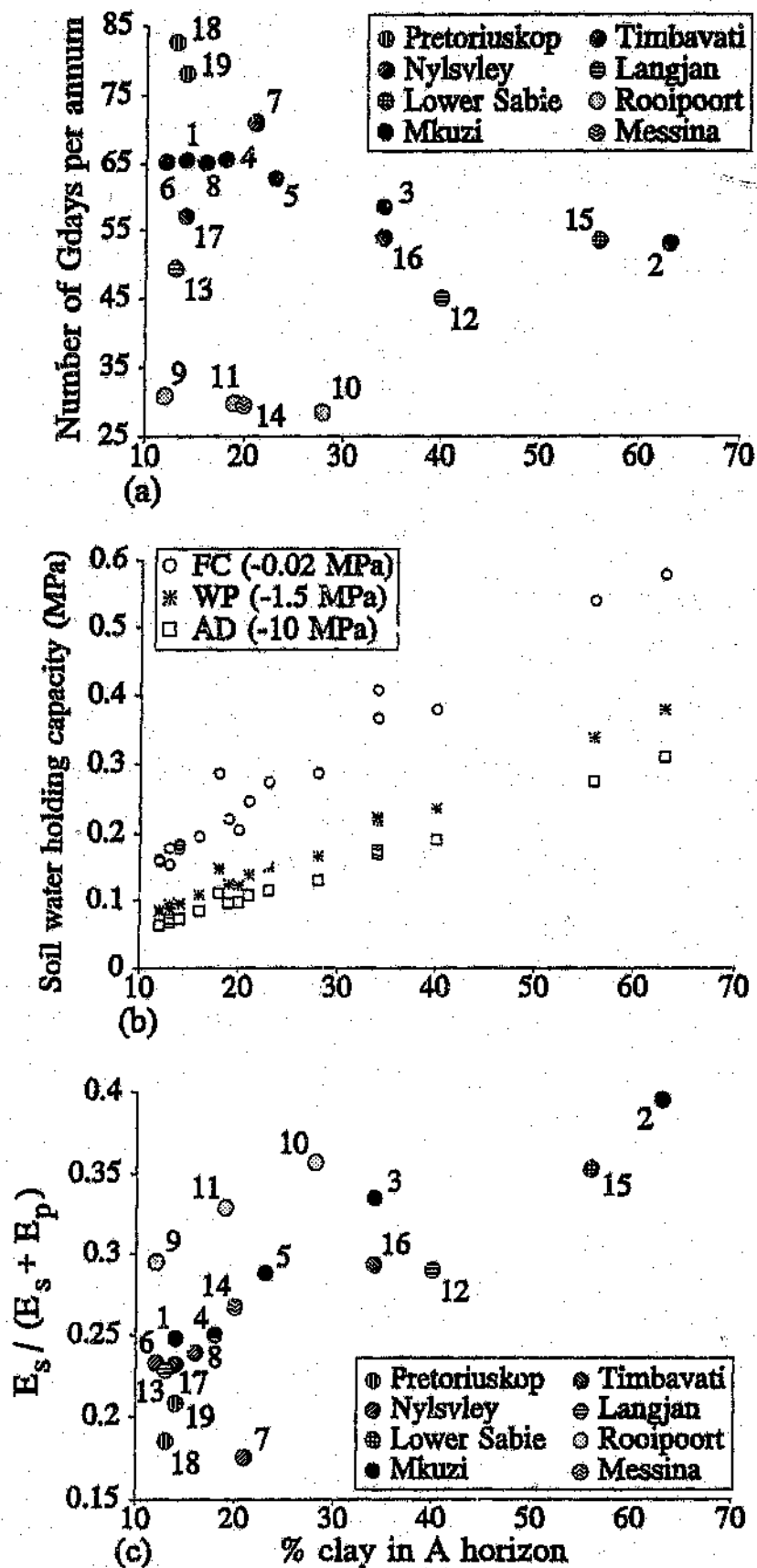


Figure 3.5 Trends in (a) Gdays, (b) A horizon soil water content and (c) the relative amount of evaporation from the soil (E_s) with soil texture. E_p refers to evapotranspiration.

productivity. This is supported by the statement that biotic characteristics of savannas in southern Africa do not reveal consistently sharp discontinuities related to thermal gradients (Huntley 1982). The apparent lack of influence of temperature within the savanna biome is contrasted with the finding by Ellery *et al* (1991) that the savanna and grassland biomes may be differentiated on the basis of dry season temperature. If temperature is having a direct effect on the vegetation it is likely to be the minimum temperature and the occurrence of frost that is important and hence would have been evident between the frosted sites (Nylsvley and Rooipoort) and the rest.

The year round monthly water deficit observed in this study is characteristic of semi-arid savannas (Walker 1985).

3.4.2 PAM INDICES

Although mean annual rainfall has been used in many studies to define climatic gradients (Seeley 1978, Rutherford 1980 and Deshmukh 1984), indices based on rainfall alone provide only a crude estimate of moisture availability. The simultaneous effects of water supply and demand are not integrated (Ellery *et al* 1991). Considering a demand component, as well, is important for deriving a biologically meaningful index. Frost *et al* (1986) considered mean annual rainfall too simple an index to adequately account for savanna floristic, structural and functional diversity and high-lighted the need for an index that integrated water and energy budgets. Mean annual rainfall is useful as a gross index of PAM, e.g. to define moisture gradients at a broad spatial scale but in order to derive a more detailed index, the PET component should be included.

The 'days of growth opportunity' index derived by the bucket model integrates both the supply-side (precipitation) and the demand-side (evaporation) of plant water relations and is therefore more robust than an index derived from rainfall or evaporation data alone. This is a simplistic model because in reality plant growth does not end abruptly when the soil dries out, but declines over a period of time. 'Growth days' as calculated will therefore be shorter than the observed growing period in the field, but should correlate well with plant productivity (Ellery *et al* 1991), since productivity also declines as water becomes limiting.

It remains an index rather than a field-verifiable measurement, since it represents the equivalent number of days where profile available water fully satisfies potential evaporation, rather than the days when the plant is physiologically active (Ellery et al 1991). An important feature of this index is that it illustrates differences in growing seasons. An index that reflects seasonality is important in savannas because all savanna regions are characterised by a marked seasonal effect (Walker 1985).

Although the bucket index provides a more realistic index of PAM than mean annual rainfall alone, it, too, is only useful at the regional scale and does not provide an index for each site.

The inclusion of the modifying effects of soil properties in the calculation of the water balance provides an index that is suitably detailed for use at the local scale. This index is biologically meaningful as it reflects the availability of moisture to plants as modified by the soil environment.

Of all the soil properties included, soil texture, depth and stone content are particularly important. Fine textured soils were more xeric than coarse textured soils for the same water and energy budgets because soil texture affects soil water holding capacity and hydraulic conductivity. Sandy soils have a lower water holding capacity because they have a larger non-capillary porosity than clayey soils. Clay soils have a more gradual slope of water potential verses water content indicating a more gradual release of water than sandy soils. Sandy soils release most of their soil water within a narrow range of potentials because of the predominance of large pores. Most of the moisture in sandy soils occurs between field capacity and wilting point and hence is available to plants. Finer textured soils have a wider range of water between field capacity and wilting point than coarser textured soils but a greater proportion of water is held at tensions below wilting point and hence is inaccessible to plants.

Evaporation from the soil surface on clayey soils is higher than on sandy soils because the higher water holding capacity in clayey soils means that a given amount of rainfall penetrates less deeply on clayey than on sandy soils. Deeper penetration and a narrower capillary fringe on coarse-textured soils conserves moisture by protecting it from evaporation (Scholes 1987). Also, the soil water held at tensions below the plant wilting point on fine textured

soils is not available to plants but still susceptible to evaporation. Knoop and Walker (1985) observed this difference between fine textured soils and sands. Soil with a high clay content experienced extended periods where soil moisture was below -1.5 MPa over the whole profile while water in the sub-soil layers of a sandy soil was not limiting in wet years and only occasionally limiting in dry years.

The use of Zucchini and Adamson's model for generating rainfall sequences overcomes the problem that site specific long term rainfall records are often unavailable. The facility to generate long term rainfall sequences in some measure overcomes the effects of the large spatial and temporal variability of rainfall, that is characteristic of semi-arid savannas (Green 1969, Barnes and McNiell 1978).

3.4.3 USEFULNESS OF THE PAM INDICES

The choice of a suitable PAM index must be based on a number of criteria. The index must be biologically meaningful, simple to calculate and the potential for its extrapolation must be assessed, especially in the light of availability of the required data.

Mean annual rainfall provides a suitable general index of water availability. The advantages of this index are that rainfall data are available, the index does not require any calculation and it is easily extrapolated. The major problem with this index is that it provides no information on how climate relates to plant growth. The usefulness of mean annual rainfall in predictive modelling of vegetation change is limited therefore.

The index derived from the bucket model is considered to be useful at the regional scale. This index is biologically meaningful. The rainfall and temperature data required are likely to be available and hence the index has a good potential for extrapolation. One disadvantage is that the index is not simple to calculate since a modelling procedure is required.

The index derived from the soil model is biologically meaningful and detailed enough to be used at the local scale. This index yields a high degree of information but requires a fairly detailed data input (e.g. the information on soil properties) and is not simple to calculate.

The extrapolation of this index would be limited by the availability of the detailed data.

3.5 CONCLUSION

The number of growth days per annum (Gdays) derived by the soil water balance model will be used as a PAM index for the interpretation of plant floristic, structural and functional trends in relation to moisture availability. This index is considered to be biologically meaningful and to suit the scale of application and purpose of this study.

4.0 AVAILABLE NUTRIENTS

4.1 INTRODUCTION

The availability of nutrients in the soil is determined by the size of the available nutrient pool and its rate of replenishment. These factors are controlled by the mineral content and rate of weathering of the parent material, the rate of turnover of organically bound nutrients, the effective soil thickness, the ability of a soil to hold nutrients against leaching and plant demand for nutrients (Solbrig, Medina & Mott 1988). Thus soil fertility is a complex phenomenon involving interactions of climate, soil, nutrients and plants.

Plant response to nutrient availability appears to be controlled by the principle of limiting factors (Chapin, Vitousek & van Cleve 1986). Nutrient limitation is recognized by an increase in growth in response to the addition of a limiting nutrient, given that all other factors are non-limiting. This positive response will persist until the concentration of the nutrient reaches a point beyond which there is no longer an increase in plant growth. This is hypothesised to be the optimal or threshold concentration of the nutrient for plant growth and any further uptake is considered to be a luxury consumption. A continued increase in the concentration of the nutrient may result in a decrease in growth as a result of a toxicity response.

Plants need nutrients in different quantities. Nitrogen, phosphorus and to a lesser extent potassium appear to be the nutrients that most frequently limit plant productivity in natural ecosystems (Chapin *et al* 1986, McLendon & Redente 1991). Lopes and Cox (1977) reported significant correlations between woody basal area per hectare and soil levels of nitrogen, phosphorus and potassium in cerrado vegetation in Brazil. Nitrogen, phosphorus and potassium have been found to limit the productivity of *Trachypogon* savannas of the Orinoco Llanos in South America (San José, Montes & Nikonova-Crespo 1991). Low availability of nitrogen and phosphorus is considered to be more limiting to plant growth than low rainfall in the southern Sahel (Breman and de Wit 1983). South African savanna soils are considered to be nitrogen, phosphorus and potassium limited (Medina 1987) with

fertilizer trials indicating that nitrogen plays a greater controlling role in plant production than phosphorus and potassium (Grunow, Pienaar and Brøytenbach 1970, Walker and Knoop 1987).

Although the availability of plant nutrients is hypothesised to be a primary determinant of savanna structure and function, there is as yet no single standard way of establishing a synthetic nutrient index for savanna soils (Solbrig 1990). There has been much debate within the forum of the Responses of Savannas to Stress and Disturbance programme as to how to index the available nutrients (AN) axis of the PAM-AN plane and several approaches have been identified (Frost *et al* 1986, Solbrig *et al* 1988). The suggested approaches encompass various degrees of complexity, both in method of determination and in the indices derived.

There are several criteria for the choice of a suitable AN index. It is very important that the soil fertility index should be ecologically meaningful. An ecologically meaningful index is one that relates soil physical and chemical properties to plant growth responses and hence reflects the interactions of climate, soil, nutrients and plants that determine plant productivity. In the development of an AN index that is generally applicable to all savanna soils, the potential for extrapolation, simplicity of calculation and the constraints imposed by the limited availability of soil physical and chemical data must be taken into account.

The availability of nutrients to plants is difficult to index in natural environments. One approach is to measure the instantaneously available pools of nutrients (Chapin *et al* 1986). This is achieved by means of soil chemical analyses. The aim would be to use variables that are easy to measure and for which data are generally available. This approach would provide simple AN indices and would help to overcome the problem of paucity of detailed soil physical and chemical data. This is a simplistic approach, however, because it does not take into account the flux of nutrients through the available pools which is as important as instantaneous pool sizes in determining the availability of nutrients to plants (Chapin *et al* 1986). Simple indices of this nature do not convey information about nutrient-soil, nutrient-nutrient and nutrient-plant interactions. One solution to this problem is to assess the usefulness of a single variable as an AN index by comparing it with indices that represent an integration of the soil-plant response, e.g. biomass production. A good correlation

between the simple and integrated indices would suggest the potential for using only the simple index.

A number of approaches have been used to provide indices that reflect the dynamic aspect of nutrient availability in natural environments. These include incubations to measure nitrogen turnover, bioassays of soil and the use of ion-exchange resins in the field (Chapin *et al* 1986).

The soil bioassay approach was suggested as a way of assessing AN in savanna soils by Solbrig *et al* (1988). Bioassays have been used elsewhere to assess the fertility of natural soils e.g. Harrison & Helliwell (1979), Olsvig-Whittaker & Morris (1982), Kinako (1983) and Gough and Marrs (1990). In these studies, soil chemical analyses were used to indicate the potential availability of nutrients while plant responses such as height, biomass production, root length, root to shoot ratio and plant tissue nutrient content were assumed to indicate actual nutrient availability. Plant responses can be used to assess the fertility of a soil assuming that a fertile soil will have physical and chemical properties that maximize nutrient uptake and plant productivity. Under controlled environmental conditions, plant responses to soils with different chemical and physical properties can be investigated. Plant responses such as biomass production are assumed to reflect the dynamics of the soil-plant interaction and consequently should provide ecologically meaningful AN indices.

A consideration of the concentrations of the most limiting nutrients is another potential approach for the development of AN indices. The availability of nitrogen, phosphorus and potassium has been used for the development of AN indices (Noble 1989) and for soil fertility assessments (Keliman 1979, Gough and Marrs 1990). Nobel (1989) used soil levels of nitrogen, phosphorus, potassium, boron and sodium to develop individual multiplicative indices for determining the influence of these elements on the productivity of agaves and cacti. This index was found to satisfactorily explain the variation in productivity of these plants with soil nutrient availability at a number of sites (Noble 1989).

For the purposes of this study, an AN index that best reflects the average condition of available nutrients at the community level will be sought. The temporal (seasonal) and

spatial (patch scale) dynamics of nutrient availability that occur within any one savanna community (Kellman 1979, Bate & Gunton 1982, Medina 1987) will not be considered.

The aim of this chapter is to present and discuss the development of potential AN indices for the quantification of the nutrient axis of the PAM-AN plane. This chapter partly addresses study objective 1.

Three main approaches were taken. The first was the determination of indices that represented an integration of the soil-plant response. The second approach investigated the potential usefulness of individual soil properties as AN indices and the third approach considered the development and use of indices derived from combinations of soil properties. The indices derived from the first approach were used as reference indices for the assessment of the fertility gradients derived from the other approaches. The approaches encompassed various degrees of complexity, both in method of determination and in the indices derived. Both absolute and relative fertility indices were experimented with.

Section 4.2 of this chapter presents the methods that were used to determine the various AN indices. Section 4.3 presents the AN indices derived from the various approaches and these are discussed in section 4.4.

The methods of soil data collection and of the determination of soil physical and chemical properties are presented in chapter 2, section 2.2. Sites are referred to by number as in Table 2.1.

4.2 METHODS

4.2.1 REFERENCE INDICES

4.2.1.1 Fertility rankings by experts

One approach to developing an AN index was to use the knowledge of soils experts - people who work with aspects of assessing soil fertility on a daily basis. Five soils experts were

provided with a table of soil analysis data (topsoil only) for the nineteen sites and asked to rank the soils in order of increasing fertility (1 = least fertile) (Appendix 9). For the purposes of this exercise, fertility was defined as above ground grass productivity, in the absence of water limitation or competition from trees. The soil fertility rankings given by each expert were compared using a Spearman's rank correlation. A mean ranking was calculated for each soil from the rankings given by each expert. This approach was used as a subjective reference index for assessing other potential AN indices by rank correlation.

4.2.1.2 Bioassay experiment

A bioassay approach was adopted for A horizon soils from each of the nineteen sites sampled (Feuchtenbeiner-Walsh 1990). A constant amount of each of the bulked samples of top soil from each site was placed in a polystyrene cup, with four replicates per soil. Sufficient seed of a grass species, *Panicum maximum*, was sown in each cup to achieve maximum rooting density. *Panicum maximum* was chosen since it establishes easily, grows rapidly and is a relatively widespread C4 savanna grass, occurring naturally on both nutrient rich and poor soils. The use of *P. maximum* as a bioassay species was recommended by Solbrig *et al* (1988). The grass was grown under controlled conditions of day temperature, day length, night temperature, humidity and irradiance in the phytotron at the University of the Witwatersrand. Plants were watered regularly to 75 % of the field capacity determined for each soil.

Plants were grown for a 15 week period. Four harvests of above-ground biomass (excluding crown material) were made, one after 2 weeks and then at 3 weekly intervals. A fifth and final harvest included above-ground, crown and root material. Harvested material was dried at 70°C for 2 days and massed to determine shoot production (total mass (grams) of above-ground biomass produced over 15 weeks) and whole-plant production (total mass (grams) of shoot production plus root and crown biomass produced over 15 weeks). The dry shoot, crown and root tissue was analysed for nitrogen, phosphorus and carbon content (total content over 15 weeks).

The AN gradients based on whole-plant and shoot production were compared with one

another and correlated with the experts' rankings using a Spearman's rank correlation. The root to shoot ratios of plants grown on each soil were compared. Biomass production was used as an objective reference index for assessing other potential AN indices by correlation and the gradient of sites based on shoot production was considered a potential AN index.

4.2.2 SINGLE FACTOR INDICES

4.2.2.1 Biomass production relative to soil nutrient content

Samples of the same soils as used for the bioassay experiment were analysed for a variety of chemical properties (details in chapter 2). Biomass production was compared with soil total nitrogen (TotN), nitrogen mineralization rate (Nmin), resin extractable phosphorus (P), 1M ammonium acetate extractable potassium (K) and percentage organic carbon (% OC). These soil chemical properties were chosen because N, P and K are macro-elements with well documented limiting effects on plant growth (Chapin 1980). Percentage organic carbon is a standard measure, highly correlated with total nitrogen and a consequence of production.

Biomass production and soil nutrient content were related using the procedure described by Cate and Nelson (1971). This is a simple graphical procedure for determining a threshold concentration of a particular soil nutrient above and below which there is a high and low probability of plant response respectively (Fig. 4.2.1). This graphical technique amounts to maximizing the computed chi-square value representing the test of the null hypothesis that the number of observations in each of the four quadrants is equal, the hypothesis that the data consist of one random population (Cate and Nelson 1971).

In order to determine plant response to individual soil nutrients and to determine the associated soil nutrient thresholds, whole-plant and shoot production were plotted against each of the five soil chemical properties chosen and the graphical technique applied. Comparisons of plant response were made on the basis of the inclusion or exclusion of sites from either of the response groups and on the consistency of groupings, rather than on the specific positions of sites on the scatter plots and how these changed with different nutrients.

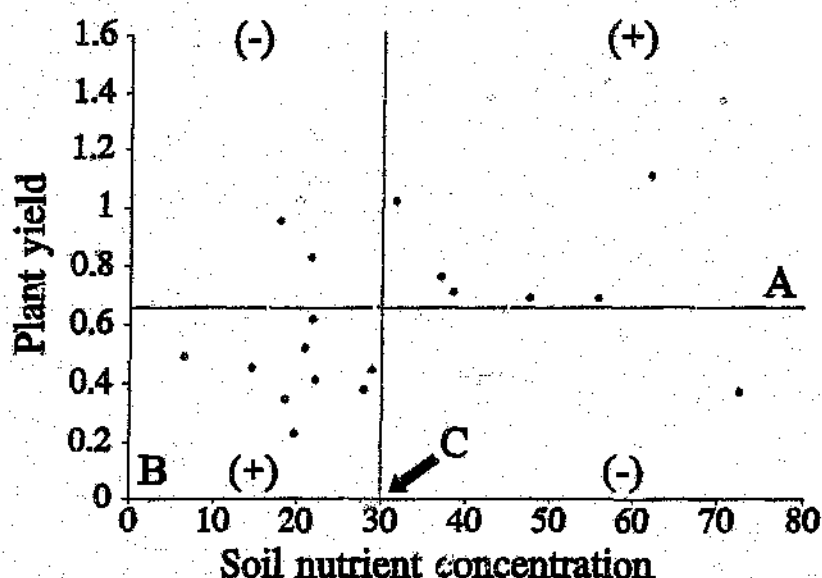


Figure 4.2.1 The Cate-Nelson (1971) procedure for determining threshold nutrient concentrations in relation to plant response. The high (A) and low (B) response groups are determined by superimposing two perpendicular lines on the plant production - soil nutrient scatter plots so as to maximize the number of data points in the positive quadrants (+). The point where the vertical line intersects the X axis (C) indicates a critical threshold value of the soil nutrient above which it is assumed to have no limiting effect and below which nutrient limitation is assumed to control plant nutrient uptake and productivity.

4.2.2.2 Nutrient accumulation in plant tissues

The tissue nutrient content of the bioassay plants (determined by Feuchtenbeiner-Walsh (1990)) was compared with the reference indices to see if tissue nutrient content was related to soil fertility.

4.2.2.3 Individual soil properties

The potential for using parent material geology and A horizon texture, pH, TotN, Nmin, P and % OC as single factor AN indices was considered. The AN gradients based on these individual soil properties were compared with the reference indices.

4.2.3 MULTIFACTOR INDICES

4.2.3.1 Effective cation exchange capacity

Effective cation exchange capacity (ECEC) and base saturation were calculated for each soil (Anon. 1982). The order of sites based on ECEC and on base saturation was compared with the reference indices.

4.2.3.2 Index of N, P and K availability using plant biomass

The approach to combining N, P and K availability into a single index was based on that taken by Noble (1989). For the purposes of this study, N availability was measured as the amount of ammonium (mg/kg) produced per week in water-logged soils under laboratory conditions, (the anaerobic potential nitrogen mineralization rate). The concentrations of both resin-extractable P and 1M ammonium acetate extractable K were used as measures of the potential availability of these nutrients in the soil. The threshold levels of N, P and K, above which these nutrients were not limiting plant growth, were estimated using the Cate and Nelson (1971) procedure.

The AN index was calculated as follows: if the concentration of a soil nutrient was above its estimated optimum supply threshold value, the availability index for that nutrient at that site was unity i.e. the nutrient was assumed not to limit plant growth. If the concentration of the nutrient was below the estimated threshold value, the availability index was calculated as the quotient of the nutrient concentration value and the estimated threshold value i.e. the ratio indicated the extent of nutrient limitation. A ratio close to 1 indicated only slight limitation while a ratio close to 0 indicated severe limitation. The AN indices were derived by multiplying the availability indices for Nmin and P and for Nmin, P and K at each site. These AN indices were compared with the reference indices.

4.2.3.3 Index of N, P and K using multivariate analysis

Multivariate analysis was used as a way of integrating soil variables to provide a simple

fertility gradient. Total nitrogen and P, and TotN, P and K were analysed by principal components analysis and the first axis eigenvalues were considered as potential fertility gradients. The multivariate indices were compared with the reference indices.

4.3 RESULTS

4.3.1 REFERENCE INDICES

4.3.1.1 Fertility rankings by experts

The soil data sent to the experts was not stone-content corrected and this is likely to have resulted in an over-ranking of soils 4 and 7. Both these soils have a high stone content (Appendix 10) and the stone correction substantially reduces the absolute amount of nutrients available in the soils at each of these sites. To accommodate this problem, sites 4 and 7 were excluded from the AN index derived from the experts' rankings.

The experts' rankings were found to be significantly correlated with one another, (Table 4.3.1) indicating that the experts independently arrived at similar fertility rankings of the soils. The mean ranking of each soil at each site was considered a potential AN index (Fig. 4.3.1 a). The order of sites based on the mean rankings was used as a subjective reference index for assessing other potential AN indices. The mean rankings ranged from 1.7 to 17.0 and the fertility gradient based on mean rankings (Fig. 4.3.1 a) indicated two groupings of sites. There were low AN sites with a mean ranking of 8.2 or less and high AN sites with a mean ranking of 11.4 or more.

4.3.1.2 Biomass production

Site 2 was excluded from the AN index based on biomass production because plants on this soil became water stressed during early stages of the experiment, and plant productivity was consistently much lower than expected from field observations. Sites 4 and 7 were also excluded because soils used for the bioassay experiment were not adjusted to the correct

stone content.

Table 4.3.1 Spearman's rank correlation coefficients of the fertility ratings provided by the five soils experts.

Expert		2	3	4	5
1	r_s	0.87	0.86	0.73	0.84
	p	0.0001	0.0001	0.0004	0.0001
2	r_s		0.83	0.86	0.84
	p		0.0001	0.0001	0.0001
3	r_s			0.74	0.86
	p			0.0003	0.0001
4	r_s				0.84
	p				0.0001

Available nutrient gradients were derived from biomass production of *P. maximum* assuming that a gradient in production reflected a gradient in AN. There was a relatively even spread of sites along the whole-plant and shoot production gradients (Fig. 4.3.1 b & c). Neither the rank order of sites based on whole-plant or shoot production was significantly correlated with the experts' rankings. There were, however, similarities in the relative positions of sites along the gradients depicted in Figure 4.3.1.

Greater amounts of whole-plant and shoot production were generally associated with a higher nutrient availability as indexed by the experts' rankings. Soils from sites 3, 5, 8, 12, 15 and 16, which were in the experts' high AN group (Fig. 4.3.1 a), were positioned on the high AN side of the gradients based on biomass production (Fig. 4.3.1 b and c). Soils 17, 18 and 19 and soils 1 and 19, however, produced higher whole-plant and shoot biomass, respectively, than expected from the experts' rankings (Fig. 4.3.1).

The order of sites along the whole-plant and shoot production gradients was not correlated although there were similarities in the relative positions of sites along the gradients (Fig.

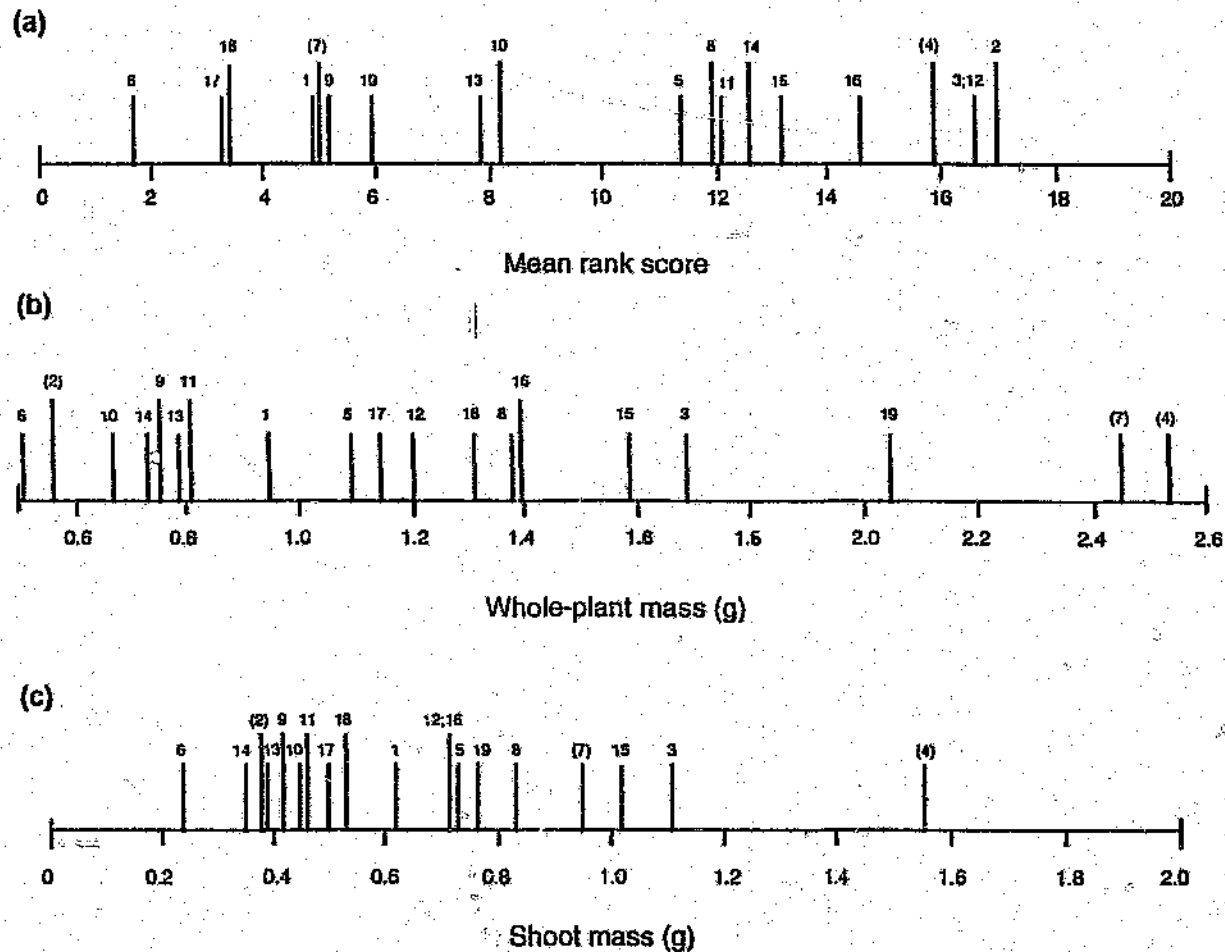


Figure 4.3.1 Reference indices of available nutrients based on (a) mean score of rankings by soils experts, (b) *Panicum maximum* whole-plant production and (c) *P. maximum* shoot production. The vertical lines indicate the position of each site along the index axis. Site numbers are as given in Table 2.1. Sites that were excluded from each of the reference indices are shown in parenthesis (see section 4.3.1.1 for details).

4.3.1 b & c). The inclusion of crown and root biomass (whole-plant production gradient) elevated the positions of soils 17, 18, and 19 relative to their positions along the gradient based on shoot production alone. The root-to-shoot ratio (r:s) of *P. maximum* on low AN soils 17 (r:s = 0.95), 18 (1.49) and 19 (1.68) was high relative to the other soils eg high AN soils 3 (r:s = 0.53), 5 (0.54) and 15 (0.56).

For the purposes of this study, whole-plant production and shoot production of *P. maximum* were used as objective reference indices for assessing other potential AN indices.

4.3.2 SINGLE FACTOR INDICES

4.3.2.1 Biomass production relative to soil nutrient content

For the reasons stated in section 4.3.1.2, sites 2, 4 and 7 were excluded from these indices.

The threshold levels of total nitrogen (TotN) (500 mg/kg), nitrogen mineralisation rate (Nmin) (30 mg/kg/week), resin-extractable phosphorus (P) (10 mg/kg), extractable potassium (K) (0.78 cmol(+)/kg) and percentage organic carbon (% OC) (0.90%) were estimated using the graphical procedure of Cate and Nelson (1971) (Fig. 4.3.2).

Soils from sites 3, 5, 12, 15 and 16 were consistently grouped above the estimated threshold levels of all the nutrients considered (Fig. 4.3.2). These soils produced consistently high shoot and whole-plant biomass associated with relatively high levels of soil nutrients and corresponded with those in the experts' high AN group.

Soils from sites 1, 6, 9, 10, 11, 13 and 14 were consistently grouped below the estimated threshold levels of all the nutrients considered except P and K (Fig. 4.3.2). These soils produced consistently low shoot and whole-plant biomass associated with relatively low levels of soil nutrients and corresponded with those in the experts' low AN group. Biomass production on soil 14 was low relative to the soil P content (Fig. 4.3.2 c) as was biomass production on soil 10 relative to the soil K content (Fig. 4.3.2 d).

Shoot and whole-plant biomass production on soil 8 was high relative to the availability of all the nutrients considered in that soil except TotN and P (Fig. 4.3.2). Shoot and whole-plant biomass production on soil 19 was high relative to the availability of all nutrients in that soil except Nmin (Fig. 4.3.2). The soil at site 19 had a nitrogen mineralization rate above the estimated threshold level. Shoot production on soils 17 and 18 was consistently low but these soils produced a high whole-plant biomass relative to the availability of the nutrients considered.

The individual soil chemical properties that best explained the observed trends in biomass production were TotN and Nmin, each with only one outlier site (a site that did not fall into either the low or high response groups) (Fig. 4.3.2a,b). The order of sites based on shoot production was correlated with the order based on TotN ($r_s=0.73$, $df=14$, $P<0.01$). Soil % OC and P were each associated with two outlier sites (Fig. 4.3.2c,e). The order of sites based on the shoot production gradient was correlated with the order based on the gradient of % OC ($r_s=0.63$, $df=14$, $P<0.01$, $n=14$) but not significantly correlated with the gradient based on P content. Potassium was associated with three outlier sites (Fig. 4.3.2d).

On the basis of the observed response of *P. maximum* to individual soil nutrients, TotN, Nmin and % OC were considered to be potential indices of AN.

4.3.2.2 Nutrient accumulation in plant tissues

The order of sites along the gradients based on both shoot N content and whole-plant N content were similar. The order of sites based on tissue N content was not correlated with either the experts' rankings or with shoot production. Contrary to expectations, plants grown on experts' low AN soils 1, 6, 17, 18 and 19 had shoot tissue N concentrations, (ranging from 23800 to 31500 $\mu\text{gN g}^{-1}$), that were comparable with those from plants grown on high AN soils 3, 8, 12, 15 and 16 (ranging from 23900 to 26100 $\mu\text{gN g}^{-1}$).

Both shoot N content ($r=0.81$, $df=14$, $P<0.001$) and whole-plant N content ($r=0.82$, $df=14$, $P<0.001$) were positively correlated with site PAM, despite the fact that the soils in the laboratory growth trial were all watered to 75% of field capacity. This observation

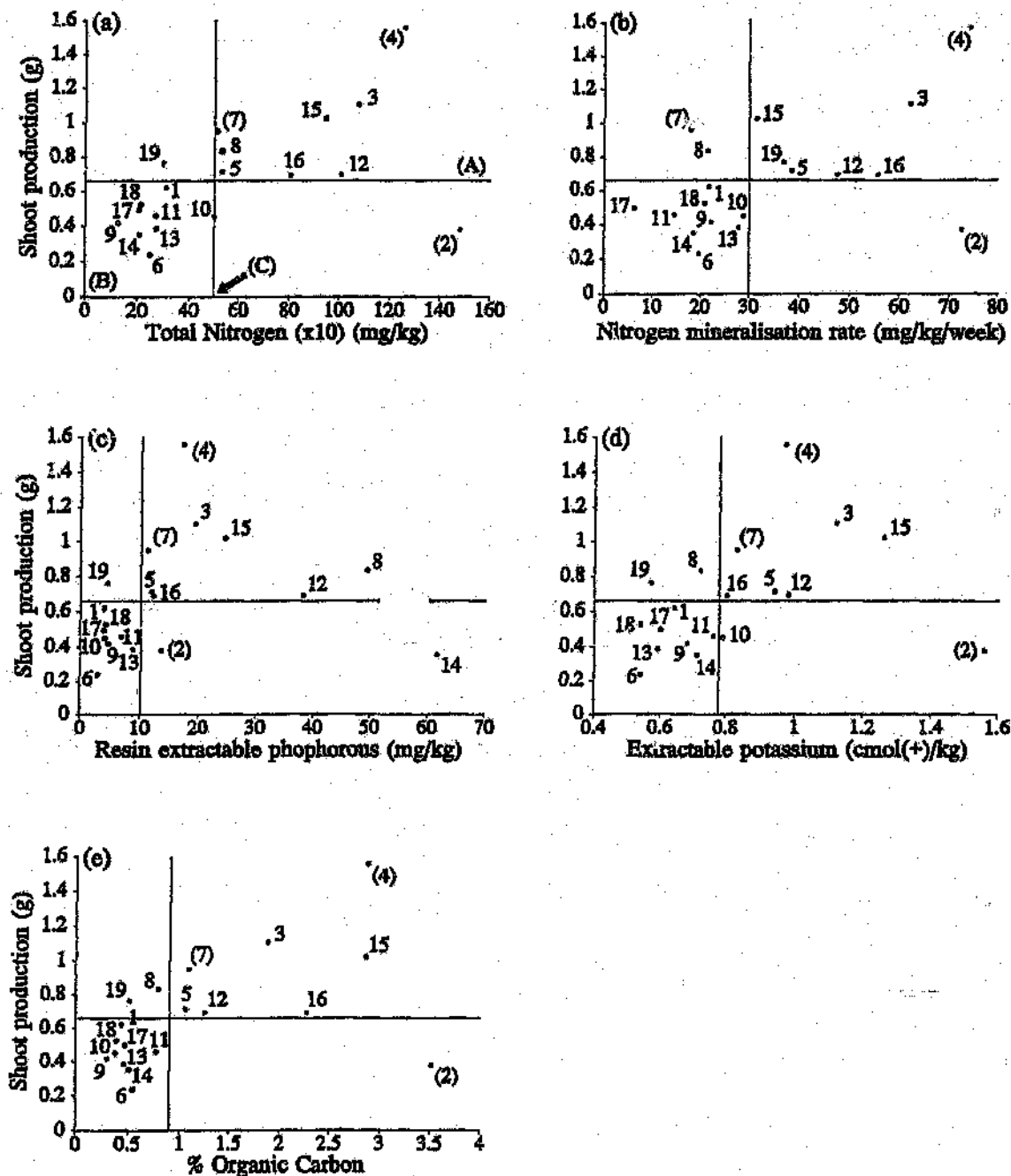


Figure 4.3.2 Biomass production of *Panicum maximum* relative to (a) total nitrogen, (b) nitrogen mineralization rate, (c) resin extractable phosphorus, (d) exchangeable potassium and (e) percentage organic carbon measured in each soil at each site. The critical threshold levels of nutrient availability (C) above and below which there was a high (A) and low (B) plant response respectively were determined by the Cate and Nelson (1971) procedure (perpendicular lines). Sites in parenthesis were not included in the fertility assessments. Sites positioned in either of the negative quadrants (-) were considered as outlier sites since biomass production on these soils was either higher or lower than expected from the availability of nutrients in the soil.

suggested some relationship between PAM and the microbial flora in each of the soils although nitrogen mineralization rate was not correlated with PAM. Based on the strong correlation of tissue N content with PAM and the lack of pattern with soil fertility, tissue N concentration was not considered a potential AN index. Similarly, tissue P content was not considered a potential AN index because no relationship was found between the concentration of P in *P. maximum* tissue and the concentration of P in the soil (Feuchtenbeiner-Walsh 1990).

4.3.2.3 Individual soil properties

A horizon soil data were used since these are likely to be more readily available than B horizon data, although the nutrient content of B soils is less likely to have been influenced by past land-use history. A and B horizon % clay ($r=0.93$, $df=16$, $P<0.001$), P ($r=0.83$, $df=16$, $P<0.001$), Ca ($r=0.87$, $df=16$, $P<0.001$), Mg ($r=0.82$, $df=16$, $P<0.001$), and K ($r=0.90$, $df=16$, $P<0.001$) were found to be significantly positively correlated indicating that, certainly in this study, A horizon soil properties could be used to represent soil fertility. B horizon soil chemical data are tabulated in Appendix 11.

4.3.2.3.1 Geology

The sites were divided into four groups on the basis of their parent material geology, ranging from acid, nutrient poor (group 1) to basic, nutrient rich (group 4) (Table 4.3.2). Sites in geological group 4 were the same as those in the experts' high AN group and in the high biomass production group. Group 1 contained predominantly low AN sites. Comparison with the reference indices suggested that geology was useful as a rough estimate of potential soil fertility but there were instances where this relationship did not hold. Soil 8, for example, although on the same geological substrate, had a much higher nutrient status than soil 6. Soils 4 and 7 had a much lower nutrient status than predicted from the geology of these sites.

4.3.2.3.2 Texture

The sandiest soils were in geological group 1 and the clayiest in group 4 indicating a rough correlation with geology (Table 4.3.2). The rank order of sites (excluding site 8) based on % sand and on experts' mean rankings was significantly correlated ($r_s=0.82$, $df=14$, $P<0.001$) suggesting that % sand content may be a useful single index of fertility. Percentage sand was also correlated with shoot production ($r=0.65$, $df=13$, $P<0.01$). Percentage clay was also considered a potential AN index (Fig. 4.3.3 a). Although textural data is relatively easy to obtain, its use has the same limitations as discussed for geology.

4.3.2.3.3 pH

The pH of the soils ranged from 4.1 to 6.25 with large ranges in each of the geological groupings (Table 4.3.2). Comparisons of pH and ECEC and pH and P yielded no pattern of increased nutrient availability with increased pH and pH was not correlated with either the experts' rankings or with shoot production. A pattern with PAM was expected, with low pH soils in high PAM areas and *vice versa*, but PAM and pH were not significantly correlated. These results suggested that pH was not suitable for use as a single AN index. The value of using pH in a combined index needs to be considered.

4.3.2.3.4 Nitrogen

It has already been shown that TotN and Nmin are good indicators of *P. maximum* biomass production (section 4.3.2.1) and that nitrogen appears to be the limiting factor in these soils. Both TotN and Nmin were correlated with the experts' rankings although Nmin ($r_s=0.68$, $df=15$, $P<0.01$) not as strongly as TotN ($r_s=0.76$, $df=15$, $P<0.001$).

There was a fairly even spread of sites along the AN gradient based on Nmin in comparison with the gradient based on TotN (Fig. 4.3.3 b & c). The sites along the TotN gradient were grouped into obvious low AN (less than 310 mg/kg), intermediate AN and high AN (more than 790 mg/kg) groups (Fig. 4.3.3 c).

Table 4.3.2 A horizon soil properties (stone content corrected). Sites were divided into geological groups and ordered within each group according to percentage sand in the A horizon. Site numbers are as given in Table 2.1. Key to the geological parent material at each site: Kar sand = Karoo sandstone; Wat sand = Waterberg sandstone; Quat sand = Quaternary sands; Kala sand = Kalahari sands; Quar = Quartzite; Wat sand (+) = Waterberg sandstone + nutrient enrichment; Gran midl = Granite midlands; Gran upld = Granite uplands; Mar sand = Marine sandstone; Mud = Mudstone; Ande = Andesite; Fels = Felsite; Rhyo = Rhyolite; Tim gabb = Timbavati gabbro; Kar bas = Karoo basalt; Alluv = Alluvium; SR bas = Sabie River basalt; Bas = Basalt.

	(1) Acidic & nutrient poor					(2)						(3)			(4) Basic & nutrient rich				
Site	13	6	1	8	14	8	18	19	17	5	10	11	7	4	16	12	3	15	2
Geology	Kar sand	Wat sand	Quat sand	Kala sand	Quar	Wat sand+	Gran midl	Gran upld	Gran upld	Mar sand	Mud	Ande	Fels	Rhyo	Tim gabb	Kar bas	Alluv	SR bas	Bas
Texture																			
% sand	84	83	80	78	70	78	77	76	75	52	50	73	63	54	54	48	28	22	16
% silt	3	5	8	9	10	6	10	10	11	25	22	8	16	28	12	12	38	22	21
% clay	13	12	14	12	20	16	13	14	14	23	28	19	21	18	34	40	34	56	63
Textural class	ls	ls	sl	sl	sl	sl	sl	sl	sl	scl	pel	sl	scl	sl	scl	sc	cl	c	c
pH (1M KCl)	6.25	4.10	4.55	5.20	5.55	4.90	4.55	5.20	5.00	5.00	5.30	4.90	4.00	5.85	6.10	6.20	6.10	4.88	4.90
Cations (cmol(+) / kg)																			
Ca	3.51	1.05	3.46	4.83	13.07	5.14	1.41	2.96	2.24	8.04	6.37	15.94	0.58	1.39	33.03	30.98	20.97	17.39	13.99
Mg	1.09	0.72	1.28	1.28	1.81	0.90	0.68	0.82	0.82	2.57	1.66	3.80	0.28	0.18	4.05	3.51	4.65	3.49	3.87
K	0.59	0.54	0.64	0.68	0.83	0.71	0.51	0.51	0.54	0.93	0.71	0.71	0.28	0.10	0.79	0.88	1.12	1.25	1.39
Acidity (cmol(+) / kg)	0.03	0.40	0.07	0.02	0.04	0.05	0.19	0.06	0.14	0.13	0.13	0.07	0.29	0.02	0.47	0.23	0.14	0.18	0.20
Effective cation exchange capacity (cmol(+) / kg)	5.22	2.79	5.45	6.81	15.55	6.80	2.79	4.35	3.74	9.67	8.87	20.52	1.39	1.69	38.34	35.61	26.88	22.31	19.55
Base saturation (cmol(+) / kg)	5.19	2.60	5.38	6.79	15.51	6.75	2.60	4.29	3.80	9.54	8.74	20.45	1.10	1.67	37.87	35.38	26.74	22.13	19.35
% Organic carbon	0.49	0.55	0.44	0.30	0.45	0.78	0.37	0.48	0.43	1.04	0.37	0.72	0.34	0.29	2.24	1.12	1.87	2.82	3.12
Phosphorus (mg/kg)	8.74	2.91	3.95	4.64	54.82	49.10	4.69	4.11	3.54	11.81	4.01	6.43	3.47	1.71	12.00	34.34	19.36	24.40	12.01
Total nitrogen (mg/kg)	268.50	247.01	307.35	125.16	185.51	527.86	201.96	287.92	184.45	528.08	483.33	248.72	158.07	125.40	794.30	905.56	1075.28	834.05	1316.76
Nitrogen mineralization rate (mg/kg/week)	25.77	19.89	21.79	22.14	16.50	21.34	19.78	33.13	5.70	38.17	26.00	13.50	5.54	7.41	55.17	42.84	62.07	31.16	64.51
Nitrogen mineralization rate (mg/kg/day)	3.68	2.81	3.11	3.16	2.36	3.05	2.83	4.73	0.81	5.45	3.71	1.93	0.79	1.06	7.88	6.12	8.87	4.45	9.22

Two major differences between the two indices were the relatively low fertility estimate for soil 15 and the close grouping of soils 1 and 8 along the Nmin gradient. Because TotN and Nmin were correlated ($r=0.81$, $df=17$, $P<0.001$), both of these were considered as potential single factor AN indices.

4.3.2.3.5 Phosphorus

Phosphorus availability was correlated with the experts' rankings ($r_s=0.82$, $df=15$, $P<0.001$) but not with the order of sites based on shoot biomass production. The relationship between phosphorus availability and *P. maximum* biomass production was not clearly defined.

Soils 8 and 14 had a high P content relative to the other sites and to the other available nutrients (Fig. 4.3.3 d). The fact that soil 8 came from an old settlement site accounted for the high soil P content here. Site 14 supported a *Colophospermum mopane* community. Soils under *C. mopane* elsewhere have been found to be P rich (Scholes, RJ pers. comm.). Phosphorus availability was not considered a potential single factor AN index but was used in combination with nitrogen (section 4.3.3).

4.3.2.3.6 Percentage organic carbon

It has already been shown that % OC was related to *P. maximum* biomass production (section 4.3.2.1). Percentage organic carbon was correlated with the experts' rankings ($r_s=0.76$, $df=15$, $P<0.001$) and was also significantly correlated with TotN ($r=0.87$, $df=17$, $P<0.001$). Percentage organic carbon was considered a potential single factor AN index (Fig. 4.3.3 e) especially since it is relatively easy to measure and data are likely to be available.

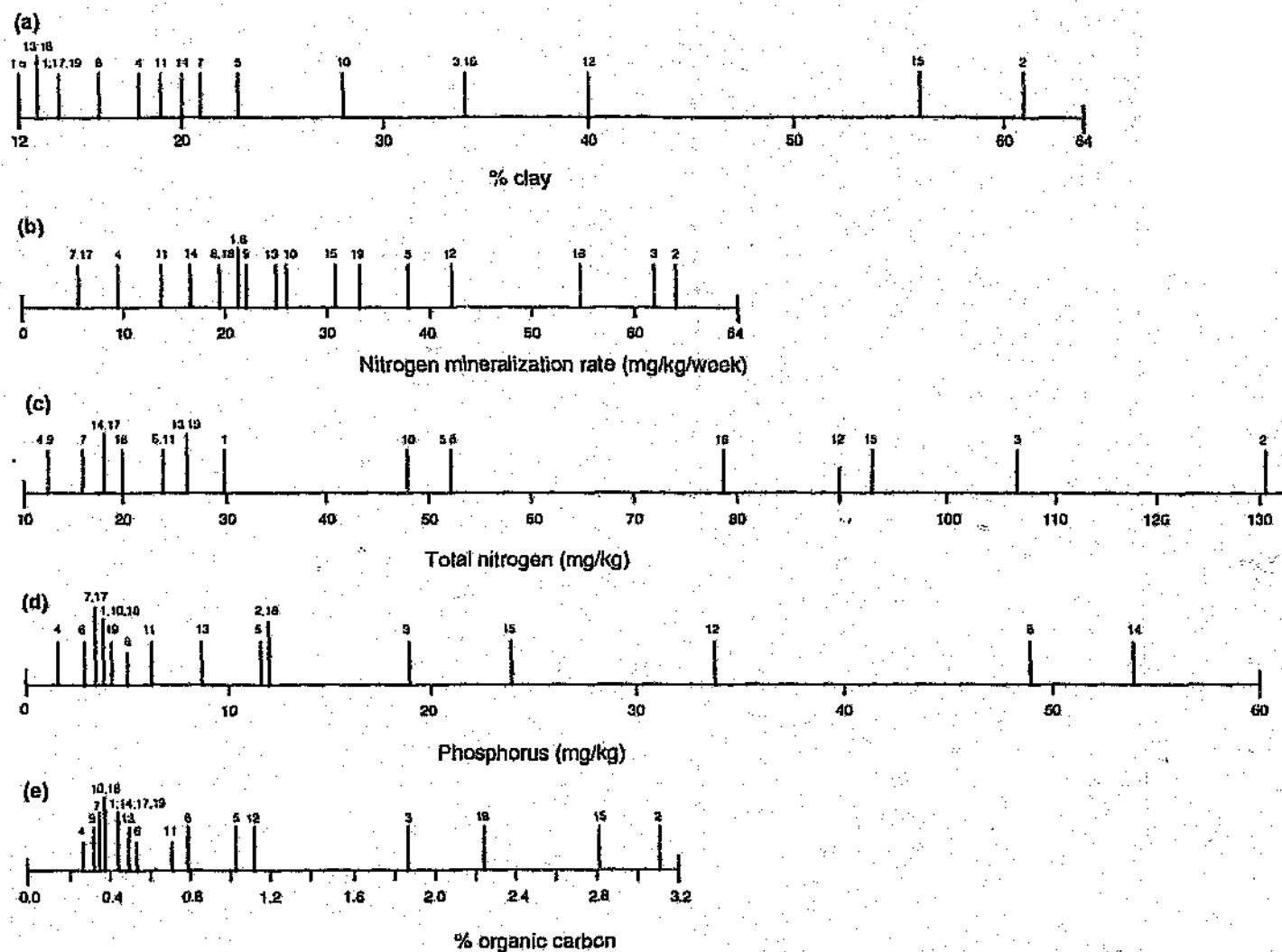


Figure 4.3.3 Single factor indices of available nutrients based on individual A horizon soil properties of (a) percentage clay, (b) nitrogen mineralization rate, (c) total nitrogen, (d) phosphorus and (e) percentage organic carbon. Vertical lines indicate the position of each site along the index axis. Site numbers are as given in Table 2.1.

4.3.3 MULTIFACTOR INDICES

4.3.3.1 Effective cation exchange capacity

A significant correlation was found between ECEC and the experts' rankings ($r=0.89$, $df=15$, $P<0.001$) but not between ECEC and shoot production (Fig. 4.3.4 a). The values of base saturation were very similar to the ECEC values (Table 4.3.2) and hence provided a similar AN index, suggesting that the experts were largely guided by base saturation considerations. Both of these measures were considered to be potential AN indices.

4.3.3.2 Index of N, P and K availability using plant biomass

The threshold levels of Nmin, P and K (estimated using the Cate and Nelson (1971) procedure) were 4.286 mg/kg/day, 10 mg/kg and 0.78 cmol(+)/kg respectively. Sites 2, 4 and 7 were excluded from this index as were sites 8, 10, 14 and 19, the outlier sites for Nmin, P and K (see section 4.3.2.1).

The order and relative positions of the sites along the gradients based on the N-P and N-P-K indices were very similar but the values of the N-P-K index were comparably lower than those of the N-P index (Table 4.3.3). The groupings of sites along the N-P and N-P-K gradients (Fig. 4.3.4 b) were related to the groupings based on the expert's rankings (Fig. 4.3.1 a) with a definite high AN, low AN split. Soil 13, with a high N-P and N-P-K AN index relative to the experts' fertility ranking, and soils 10 and 11 with low N-P and N-P-K indices relative to the experts' rankings were exceptions.

Both the N-P and N-P-K indices (based on shoot mass) were considered potential multifactor AN indices.

4.3.3.3 Index of N, P and K using multivariate analysis

The first axis of a PCA of TotN and P accounted for 78 % of the variation. The site order based on the first axis eigenvalues was significantly correlated with the experts' rankings

Table 4.3.3 (a) Availability indices of nitrogen mineralisation rate (Nmin), extractable phosphorus (P) and extractable potassium (K) based on the procedure of Noble (1989), (b) AN indices derived from the multiplication of the availability indices. Sites that did not fall within either the high or low response groups (section 4.3.2.1) for a particular nutrient were excluded from the indices. These are indicated as 'out' sites.

(a) Site	NMin		P		K	
	shoot	plant	shoot	plant	shoot	plant
1	0.73	0.73	0.40	0.40	0.82	0.82
3	1.00	1.00	1.00	1.00	1.00	1.00
5	1.00	1.00	1.00	1.00	1.00	1.00
6	0.66	0.66	0.29	0.29	0.69	0.69
8	out	out	1.00	1.00	out	0.92
9	0.74	0.74	0.46	0.46	0.87	0.87
10	0.96	0.96	0.41	0.41	out	out
11	0.48	0.48	0.69	0.69	0.97	0.97
12	1.00	1.00	1.00	1.00	1.00	1.00
13	0.93	0.93	0.88	0.88	0.76	0.76
14	0.62	0.62	out	out	0.91	0.91
15	1.00	1.00	1.00	1.00	1.00	1.00
16	1.00	1.00	1.00	1.00	1.00	1.00
17	0.21	out	0.39	out	0.77	0.77
18	0.69	out	0.43	out	0.69	0.69
19	1.00	1.00	out	out	out	out

(b) NMin x P				NMin x P x K		
Site	shoot	plant		Site	shoot	plant
17	0.08	out	Low AN	17	0.06	out
6	0.19	0.19		6	0.13	0.13
1	0.29	0.29		18	0.21	out
18	0.30	out		1	0.24	0.24
11	0.33	0.33		9	0.30	0.30
9	0.34	0.34		11	0.32	0.32
10	0.40	0.40		13	0.62	0.62
13	0.82	0.82		3	1.00	1.00
3	1.00	1.00		5	1.00	1.00
5	1.00	1.00		12	1.00	1.00
12	1.00	1.00	High AN	15	1.00	1.00
15	1.00	1.00		16	1.00	1.00
16	1.00	1.00		8	out	out
8	out	out		10	out	out
14	out	out		14	out	out
19	out	out		19	out	out

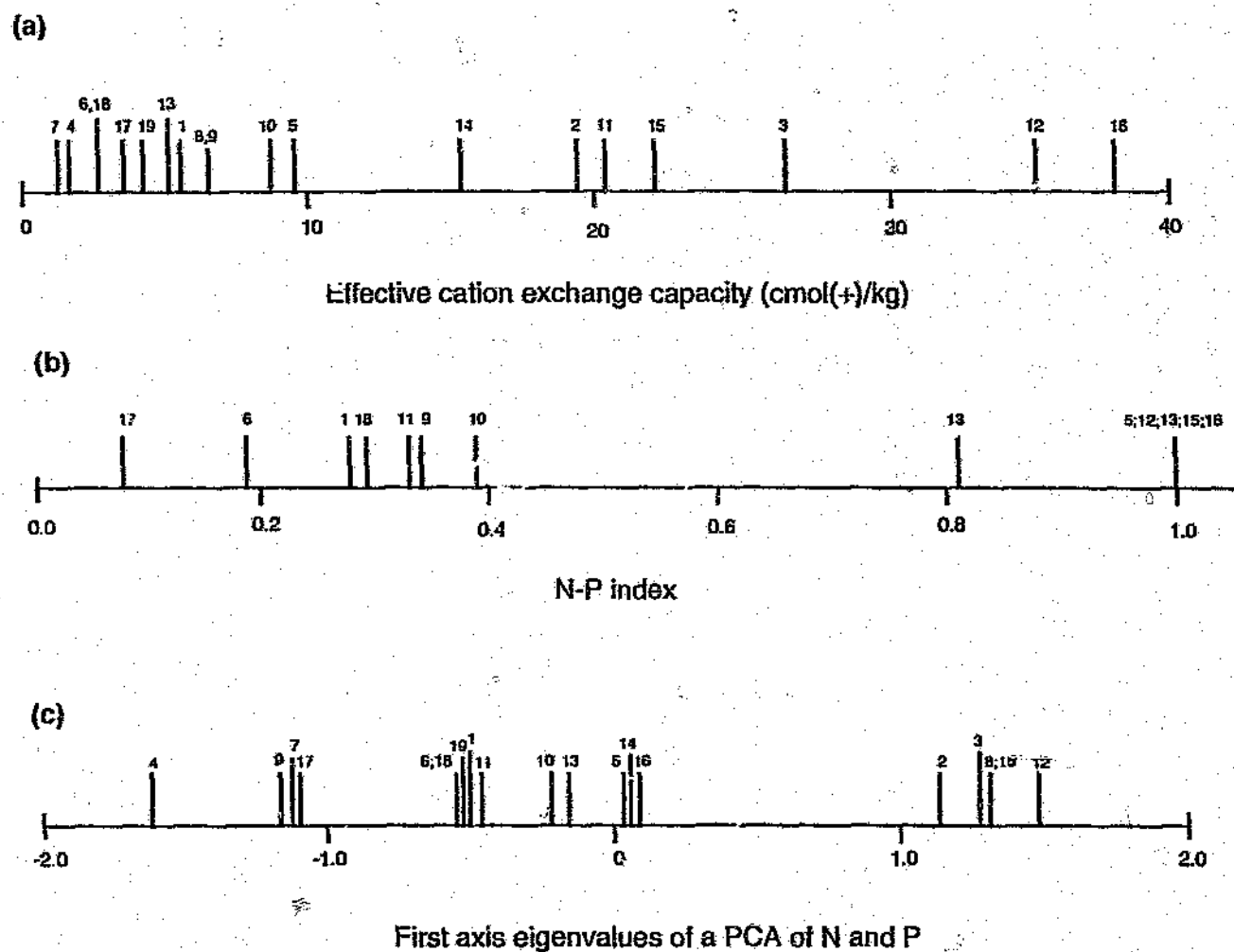


Figure 4.3.4 Multifactor indices of available nutrients based on (a) effective cation exchange capacity, (b) N, P and K availability and (c) first axis eigenvalues of a PCA of N and P. The vertical lines indicate the position of each site along the index axis. Site numbers are as given in Table 2.1.

($r_s=0.80$, $df=15$, $p<0.001$) and relative positions along the gradient (Fig. 4.3.4 c) were similar to those provided by shoot production (Fig. 4.3.1 c) and by the N-P and N-P-K indices (Fig. 4.3.4 b). The inclusion of K as a variable in the PCA did not change the percentage of the variation accounted for by the first axis but did slightly alter positions of certain sites on the AN gradient, particularly sites 8 and 14.

The use of P in the multivariate indices elevated the fertility of sites 8 and 14 relative to the high and intermediate AN sites. The inclusion of K, however, lowered the position of these sites on the fertility gradient. The best combination of variables was considered to be that of TotN, P and K. This decision was based on comparisons of eigenvalue fertility gradients and of these with the other multifactor indices.

4.4 DISCUSSION

4.4.1 REFERENCE INDICES

4.4.1.1 Fertility rankings by experts

This approach provided a means for obtaining a single fertility index that represented the integration of a number of soil properties based on the knowledge and opinions of soils experts. A relative index (a gradient of sites) was obtained from the fertility rankings that was useful for comparison with other indices.

This index was considered ecologically meaningful and required only simple computation. Because it is a relative gradient, one drawback to its use is that the ranking exercise would have to be repeated every time additional soils were added to the gradient. Another problem with this approach is that it requires relatively detailed soil physical and chemical data which are not generally available. Bell (1982) states that data on nutrient availability in savanna soils is scattered and of variable quality.

In order to improve this approach, the experts should be consulted as to what other soil

properties or information, if any, they needed to assist their fertility assessments. A knowledge of the criteria used by each expert to rank the soils would give insight into the relative importance of each of the soil properties.

A cautionary note is that the particular experience of the expert will influence their assessment of fertility. The ranking of soils by a pedologist, considering mostly soil physical properties, provided an AN gradient opposite from that of the other experts who were guided mostly by soil chemical properties. The pedologist rated sandy soils best and clayey soils least favourable for plant growth.

4.4.1.2 Biomass production

Biomass production provided an absolute index that reflected nutrient availability in terms of soil-plant interactions. This approach provided an objective reference index to which the other indices could be compared.

An index based on biomass production was considered to be ecologically meaningful. The index required only simple computation but a large amount of effort was required to obtain the biomass data. A drawback of this approach is that the whole growth trial would have to be repeated to determine biomass production on additional soils. As for the subjective reference index, this approach requires a relatively detailed knowledge of soil chemical properties.

A limitation of using only one indicator species to assess soil fertility is that species specificity of the soil-plant interaction is not considered. Different species have different tolerance levels of low nutrient availability e.g. grasses that are nitrogen limited and legumes that are phosphorus limited (Högberg 1986, Medina 1987). Ideally, a range of indicator species should be considered.

There is a problem with using soils that have been prepared for chemical analysis since soil structure is totally disturbed and does not represent conditions in the field. The soils used in this growth trial should have been re-adjusted to the correct stone content after sieving.

This approach could be extended to consider plant response on a single soil type to changes in climatic factors, or changes in nutrient availability or a combination of these. A bioassay approach in the field should also be considered.

Plant root-to-shoot ratios have been used to assess plant response in other bioassay approaches. The high root:shoot ratio of plants grown on low AN soils in this study can be explained as an adaptation to low nutrient availability. A high root:shoot ratio reflects the production of a large root stock which increases the root surface area for nutrient uptake. This is a strategy commonly found in grasses growing on soils with low fertility (Chapin 1980, Medina 1987).

4.4.2 SINGLE FACTOR INDICES

4.4.2.1 Biomass production relative to soil nutrient content

Although this approach did not provide specific AN indices, it provided useful information for the other approaches experimented with. This approach enabled an investigation of the response of *P. maximum* to individual soil nutrients and was important for determining nutrient limitations or threshold values for use in other indices e.g. the N-P-K index. The results of this approach were also useful for the interpretation and assessment of the single factor indices.

4.4.2.2 Nutrient accumulation in plant tissues

The similarities in tissue nitrogen content of *P. maximum* grown on experts' low and high AN soils was unexpected because low tissue nutrient concentrations of plants grown on infertile soils have been documented (Chapin 1980). Chapin (1980) states, however, that tissue nutrient content is not necessarily a good index of nutrient availability and that plant tissue concentrations of natural species are less sensitive indicators of soil nutrient availability than crop species. Olsvig-Whittaker & Morris (1982) attribute the difficulty of interpreting tissue nutrient status to the fact that the uptake of ions by plants does not take place in direct

proportion to the concentration of ions in the soil solution. Chapin (1980) suggests the use of the availability of soil nutrients determined by chemical analysis or a combination of tissue nutrient concentration and plant production as AN indices. The latter suggestion warrants investigation and may shed light on the high biomass produced at sites 1, 17, 18 and 19 in this study.

4.4.2.3 Geology

The use of geology to estimate soil fertility is based on the assumption that the soil present at a site has developed from the underlying parent material with no major nutrient inputs from outside the system. Dystrophic soils with low activity clays form from acidic parent materials such as granite and quartz while soils from basic igneous rocks have high activity clays and are eutrophic. A strong correlation between geology and soil characteristics has been found for the major geological units in the Kruger National Park (Venter 1986).

Geological data are freely available for most savanna areas and provide a relative AN index. An index based on geology requires empirical calibration to be ecologically meaningful but is easy to obtain and allows for extrapolation.

Geology and geomorphology have been used as a basis for assessing the effect of AN on community structure (Bell 1982, Cole 1982) and large mammal biomass in savannas (East 1984). The main problem with the classification of regions or landscapes as fertile or infertile on the basis of their geology is that the marked spatial heterogeneity in nutrient distribution within the savanna landscape, e.g. along catenas is not taken into account (Scholes 1991).

This landscape scale heterogeneity in nutrient distribution accounts for the discrepancy in geology and soil nutrient status at site 6. This was an old settlement site and the soil nutrient status reflected the nutrient enrichment from outside the system that has occurred here (Blackmore, Mentis and Scholes 1991). The rate of weathering of the parent material may also alter the geology - soil fertility relationship. Although the potential exists for nutrient rich soils to develop at sites 4 and 7, the parent material of these soils is resistant to

weathering (Venter 1986) and hence the soils have a much lower actual fertility than predicted from their geology.

4.4.2.4 Texture

Soil texture is considered to indicate the fertility potential of a soil, since the soil nutrient holding capacity is proportional to the soil clay content (Brady 1974). The capacity of a soil to accumulate organic carbon is also highly correlated to its clay content (Birch & Friend 1956, Jones 1973). Texture also influences nutrient dynamics, e.g. the rate at which organic matter decomposes is limited by soil aeration which is determined by soil texture (Bate and Gunton 1982).

The catenal sequence on slopes, e.g. on granitic surfaces in the Eastern Transvaal Lowveld, illustrates the texture-nutrient association. The top of the catena is associated with sandy, easily leached and nutrient poor soils while clayey, nutrient rich soils occur at the bottom (Walker 1985, Ben-Shahar 1990).

Walker (1985) used soil texture and rainfall to formulate a model that predicts an increase in tree density along a gradient of increasing rainfall. Soil texture has also been used in a model formulated by Johnson and Tothill (1985) to account for the variation in structure and composition of tropical savannas. Both of these models represent precursors of the current PAM-AN plane hypothesis.

Both percentage clay and percentage sand were considered to be potential AN indices. Soil texture is relatively easy to measure and because it provides an absolute index, additional sites can easily be added to the gradient.

The main problem with the use of this index is that a measure of soil texture alone makes no distinction between types of clay. A given percentage of a low-activity clay such as kaolinite has very different nutrient supplying properties to a high-activity clay such as montmorillonite. Low-activity, 1:1 lattice clays have a low effective cation exchange capacity, small amounts of exchangeable bases and low levels of P in contrast to high

activity, 2:1 lattice clays that are eutrophic (Frost *et al* 1986). Venter (1986) states that most of the ecologically essential soil properties of the different basic igneous rocks that occur in the Kruger National Park are determined by the type and quantity of clay minerals present in the soil. In West African the soils with clays other than kaolinite, have above average amounts of organic matter (Jones 1973).

4.4.2.5 pH

Soil pH influences nutrient availability in several ways, e.g. by affecting the solubility of P, by influencing the rate of nitrogen mineralization and by influencing the cation exchange capacity. At a low pH, for example, ions such as aluminium and iron are soluble and combine with and reduce P availability and compete with cations for absorption sites on the soil colloid (Brady 1974). Although pH was not considered a suitable single AN index, the value of using pH in a combined index needs to be considered.

4.4.2.6 Nitrogen

The indices based on TotN and Nmin related well to both the reference indices. This indicated that, although they were single factor indices, they were a good reflection of soil fertility and in the light of this were considered to be ecologically meaningful. Both of these measures of soil nitrogen content have been used in other studies. Noble (1989), for example, found that TotN accounted for productivity differences between sites of agaves and cacti. Nitrogen mineralization rate has been successfully evaluated as an index of forest soil fertility and above-ground productivity (Powers 1980, Pastor, Aber, McClaugherty and Melillo 1984).

Using a measure of nitrogen content of the soil provides an absolute index and one to which new sites could easily be added. Total nitrogen and Nmin data are relatively easy to obtain although the Nmin analysis requires incubation of the soil and hence is more time consuming.

Total nitrogen is the mineralisable reserve of organic nitrogen which through ammonification and nitrification replenishes the plant-available pool of ammonium-nitrogen

and nitrate-nitrogen respectively (Hatton & Smart 1984). Total nitrogen therefore represents the potential availability of nitrogen in the soil. Total nitrogen content is correlated with organic matter content. Nitrogen mineralisation rate reflects the rate at which nitrogen is mineralised into ammonium and hence provides a measure of one aspect of nitrogen dynamics within the soil. As already stated, nitrogen is considered to be a limiting nutrient in savanna soils. Plant functional responses are therefore expected to be strongly influenced by nitrogen availability.

Nitrogen is a volatile element and is considered to be the main nutrient lost as a result of fire. Net nitrogen losses do not appear to occur in all savanna systems (Medina 1987). Fire decreases the amount of total nitrogen through volatilisation but increases nitrogen supplies in other ways e.g. a stimulation of nitrogen mineralisation rate (Singh 1993).

4.4.2.7 Phosphorus

Although phosphorus availability has been used as an AN index in other studies e.g. Day, Keddy, McNeill and Carleton (1988) it was not considered a potential single factor index in this study because of the lack of a clear relationship between phosphorus availability and biomass production.

Phosphorus is considered to be a limiting nutrient, e.g. in semi-arid savannas in Botswana (Tolsma, Ernst, Verweij and Vooijs 1987). A large portion of both organic and inorganic forms of P are bound with iron and aluminium compounds or clay particles rendering them insoluble. The bound fractions do not take part in normal soil biochemical processes and are unavailable for plant uptake. Inorganic P is the form that plants can utilise and only a small fraction of this is labile (Hatton & Smart 1984). The characteristic low availability of P is related to the fact that the size and charge of the ion enables it to be held tightly within the soil and hence there is no movement in the soil by diffusion and mass flow. Therefore P is only available to plants through root interception and the use of mycorrhizas.

Fire plays an important role in P dynamics in savannas since it causes the rapid mineralisation of organic matter and results in the release of inorganic P (Holt & Coventry

1991, Singh 1993). Unlike nitrogen, phosphorus has high volatilisation temperature and is rarely lost through burning. Burning usually results in higher concentrations of inorganic P in the upper soil layer (Singh 1993).

4.4.2.8 Percentage organic carbon

Organic carbon is not a plant nutrient but it is the main constituent of soil organic matter. It provides the energy source for the mineralization of macro- and micronutrients, which are bound with carbon into organic forms that are unavailable to plants. Soil organic matter has an important influence on soil physical and chemical properties (O'Connell 1987).

The % organic carbon of a soil is highly correlated with organic P and N concentrations. Most of the soil store of N & P occurs bound with C in organic forms.

Percentage organic carbon related well to the reference indices and hence is considered to be a potential single factor AN index. The index based on % OC is an absolute one and would enable the addition of new soils to the index. Data on % OC are relatively easy to obtain.

One caution about the use of % OC as a fertility index is the circularity of the argument that high % OC results in high productivity since there is a positive feedback between productivity and % OC.

4.4.2.9 Summary of the single factor approach

Percentage clay, % sand, TotN, Nmin and % OC were considered to be the simple indices with the most potential for indexing AN. This assessment was made on the basis of the criteria listed in section 4.1, and on comparisons between simple indices and between simple and reference indices.

4.4.3 MULTIFACTOR INDICES

Effective cation exchange capacity (ECEC) has been used in other studies as an index of soil fertility e.g. Kinako (1983) on the assumption that the cation exchange capacity is a measure of the soil's ability to hold nutrients against leaching (Brady 1974). Solbrig *et al* (1988) consider that % base saturation provides a better estimation of soil fertility than ECEC.

The rationale for developing indices on the basis of combinations of nutrients, especially limiting ones is that plants do not respond independently to different nutrients. For example, P is needed for maximum N mineralisation and nitrification (West 1991). The choice of combinations of N, P and K in this study was based on the fact that these are considered to be limiting in savanna soils. *Panicum maximum* plants in the growth trial related to this study showed both N and P deficiency symptoms (Feuchtenbeiner-Walsh 1990) after eight to eleven weeks of growth suggesting that these nutrients were having a limiting effect on plant response.

One problem with these multifactor indices is that they require detailed soil chemical data. Another problem is that a relatively large amount of calculation is required, especially for the N-P-K eig. index which requires the use of multivariate statistics.

4.4.4 EFFORT TO INFORMATION RATIO

4.4.4.1 Reference indices

The index based on fertility rankings by experts required a relatively large amount of effort but there was a good information return. A high number of man hours were required, both for the collection of soil data and for the ranking by experts. This is considered a useful way of providing a reference index, however.

The index based on biomass production also had a high effort factor but there was a good information return since this approach provided an index that reflected plant response. This

was also considered a useful way of providing a reference index.

Both of these indices have the major drawback that the whole approach would have to be repeated every time a new soil was added to the gradient.

4.4.4.2 Single factor indices

The single factor indices that required the least effort to obtain, such as geology, were only considered suitable for broad generalisations of soil fertility estimates. The single factor indices considered to be potentially useful are considered to yield a high information return for a relatively small amount of effort although the chemical analysis of soils is required for all of these.

4.4.4.3 Multifactor indices

The multifactor approaches required a relatively high level of computation in combination with a need for detailed soil chemical data. These indices were considered to have a relatively high effort to information ratio.

4.5 CONCLUSION

The following ten AN indices were considered worth using on the PAM-AN plane (1) mean score of experts' ratings, (2) shoot production, (3) TotN, (4) Nmin, (5) % clay, (6) % OC, (7) % base saturation, (8) N-P, (9) N-P-K, and (10) eigenvalues of N,P,K. For the purposes of this study TotN was chosen as the main AN index for the quantification of the PAM-AN plane. In addition to TotN, the floristic data were related to indices based on the mean score of experts' ratings, shoot production, Nmin, %clay, %OC, N-P and eigenvalues of N,P,K. The structural data were related to TotN and textural gradients and the functional data to the TotN gradient.

5.0 FLORISTIC CLASSIFICATION

5.1 INTRODUCTION

To date, the floristic approach to the classification of savanna vegetation has predominated (e.g. Bouxin 1975, Gertenbach 1983, le Roux, Grunow, Morris, Bredenkamp & Scheepers 1988, San José & Montes 1991). This approach has been useful for the identification of savanna floristic types but does not provide a basis for the prediction of vegetation change, or a means for inter-site comparisons and extrapolations. The RSSD forum has proposed the use of a structural-functional approach to address these limitations and floristic classifications offer a reference point against which to judge the success of structural and/or functional classifications. Floristic and structural-functional approaches have been compared in other studies (e.g. Werger & Sprangers 1982, Montalvo *et al* 1991).

The aim of this chapter is to present the relationships between the floristic characteristics of the savanna communities and PAM and AN. This chapter partly addresses study objectives 2 and 3. The woody and graminoid components of the vegetation were analysed separately.

The main approach was to investigate trends in woody plant and graminoid species composition in relation to PAM and AN by ordination and classification. Trends in the distribution of woody plant families and graminoid subfamilies and tribes were also considered. These higher taxonomic levels were investigated because they are considered to reflect functional traits of the vegetation. The woody plant and graminoid classifications based on species composition were compared.

Sections 5.2 and 5.3 present the results of the ordination and classification of the woody plant and graminoid floristic data. Section 5.4 considers the comparison between the two classifications. These results are discussed in section 5.5.

Plant available moisture was indexed as the mean number of Gdays per annum derived using the soil water balance model. Unless otherwise stated, the available nutrients gradient was

indexed by total nitrogen content of the A horizon (TotN). The details of these indices are given in chapters 3 and 4 respectively.

The details of the methods of floristic data collection and analysis can be found in chapter 2, sections 2.4 and 2.5 respectively. The sites are referred to by number as in Table 2.1.

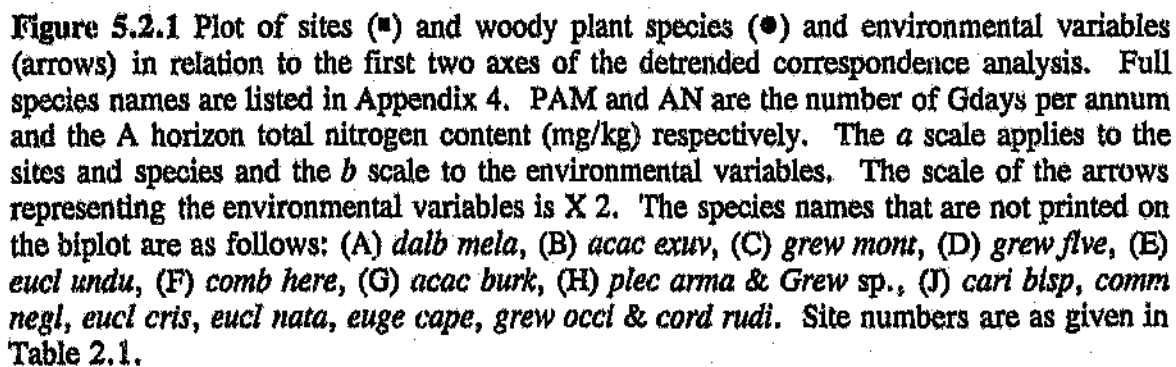
5.2 RESULTS: WOODY VEGETATION

5.2.1 SPECIES COMPOSITION

The eigenvalues of the first four DCA axes were 0.79, 0.65, 0.53 and 0.41 respectively. The cumulative percentage variance accounted for by the first two axes of the species-environment biplot was 39.0% and 62.1% and hence the first two axes were considered an adequate representation of the species and environmental variables (Fig. 5.2.1). The range of sample scores on the first axis was 9.06, indicating that sites at opposite ends of this axis shared few species in common.

The first floristic axis of the DCA was strongly negatively correlated with PAM ($r=-0.71$, $df=17$, $P<0.001$) but not correlated with AN (TotN) ($r=0.11$, $df=17$, $P>0.1$) (Fig. 5.2.1). The second floristic axis was correlated with AN ($r=0.60$, $df=17$, $P<0.01$) but not with PAM ($r=0.24$, $df=17$, $P>0.1$).

The first axis described an available moisture gradient (Fig. 5.2.1). Communities 9 to 14 at the arid end of the gradient were composed of species such as *Acacia erioloba*, *A. mellifera*, *Terminalia prunioides*, *Boscia albitrunca*, *B. foetida*, *Lycium cinereum*, *Colophospermum mopane*, *Commiphora* spp., *Grewia flava* and *G. villosa*. Communities at the moist end of the gradient were composed of species such as *Terminalia sericea*, *Combretum* spp., *Euclea* spp., *Maytenus* spp., *Albizia harveyi*, and *Ochna natalitia*. The second axis described an available nutrients gradient (Fig. 5.2.1). Communities 2, 3, 5 and 8 with a relatively high total nitrogen (TotN) content were associated with several *Acacia* spp. together with species such as *Dombeya rotundifolia* and *Diospyros lycioides*.



Communities at the low AN end of the gradient were associated with species such as *Combretum apiculatum*, *Albizia forbsii*, *Acacia burkei*, *Peltophorum africanum* and *Euclea divinorum*. Community 6, which had a low AN and relatively high PAM, was an outlier. *Burkea africana* was the most abundant species in this community and did not occur in any of the other savanna types sampled. *Strychnos pungens* was also only recorded in community 6.

The first TWINSpan division (eigenvalue 0.66) was interpreted on the basis of plant available moisture since communities 9 to 14, at the arid end of the PAM gradient, were separated from the other communities by this division (Fig. 5.2.2). The first division was

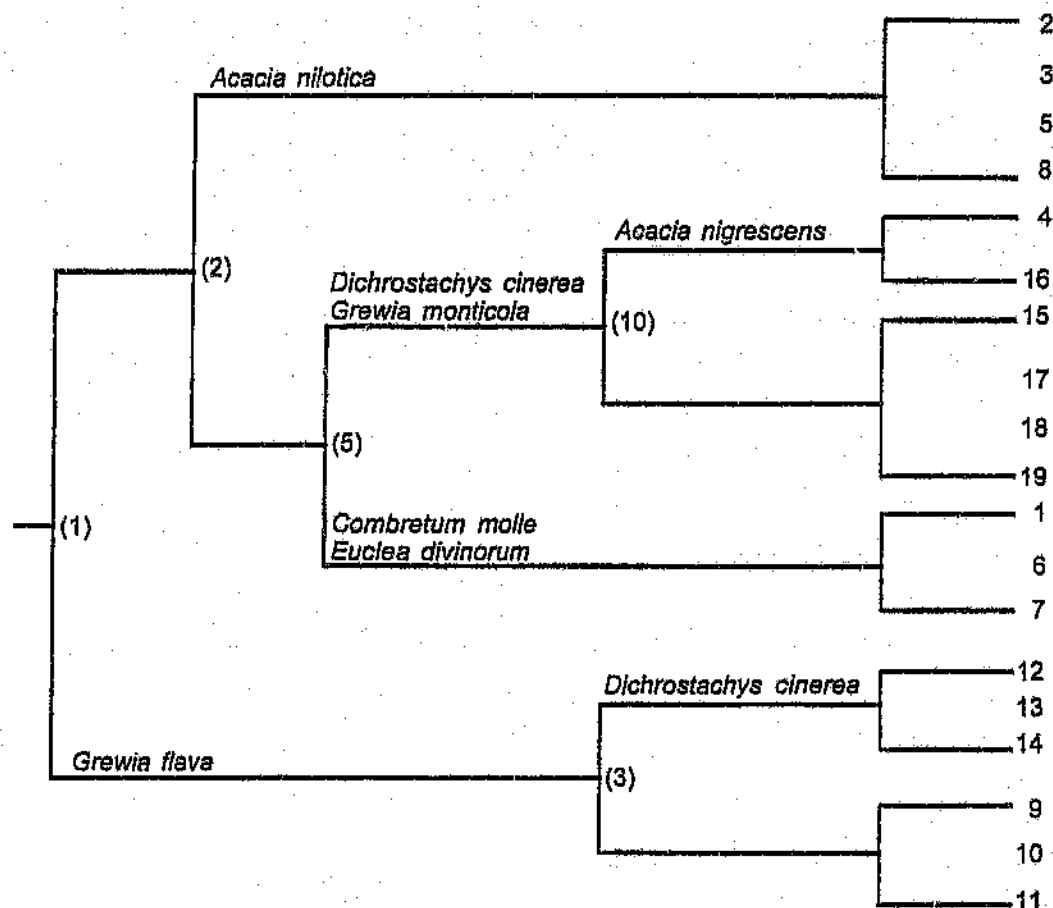


Figure 5.2.2 A dendrogram illustrating the hierarchical classification of the savanna woody plant communities on the basis of species composition. Numbers in parenthesis are the division numbers. The indicator species for each division are shown. Site numbers are as given in Table 2.1.

based on the presence or absence of *Grewia flava* and preferential species included *Acacia erioloba*, *A. mellifera* and *Boscia albitrunca*. Division two (eigenvalue 0.61), which occurred within the group of intermediate and high PAM sites, was interpreted on the basis of available nutrients since communities 2, 3, 5 and 8, at the fertile end of the AN gradient, were separated from the less fertile communities (Fig. 5.2.2). *Acacia nilotica* was the indicator species of this division. Division three (eigenvalue 0.65) split the arid communities into two groups, 9, 10 and 11 and 12, 13 and 14 (Fig. 5.2.2). The indicator species was *Dichrostachys cinerea* which did not occur in communities 9, 10 and 11.

The vegetation sampled at the nineteen sites was classified into four floristic types after TWINSpan division 3, and into seven floristic types based on the final clustering of sites by TWINSpan (Fig. 5.2.2) and on the positions of sites on the DCA biplot (Fig. 5.2.1). The groupings of sites by TWINSpan corresponded with the relative positions of sites on the biplot, with the exception of sites 4 and 6 and 16. The species composition of community 4 was interesting in that the tall woody species were similar to those found in the intermediate and low AN grouping of sites with *Combretum apiculatum* dominant, while the shrub layer had an abundance of *Acacia spp.* On the basis of the ordination result, communities 4 and 6 were considered unique floristic types and community 16 was grouped with communities 15, 17, 18 and 19.

Both the results of the ordination and the classification indicated that, of the two environmental variables considered, PAM had an overriding influence on the species distributions. The primary influence of PAM was clearly illustrated on a plot of the four and seven floristic types on the PAM-AN plane (Fig. 5.2.3). Floristic types 6 and 7 were characteristic of dry savanna areas and species in floristic types 1, 2, 3, 4 and 5 occurred under moister conditions. The species composition of communities 12, 15 and 16 appeared to reflect the PAM status at these sites since although they had a high AN status, they were grouped into floristic types on the basis of PAM. The secondary influence of AN was illustrated by the position on the plane of floristic type 1, with a high nutrient status, and floristic types 2, 4 and 5 with a low AN status. The primary influence of PAM and secondary influence of AN was not clearly illustrated in floristic type 3. A possible explanation for the grouping of these communities into a single floristic type is that they had

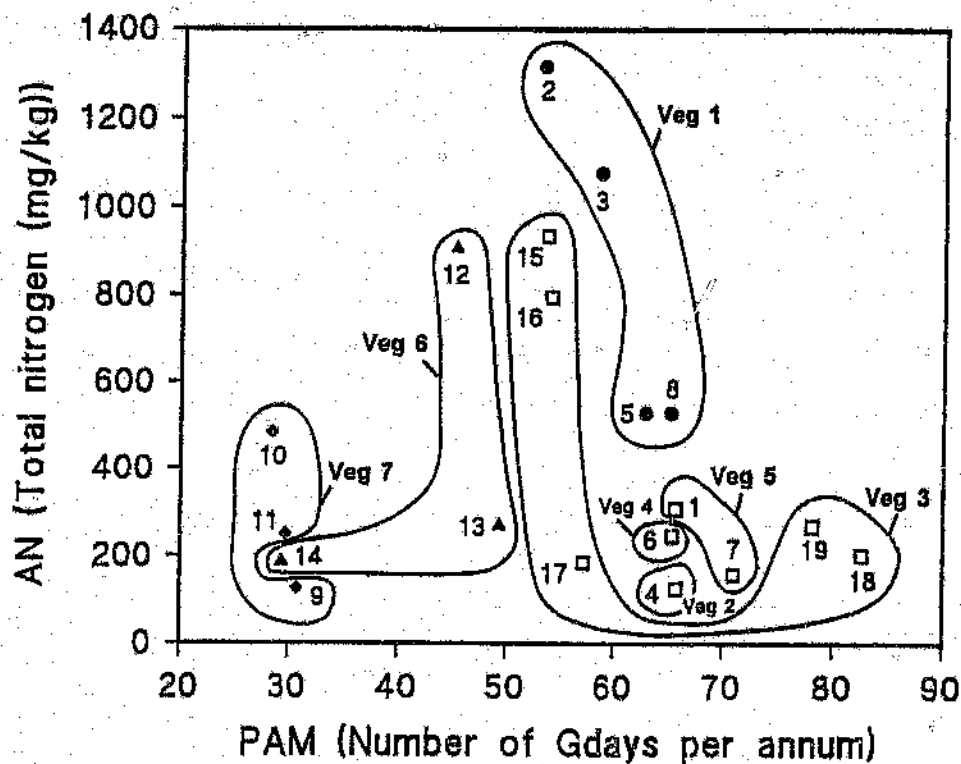


Figure 5.2.3 Woody plant floristic types (veg 1 to 7) on the PAM-AN plane. The sites were grouped according to the hierarchical classification of the species composition of the woody plant communities. The symbols represent the groupings after TWINSpan division 3. The lines indicate the groupings of the sites into the seven floristic types identified. Site numbers are as given in Table 2.1.

a relatively high number of species in common that were not sampled anywhere else, (approximately 30% of the species). These communities were all located in the eastern Transvaal Lowveld and hence were geographically separated from the other communities sampled. The position of community 14 on the PAM-AN plane and the fact that it was not grouped into a floristic type with sites close to it suggests that sites with similar conditions of PAM and AN do not necessarily have a similar species composition. There may be factors other than PAM and AN accounting for this since the arid communities comprising floristic types 6 and 7 were sampled in geographically distinct areas, (the far northern Transvaal and the north eastern Cape respectively).

5.2.2 COMPOSITION AT THE FAMILY LEVEL

There were no clear trends in PAM and AN and floristic composition based on the dominant families in each community. The first floristic axis was weakly negatively correlated with PAM ($r=-0.44$, $df=17$, $P<0.1$), and the second floristic axis was not correlated with either of the environmental variables.

5.2.3 COMPOSITIONAL TRENDS ON THE BASIS OF SELECTED FAMILIES

In contrast to the species composition results, the first floristic axis of the DCA based on the amounts of Mimosoideae, Caesalpinoideae and Combretaceae was significantly negatively correlated with AN ($r=-0.51$, $df=17$, $P<0.01$). Neither axis was correlated with PAM ($P>0.1$, $df=17$) (Fig. 5.2.4). Mimosoideae were most abundant at sites with a high AN status, while Combretaceae and Caesalpinoideae were abundant at sites with intermediate and low AN status respectively (Fig. 5.2.4).

5.2.4 OTHER AN INDICES

The first floristic axis of the ordinations of woody plant species composition with PAM and various indices of AN was significantly correlated with PAM and the first environmental axis, irrespective of the AN index used (Table 5.2.1). This illustrated the primary effect of PAM on species composition. Besides TotN, the other AN indices that were significantly correlated with the second floristic axis were experts' mean ranking, N-P and Nmin (Table 5.2.1).

5.3 RESULTS: GRAMINOID VEGETATION

5.3.1 SPECIES COMPOSITION

The eigenvalues of the first four DCA axes were 0.65, 0.54, 0.40 and 0.34 respectively. The cumulative percentage variance accounted for by the first two axes of the species-

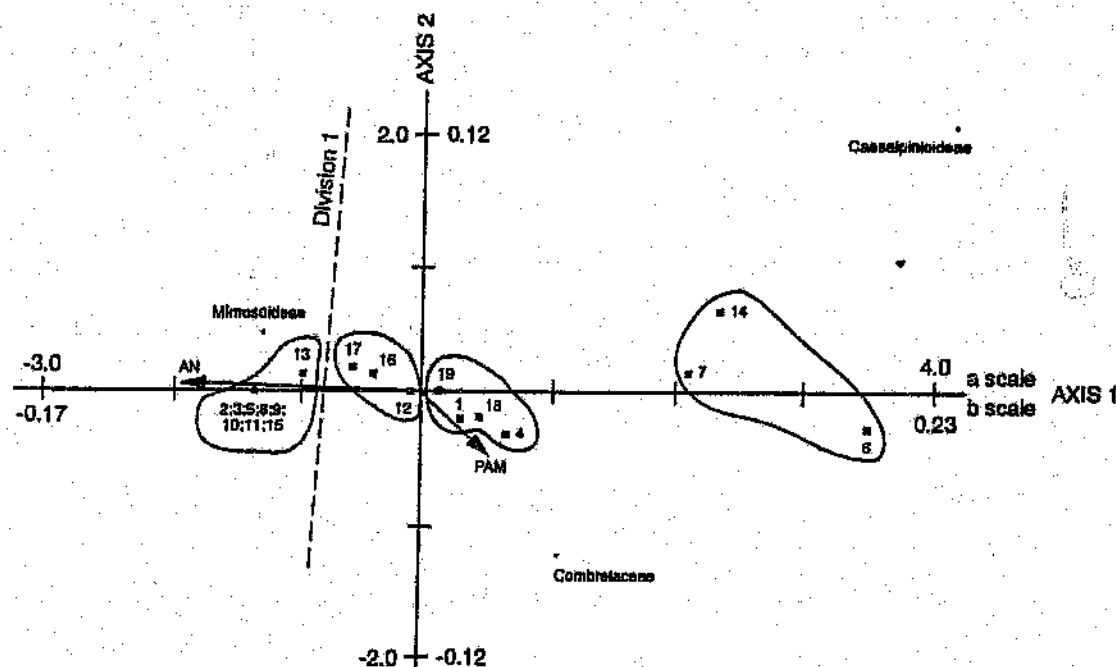


Figure 5.2.4 Plot of sites (■) and environmental variables (arrows) in relation to the first two axes of the detrended correspondence analysis based on the abundance of members of the Mimosoideae, Ceasalpinoideae and Combretaceae (●) at each site. PAM and AN are the number of Grays per annum and the A horizon total nitrogen content (mg/kg), respectively. The *a* scale applies to the sites and families and the *b* scale to the environmental variables. The scale of the arrows representing the environmental variables is X 2. The dashed line indicates the grouping of sites after division 1 and the solid lines, the groupings of sites after the final division (14) of TWINSPLAN. Site numbers are as given in Table 2.1.

environment biplot was 33.9 and 56.6% and hence the first two axes were considered an adequate representation of the species and environmental variables (Fig. 5.3.1). The range of sample scores on the first axis was 7.28, indicating that sites at opposite ends of this axis shared few species in common.

The first floristic axis of the DCA was negatively correlated with PAM ($r=-0.66$, $df=17$, $P<0.005$) and not correlated with AN (TotN) ($r=-0.09$, $df=17$, $P>0.1$) (Fig. 5.3.1). The second floristic axis was correlated with AN ($r=0.59$, $df=17$, $P<0.01$) but not with PAM ($r=0.12$, $df=17$, $P>0.1$).

Table 5.2.1 Eigenvalues and Pearson correlation coefficients (r, with *= $p < 0.05$, **= $p < 0.01$ and ***= $p < 0.001$) from ordination (DCA) of the woody floristic data with PAM (GDays per annum) and various indices of AN. A1 and A2 refer to species axes 1 and 2, E1 and E2 refer to environmental axes 1 and 2, and df = degrees of freedom. Experts = expert's mean ranking, shoot prod = shoot biomass, N-P = combination of N and P based on shoot biomass, N-P-K eig = AN index derived from the first axis eigenvalues of the multivariate analysis of N,P and K, % clay, % OC and NMin = percentage clay, organic carbon and nitrogen mineralization rate in the A horizon respectively.

AN	df	Eigenvalues			r with species A1				r with species A2				r with AN
		A1	A2	A3	PAM	AN	E1	E2	PAM	AN	E1	E2	PAM
Experts	15	0.79	0.67	0.60	0.68**	-0.44	0.77***	0.11	-0.18	-0.50*	0.08	0.56*	-0.12
Shoot prod	14	0.80	0.67	0.56	0.70**	0.14	0.71**	0.43	0.12	-0.16	0.15	0.25	0.33
N-P	11	0.84	0.71	0.63	0.73**	-0.12	0.76**	0.21	0.01	-0.65*	0.18	0.65*	0.11
% clay	16	0.80	0.66	0.53	-0.71***	0.11	0.72***	-0.30	0.28	0.41	-0.21	0.50	0.01
% OC	17	0.79	0.65	0.54	-0.72***	-0.06	0.72***	-0.29	0.22	0.43	-0.18	0.45	0.19
Nmin	17	0.79	0.65	0.54	-0.72***	0.16	0.76***	-0.06	0.22	0.52*	-0.05	0.55*	0.12
NPK eig	17	0.79	0.65	0.54	-0.72***	0.28	0.74***	-0.14	0.22	0.45	-0.10	0.53*	-0.11

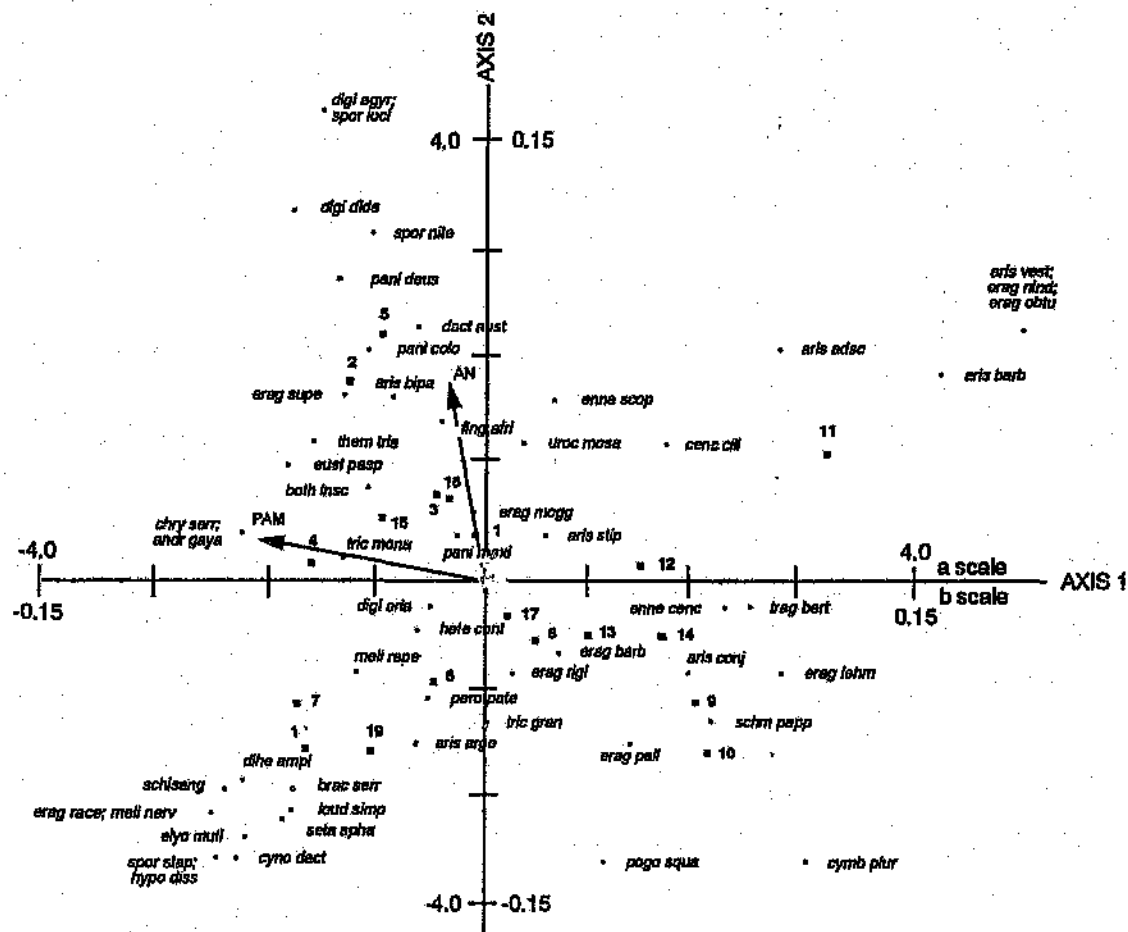


Figure 5.3.1 Plot of sites (■) and grass species (●) and environmental variables (arrows) in relation to the first two axes of the detrended correspondence analysis. Full species names are listed in Appendix 6. PAM and AN are the number of Gdays per annum and the A horizon total nitrogen content (mg/kg), respectively. The *a* scale applies to the sites and species and the *b* scale to the environmental variables. The scale of the arrows representing the environmental variables is X 4. Site numbers are as given in Table 2.1.

The first axis described an available moisture gradient (Fig. 5.3.1). Communities 9 to 14 at the arid end of the gradient were associated with species such as *Schmidtia pappophoroides* and *Enneapogon cenchroides*. *Aristida* spp. and *Eragrostis* spp. occurred predominantly at these arid sites. Communities at the moist end of the gradient were associated with species such as *Diheteropogon amplexans*, *Loudetia simplex*, *Cynodon dactylon*, *Melinis nervigloris* and *Schizocarium sanguineum*. The second axis described an available nutrients gradient (Fig. 5.3.1). Communities 2, 3, 5, 15 and 16 with a relatively high TotN content were associated with species such as *Panicum deustum*, *P. coloratum*, *Themeda triandra*, *Bothriochloa insculpta*, *Urochloa mosambicensis* and *Enneapogon scoparius*. Communities at the low AN end of the gradient were associated with species such as *Hyperthelia dissoluta*, *Elyonurus muticus*, *Pogonarthria seriarrosa* and *Cymbopogon plurinodis*. Community 11 was an outlier relative to the position of the other arid sites since it had species such as *Aristida vestita*, *Eragrostis nindensis* and *E. obtusa* that are characteristic of arid areas but occurred exclusively at site 11 in this study (Fig. 5.3.1).

The first TWINSpan division (eigenvalue 0.52) was interpreted on the basis of plant available moisture since communities 9 to 14 at the arid end of the PAM gradient were separated from the other communities by this division (Fig. 5.3.2). Communities 8 and 17 had some species in common with the arid communities and were grouped with them. The first division indicator species for the arid grouping were *Aristida congesta*, *Schmidtia pappophoroides* and *Eragrostis lehmanniana*. *Themeda triandra* was the indicator species for the moist grouping. Division two (eigenvalue 0.57), which occurred within the group of intermediate and high PAM sites, was interpreted on the basis of available nutrients since communities 2, 3, 5, 15 and 16, at the fertile end of the AN gradient, were separated from the other communities by this division (Fig. 5.3.2). The second division indicator species was *Diheteropogon amplexans*. Division three (eigenvalue 0.57) separated community 11 from the other arid communities (Fig. 5.3.2). The indicator species for this division was *Aristida adscensionis*.

The vegetation sampled at the nineteen sites was classified into four floristic types after TWINSpan division three and nine floristic types based on the final clustering of sites by TWINSpan (Fig. 5.3.2) and on the positions of sites on the DCA biplot (Fig. 5.3.1). The

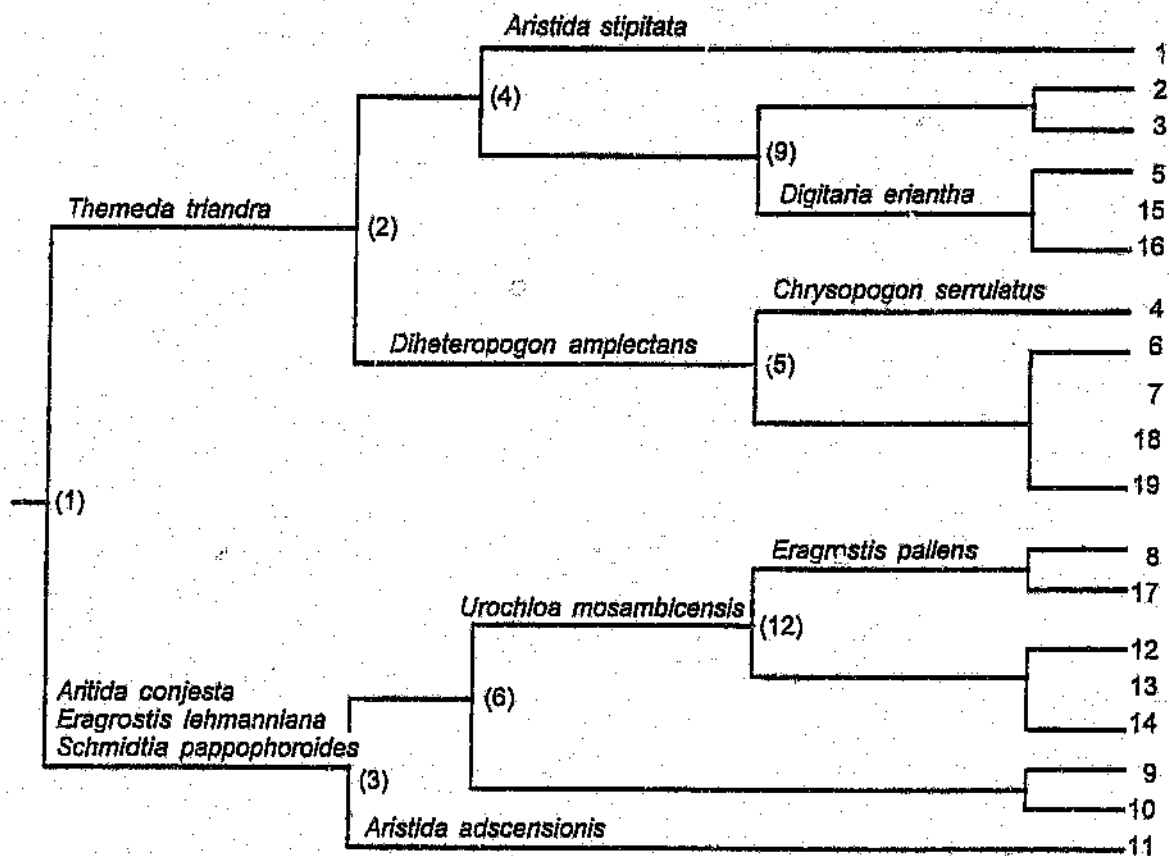


Figure 5.3.2 A dendrogram illustrating the hierarchical classification of the savanna graminoid communities on the basis of species composition. Numbers in parenthesis are the division numbers. The indicator species for each division are shown. Site numbers are as given in Table 2.1.

groupings of sites by TWINSpan corresponded with the relative positions of sites on the biplot. Communities 1 and 4 had a low AN status but were grouped with the high AN status sites. Community 1 had a high occurrence of *Panicum maximum* which was also abundant in the high AN communities. *Panicum maximum* occurred predominantly in subcanopy habitats at this site. Based on the results of the classification, communities 1 and 4 were considered unique floristic types.

Both the results of the ordination and the classification indicated that, of the two environmental variables considered, PAM had an overriding influence on the species

distributions. The primary influence of PAM was apparent from a plot of the four and nine floristic types on the PAM-AN plane (Fig. 5.3.3).

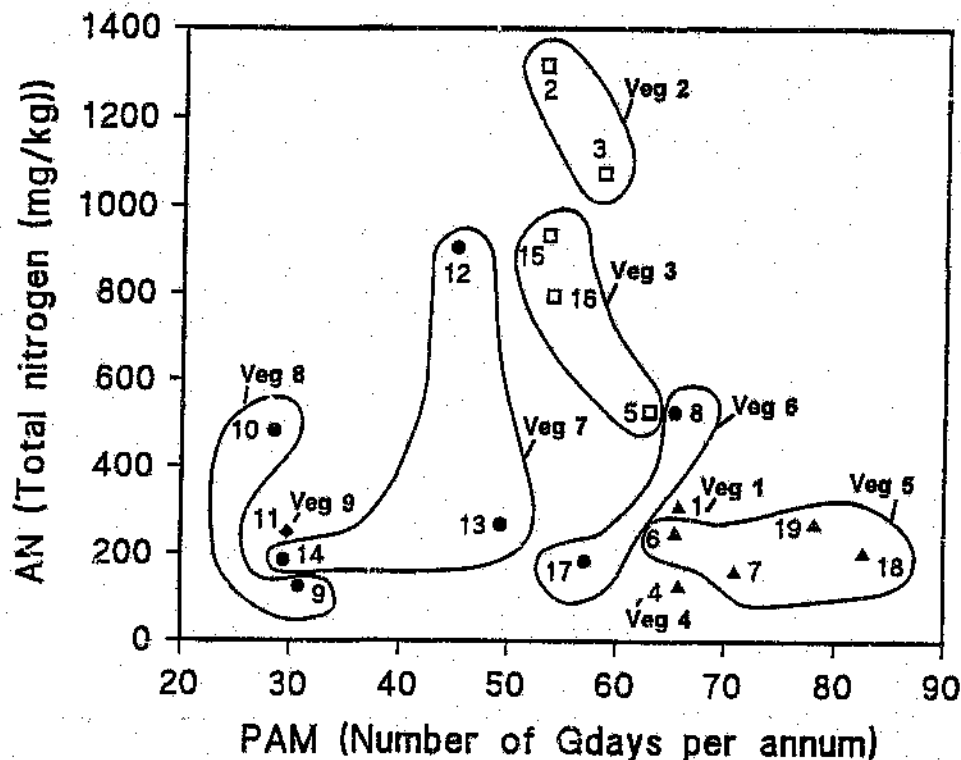


Figure 5.3.3 Graminoid floristic types (veg 1 to 9) on the PAM-AN plane. The sites were grouped according to the hierarchical classification of the species composition of the graminoid communities. The symbols represent the groupings after TWINSpan division 3. The lines indicate the groupings of the sites into the nine floristic types identified (Table 5.3.1). Site numbers are as given in Table 2.1.

Floristic types 7, 8 and 9 were characteristic of dry savanna areas and species in floristic types 1, 2, 3, 4, 5 and 6 occurred under moister conditions. The secondary influence of AN was illustrated by the position on the plane of floristic types 2 and 3, with a high nutrient status, and floristic types 1, 4 and 5 with a low AN status. As for the woody vegetation, there were communities with similar conditions of PAM and AN that were not grouped into the same floristic types, e.g. communities 5 and 8 and communities 11 and 14. The species composition of community 5 appeared to be related to AN since this community was grouped with the high AN sites. Although the availability of nutrients at site 8 was very similar to that at site 5, the species composition of community 8 appeared to be related to AN since it was grouped with the arid sites.

5.3.2 COMPOSITIONAL TRENDS ON THE BASIS OF SUBFAMILIES

The eigenvalues of the first two DCA axes were 0.53 and 0.06 respectively. The first floristic axis was negatively correlated with PAM ($r=-0.68$, $df=17$, $P<0.005$) indicating that the grasses of the Panicoideae were associated with moister sites while grasses of the Chloridoideae and Arundinoideae were associated with drier sites (Fig. 5.3.4). Neither axis

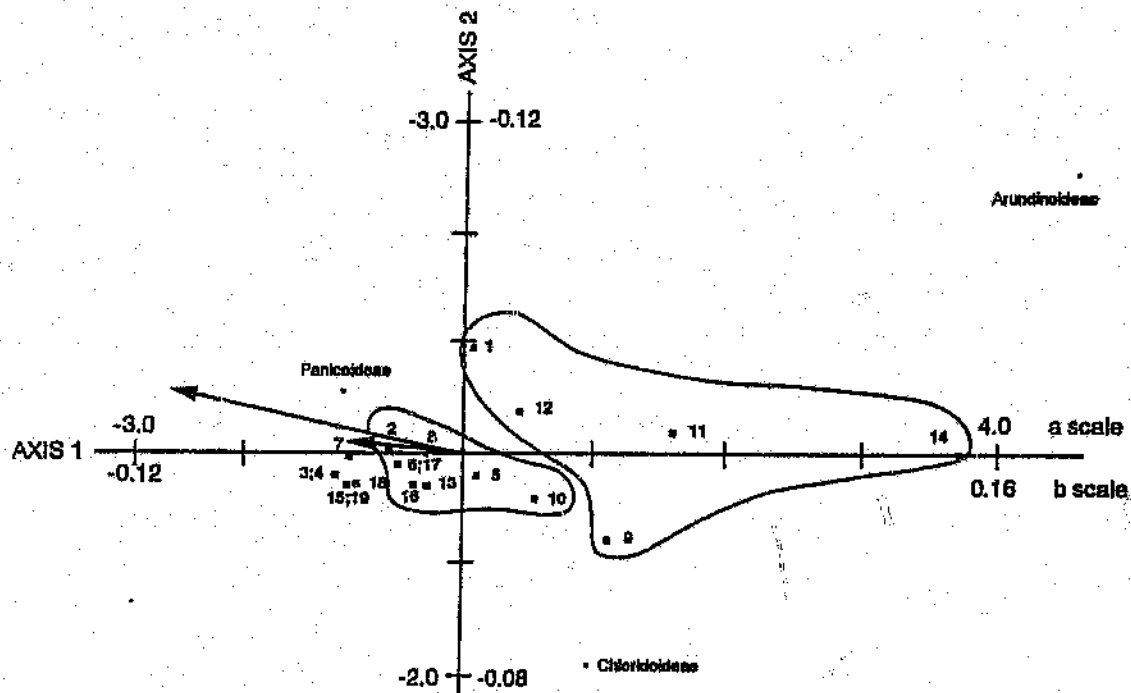


Figure 5.3.4 Plot of sites (■) and environmental variables (arrows) in relation to the first two axes of the detrended correspondence analysis based on the grass subfamilies (●) present at each site. PAM and AN are the number of Gdays per annum and the A horizon total nitrogen content (mg/kg), respectively. The *a* scale applies to the sites and families and the *b* scale to the environmental variables. The scale of the arrows representing the environmental variables is X 4. The grouping of sites after the second division of TWINSpan is indicated. Site numbers are as given in Table 2.1.

was correlated with AN ($P>0.1$, $df=17$).

5.3.3 COMPOSITIONAL TRENDS ON THE BASIS OF TRIBES

The eigenvalues of the first two DCA axes were 0.56 and 0.34 respectively. The first floristic axis was negatively correlated with PAM ($r=-0.59$, $df=17$, $P<0.01$) indicating that the compositional variation based on grass tribes could be explained in relation to the PAM gradient. The Aristideae, Pappophoreae and Chlorideae occurred predominantly at the arid sites while the Paniceae, Arundinelleae and Andropogonaceae were the predominant tribes at the moist sites (Fig. 5.3.5). Neither of the axes were correlated with AN ($P>0.1$, $df=17$).

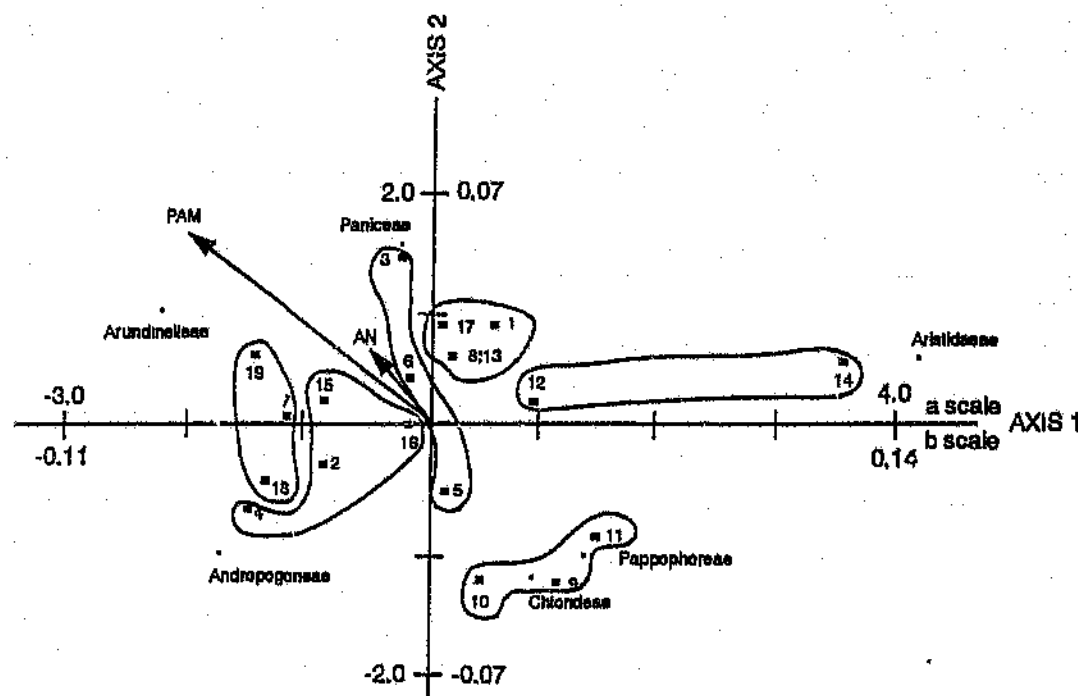


Figure 5.3.5 Plot of sites (■) and environmental variables (arrows) in relation to the first two axes of the detrended correspondence analysis based on the grass tribes (●) present at each site. PAM and AN are the number of Gdays per annum and the A horizon total nitrogen content (mg/kg), respectively. The *a* scale applies to the sites and families and the *b* scale to the environmental variables. The scale of the arrows representing the environmental variables is X 4. The grouping of sites after the sixth division of TWINSpan is indicated. Site numbers are as given in Table 2.1.

5.3.4 OTHER AN INDICES

The first floristic axis of the ordinations of the graminoid floristic data with PAM and various indices of AN was significantly correlated with PAM and the first environmental axis, irrespective of the AN index used (Table 5.3.1). This illustrated the primary effect of PAM on species composition. Besides TotN, the second floristic axis was correlated with all the other AN indices except shoot production (Table 5.3.1).

5.4 COMPARISON OF WOODY AND GRAMINOID CLASSIFICATIONS

The woody plant communities were grouped into seven floristic types and the graminoid communities into nine floristic types. A comparison of the classifications indicated that similar woody plant communities did not necessarily have similar graminoid communities associated with them and *vice versa* but there was a high degree of correlation overall (Fig. 5.4.1). Communities 1, and 7 were classified into one woody floristic type but represented two different graminoid vegetation types. Similarly, community 6 had a unique woody plant composition but the graminoid community at this site was similar to communities 7, 18 and 19. Sites 8 and 17 had a similar graminoid composition but were classified into different woody floristic types. The savanna types that had a similar woody plant and graminoid composition were high AN sites 2 and 3, and 15 and 16, high PAM sites 18 and 19 and the arid sites 12, 13 and 14, and 9 and 10. Community 4 had a unique woody plant and

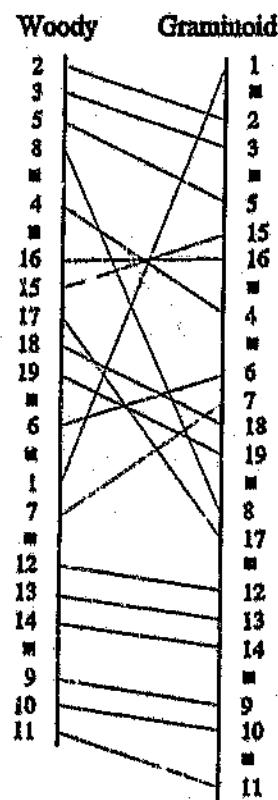


Figure 5.4.1 Comparison of the woody plant and graminoid floristic classifications. Floristic types are separated by solid squares.

Table 5.3.1 Eigenvalues and Pearson correlation coefficients (r, with *=p<0.05, **=p<0.01 and ***=p<0.001) from ordination (DCA) of the grass floristic data with PAM (GDays per annum) and various indices of AN. A1 and A2 refer to species axes 1 and 2, E1 and E2 refer to environmental axes 1 and 2, and df = degrees of freedom. Experts = expert's mean ranking, shoot prod = shoot biomass, N-P = combination of N and P based on shoot biomass, N-P-K eig = AN index derived from the first axis eigenvalues of the multivariate analysis of N,P and K, % clay, % OC and NMin = percentage clay, organic carbon and nitrogen mineralization rate in the A horizon respectively.

AN	df	Eigenvalues			r with species A1				r with species A2				r with AN	
		A1	A2	A3	PAM	AN	E1	E2	PAM	AN	E1	E2	PAM	
Experts	15	0.64	0.60	0.38	-0.66**	-0.13	0.69**	0.19	0.01	-0.52*	0.15	0.52*	-0.12	
Shoot prod	14	0.63	0.56	0.42	-0.63**	-0.34	0.66**	-0.56*	0.30	0.39	-0.37	0.44	0.26	
N-P	11	0.65	0.60	0.40	-0.70**	-0.25	0.72**	0.40	-0.21	-0.60*	0.34	0.61*	0.12	
% clay	16	0.66	0.56	0.49	-0.69**	-0.13	0.72***	-0.30	0.11	0.55*	-0.24	0.56**	-0.04	
% OC	17	0.65	0.54	0.40	-0.66**	-0.20	0.67**	-0.22	0.12	0.64**	-0.21	0.64**	0.16	
Nmin	17	0.65	0.54	0.40	-0.66**	-0.09	0.66**	-0.21	0.12	0.51*	-0.17	0.52*	0.06	
NPK eig	17	0.65	0.54	0.40	-0.66**	0.13	0.66**	-0.09	0.12	0.57*	-0.08	0.61**	-0.13	

graminoid species composition. A comparison of the floristic classifications after TWINSpan division 3 indicates that all the woody plant and grass communities in the high PAM - low AN region of the plane were grouped into one floristic type (Fig. 5.2.3 & Fig. 5.3.3).

An important similarity between the two classifications was that they were both related primarily to the PAM gradient with AN having a secondary effect. The results of the DCA suggested that PAM had a slightly greater influence on the species composition of the woody vegetation than it had on the graminoid composition, since it was slightly more strongly correlated with the first woody floristic axis ($r=-0.71$, $df=17$, $P<0.001$) than with the first graminoid floristic axis ($r=-0.66$, $df=17$, $P<0.005$). The correlation between the second floristic axis of both the woody plant ($r=0.60$, $df=17$, $P<0.05$) and graminoid ($r=0.59$, $df=17$, $P<0.01$) ordinations was similar.

5.5 DISCUSSION

The influence of PAM and AN on savanna species composition has been observed in other studies (van der Meulen & van Gils 1983, Jensen & Belsky 1989, San José & Montes 1991, Ben Shahr 1991). The results of this study, for both woody plant and graminoid composition, support the conclusion of Huntley and Walker (1982) that water is the major environmental determinant of savanna species composition. Johnson and Tothill (1985) found that, within rainfall regions in Australian savannas, soil water holding capacity and internal drainage (i.e. factors relating to PAM) were important controls on floristic composition. The secondary influence of AN on species composition is likely to be most pronounced within each savanna region (i.e. under similar climatic conditions) as found by Ben-Shahr (1991) in the Sabi-Sabi Game Reserve and by O'Connor (1992) in a semi-arid savanna in the far northern Transvaal.

5.5.1 WOODY VEGETATION

Certain of the species sampled only occurred in moist or in arid communities. Species such

as *Acacia mellifera*, *Boscia albitrunca*, *Lycium cinereum*, *Colophospermum mopane*, *Commiphora africana*, *Grewia flava* and *Terminalia prunioides* have been recorded in other arid savanna areas e.g. in the Etosha National Park (le Roux *et al* 1988). Similarly, there were species that were restricted to either dystrophic or eutrophic soils. Species such as *Acacia burkei*, *Albizia forbsii*, *Combretum collinum* and *Terminalia sericea* commonly occur on sandy soil derived from granite and sandstone e.g. in the south-western Kruger National Park (Venter & Gertenbach 1986). There were also a number of species that occurred in communities over a range of PAM and AN. These included species such as *Combretum apiculatum* which occurred in both low and high PAM communities and *Dichrostachys cinerea* and *Sclerocarya birrea* that occurred on both low and high AN soils.

Nylsvley community 6 had a unique woody plant composition. This is attributed to the fact that this community represents part of the southern limit of the Zambezian Domain or phytochorion. This domain is characterised by 'miombo' taxa such as *Burkea africana* and *Ochna pulchra* growing on dystrophic soils (Huntley 1982). The uniqueness of Mkuzi community 4 is attributed to the fact that the tree and shrub components were floristically somewhat different. The tree component was composed predominantly of *Combretum apiculatum*, while the shrub layer had an abundance of *Acacia nigrescens*, *Acacia nilotica* and *Acacia tortilis*. This combination of tree and shrub species was not encountered at any of the other sites. A possible explanation is that this community has been subject to a fairly regular occurrence of fire (Goodman, P.S. pers. comm.) that may have altered the species composition of the shrub layer. The other floristic types reflected known distributions of species in relation to climate and soil fertility.

The relationship between the distribution of selected families and AN observed in this study supports the hypothesis that members of the Mimosoideae are abundant on nutrient rich soils and members of the Caesalpinoideae and Combretaceae on nutrient poor soils (Scholes 1991). The distribution of these families was not related to PAM although it has been hypothesised that members of the Caesalpinoideae are dominant in moist savannas (Huntley 1982) and members of the Mimosoideae in arid savannas (Tinley 1982). The floristic groups based on selected families could be considered as functional groups since the functional characteristics of each of these families are distinct and of ecological significance in relation to PAM and

AN. This aspect will be discussed in more detail in chapter 7.

The results of this study indicated that communities with similar conditions of PAM and AN were not always floristically similar. One explanation for this is that the species composition of a community is sensitive to the historically determined chorological pattern of distribution of its component species (Werger & Sprangers 1982). That certain species only occur in certain geographical locations, irrespective of environmental conditions, means that the comparability of the results of a floristic classification on the basis of PAM and AN, as in this study, is geographically restricted. Floristic types 3, 6 and 7 contained communities with a range of conditions of PAM and AN but in each case, the communities were sampled in the same geographical areas. The observation that communities with similar conditions of PAM and AN were not always floristically similar supports the need for an approach such as the structural-functional one for comparative and predictive purposes. The underlying hypothesis is that savannas with similar conditions of PAM and AN that differ floristically are similar structurally and/or functionally.

5.5.2 GRAMINOID VEGETATION

As for the distribution of woody plant species, there were graminoid species that occurred only under moist or arid conditions, only on dystrophic or eutrophic soils and some that occurred across a range of moisture and nutrient conditions. Genera such as *Andropogon*, *Diheteropogon*, *Schizacarium* and *Loudetia* occur predominantly in moist areas and genera such as *Stipagrostis*, *Enneapogon* and *Aristida* are common in arid areas (Huntley 1982). Genera such as *Hyparrhenia* are characteristic of dystrophic soils (Cole 1982) and genera such as *Panicum* and *Cenchrus* of eutrophic soils.

The unique floristic composition of Mkuzi community 4 and of Rooipoort community 11 may be related to the shallowness and stoniness of the soils at these sites. Species such as *Melinis repens*, *Heteropogon contortus*, *Chrysopogon serrulatus*, *Enneapogon scoparius* and certain *Aristida* and *Eustachys* species that occurred at these sites are known to be common on shallow, stony soils (Roberts 1971, Cole 1986, and Ben-Shahar 1987). Bosch, van

Rensburg & Truter (1987) found that percentage stoniness of the soil and soil depth were important habitat factors for explaining grass compositional variation in the western parts of the South African grassland biome. The classification of intermediate PAM communities 8 and 17 with the arid communities reflected the higher occurrence of *Aristida* and *Eragrostis* species at these sites than at the other intermediate and high PAM sites. *Eragrostis* and *Aristida* species are common in arid areas (Johnson & Tothill 1985).

The relationship between the distribution of graminoid subfamilies and tribes and PAM observed in this study is well known in the savanna areas of southern Africa (Gibbs Russell *et al* 1990), Australia and South America (Johnson and Tothill 1985). On all of these continents, Panicoid grasses were common in mesic areas while Aristidoid and Chloridoid grasses occurred under semi-arid conditions (Johnson & Tothill 1985). Johnson and Tothill (1985) proposed a model for the classification of the world's savannas based on tribal floristic variation in relation to gradients of annual rainfall and soil textural characteristics. On this basis they identified three major savanna types, namely a core Andropogonoid savanna, a wet Panicoid-Andropogonoid savanna and a dry Aristidoid-Eragrostoid-Chloridoid savanna. Johnson & Tothill (1985) suggest that while many of the predominant savanna grass genera are the same on different continents, geological isolation and continent specific speciation preclude global comparisons of savannas at the species level. They consider the use of a higher taxonomic level such as tribes as a basis for a global classification of savanna types as a solution to this problem. The classification of grasses into subfamilies and tribes has a high predictive value and indicates broad categories of morphology, reproductive adaptations, anatomy, physiology and geographical distribution (Gibbs Russell & Spies 1988). Thus, the floristic groups derived in this study based on the distribution of subfamilies and tribes could be considered as functional groups. This aspect will be dealt with in more detail in chapter 7.

The results of the floristic classification of the graminoid communities in the plane of PAM and AN indicated that communities with similar conditions of PAM and AN were not always floristically similar. As for the woody plant communities, these results support the need for an approach such as the structural-functional one for comparative and predictive purposes.

5.5.3 OTHER AN INDICES

The results of the ordinations of woody plant and graminoid species composition with PAM (Gdays) and various indices of AN further supported the hypothesis that PAM has an overriding influence on the distribution of savanna species. The first species axis was correlated with PAM irrespective of the AN index used. Not all the AN indices were successful in explaining the compositional variation of the woody vegetation. Apart from the experts' rankings index, all the indices that were correlated with woody composition were related to the nitrogen content of the soil. In addition to the various nitrogen indices, grass species composition was also related to % clay and % organic carbon.

5.5.4 COMPARISON OF WOODY AND GRAMINOID CLASSIFICATIONS

The differences between the woody plant and graminoid floristic classifications suggested that these components of the vegetation were responding differently to PAM and AN in a number of the communities sampled. A possible explanation for this is that woody plants and graminoids respond to environmental constraints at different spatial and temporal scales (Johnson and Tothill 1985). Another explanation is that the floristic composition of these two components of the savanna vegetation is influenced by other environmental factors e.g. the apparent effect of stoniness and soil depth on graminoid floristic composition. The effects of disturbance may also account for compositional differences e.g. communities 5 and 8 that had a similar woody plant composition but a different graminoid composition. The composition of the herbaceous component can be completely altered by grazing history and changes rapidly in response to annual rainfall variability (O'Connor 1985). The similarities between the woody plant and graminoid classifications, however, suggested that these two components of the vegetation do not respond to the influences of PAM and AN entirely independently.

5.6 CONCLUSION

Plant available moisture had a primary effect on the species composition of the savanna communities sampled and on the distribution of graminoid subfamilies and tribes. The effect

of available nutrients was less pronounced, but still significant and was strong on tree composition at the family level. The woody plant and graminoid components at each site were not always classified into the same floristic types but there was a degree of correlation indicating that these components do not act entirely independently in response to conditions of PAM and AN.

6.0 STRUCTURAL TRENDS AND CLASSIFICATION

6.1 INTRODUCTION

Although the floristic approach to the analysis of plant communities has predominated since the turn of the century (Werger & Sprangers 1982), the use of the physiognomic-structural approach has continued, as reflected in the classical works of Raunkiaer (1934), Dansereau (1951) and others. The structural approach to characterising vegetation is considered to have certain advantages over the floristic approach. For example, the structural approach does not require a detailed floristic knowledge of the vegetation under analysis (Werger & Sprangers 1982). The structural approach can be used for describing large geographic zones of vegetation (e.g. Box 1981), and for examining small scale or local environmental gradients (e.g. Bredenkamp & Theron 1985). The rationale for the use of a structural approach is considered in more detail in section 1.3 of chapter 1.

The structure of savanna vegetation has been analysed using both *a priori* (Edwards 1983, Bredenkamp & Theron 1985) and *a posteriori* (Lopes & Cox 1977, Skarpe 1990) approaches. van der Meulen & Westfall (1980) analysed the structure of bushveld vegetation using Dansereau's system of structural diagrams.

Many floristic analyses have been supplemented by profile diagrams and physiognomic-structural data (Moll, Campbell & Probyn (1976). A number of studies in savannas (e.g. Coetzee & Gertenbach 1977, Gertenbach 1983, Fraser, van Rooyen & Verster 1987, Belsky & Amundson 1990 submitted, O'Connor 1992) have used a floristic and structural approach in order to explain vegetation - environment relationships.

A knowledge of the structure of savanna vegetation is important for several reasons, for example, because it influences the distribution of wildlife. The structural approach provides a basis for predictive modelling of vegetation change because a change in structure usually reflects the reaction of the vegetation to perturbations such as disturbance (Bredenkamp & Theron 1985).

The aim of this chapter is to present the relationships between the structural characteristics of the woody plant, graminoid and forb communities and PAM and AN. This chapter partly addresses study objectives 2 and 3.

Structural characteristics of the woody plant and graminoid communities were analysed separately. The first section of the chapter considers the trends in individual woody plant structural characteristics along the PAM and AN gradients. Section 2.2 presents the trends in individual graminoid and forb structural characteristics with PAM and AN and considers seasonal changes in the structural characteristics of the herbaceous layer. The third section considers the structural relationships between the woody plant and graminoid and graminoid and forb communities. The potential for classifying the woody plant and graminoid communities on a structural basis, using both an *a priori* and an *a posteriori* approach, is investigated.

Plant available moisture was indexed as the number of Gdays per annum derived using the soil water balance model. Unless otherwise stated, AN was indexed by the total nitrogen content of the A horizon (mg/kg). The details of these indices are contained in chapters 3 and 4 respectively.

The methods of structural data collection and analysis are presented in Chapter 2, sections 2.4 and 2.5 respectively. The sites are referred to by number as in Table 2.1.

6.2 WOODY VEGETATION RESULTS

6.2.1 COMMUNITY STRUCTURE IN RELATION TO PAM AND AN

Woody plant density was not significantly correlated with either PAM ($r=0.21$, $df=17$, $P>0.1$) or AN ($r=-0.29$, $df=17$, $P>0.1$). Although there was no clear trend in woody density on the PAM-AN plane, the highest densities occurred in communities 1, 7 and 18, at the moist end of the PAM gradient on dystrophic soils (Fig. 6.2.1 a).

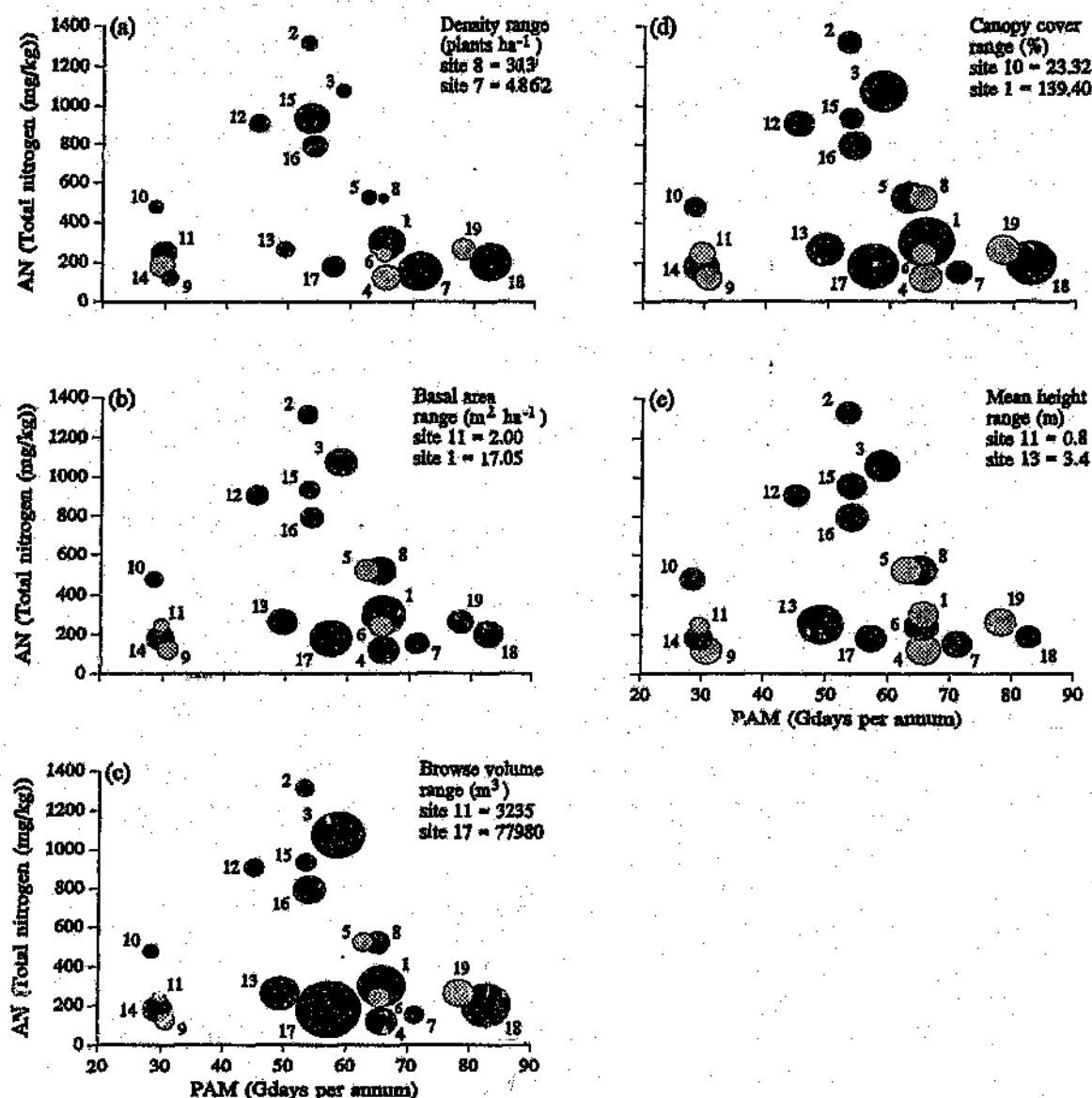


Figure 6.2.1 Trends in woody plant community (a) density, (b) basal area, (c) total browse volume, (d) canopy cover and (e) mean height on the PAM-AN plane. PAM is indexed as the mean number of Gdays per annum and AN as the total nitrogen content of the A horizon in mg/kg of soil. The circles indicate the value of each structural variable at each site. These values are contained in Appendix 2. Site numbers are as given in Table 2.1.

Total basal area was significantly positively correlated with PAM ($r=0.47$, $df=17$, $P<0.05$) indicating that woody basal area increased with an increase in moisture availability. Although the highest basal areas occurred in the high PAM and low AN region of the PAM-AN plane (Fig. 6.2.1 b), there was no significant correlation between basal area and AN

($r=-0.26$, $df=17$, $P>0.1$).

There was a weak trend in total browse volume with PAM ($r=0.41$, $df=17$, $P<0.1$) but no trend with AN ($r=-0.13$, $df=17$, $P>0.1$) (Fig. 6.2.1 c).

There were no clear trends in canopy cover with either PAM ($r=0.26$, $df=17$, $P>0.1$) or AN ($r=0.21$, $df=17$, $P>0.1$) although sites with the highest canopy covers occurred in moist areas on dystrophic soils (Fig. 6.2.1 d). (The canopy cover values represent the sum of the canopy covers of the short and tall woody plant layers at each site).

Both mean height ($r=0.58$, $df=17$, $P<0.05$) and mean maximum height ($r=0.48$, $df=17$, $P<0.05$) were positively correlated with PAM. This indicated that woody height increased with an increase in moisture availability. No trend in height occurred along the AN gradient ($P>0.1$, $df=17$) (Fig. 6.2.1 e).

These results indicated that where environmental factors were influencing woody community structure, PAM had the overriding effect.

For all structural features there was a general trend towards higher values occurring in the high PAM - low AN region of the PAM-AN plane (Fig. 6.2.1 a-e). There were exceptions to these trends, however. The high AN - intermediate PAM community 3 and the low PAM - low AN community 14 had consistently higher values than communities with similar conditions of PAM and AN (Fig. 6.2.1 a-e). The high PAM - low AN communities 6 and 7 had consistently lower values than communities with similar conditions of PAM and AN (Fig. 6.2.1 a-e). The woody plant community at site 16 had a higher browse volume and canopy cover and the woody plants at site 9 were taller than the surrounding sites. These results indicated that a range of structural features occurred within each PAM and AN region on the plane. Communities positioned in close proximity to one another on the plane, namely communities 11 and 14, 5 and 8 and 1 and 6 were different from one another for all the structural variables considered (Fig. 6.2.1 a-e). These results indicated that woody plant communities with similar conditions of PAM and AN did not consistently have similar structural features.

There were no significant correlations between the structural variables and soil texture represented as percentage clay ($P > 0.1$, $df=17$).

None of the woody plant structural features were correlated with either soil stone content or with soil profile depth. This indicated that neither of these soil structural properties had an overriding influence on the woody vegetation structure.

6.2.2 BROWSE VOLUME DISTRIBUTION

Four browse volume groups were formulated from a subjective comparison of the browse volume distribution profiles in all the woody plant communities (Fig. 6.2.2).

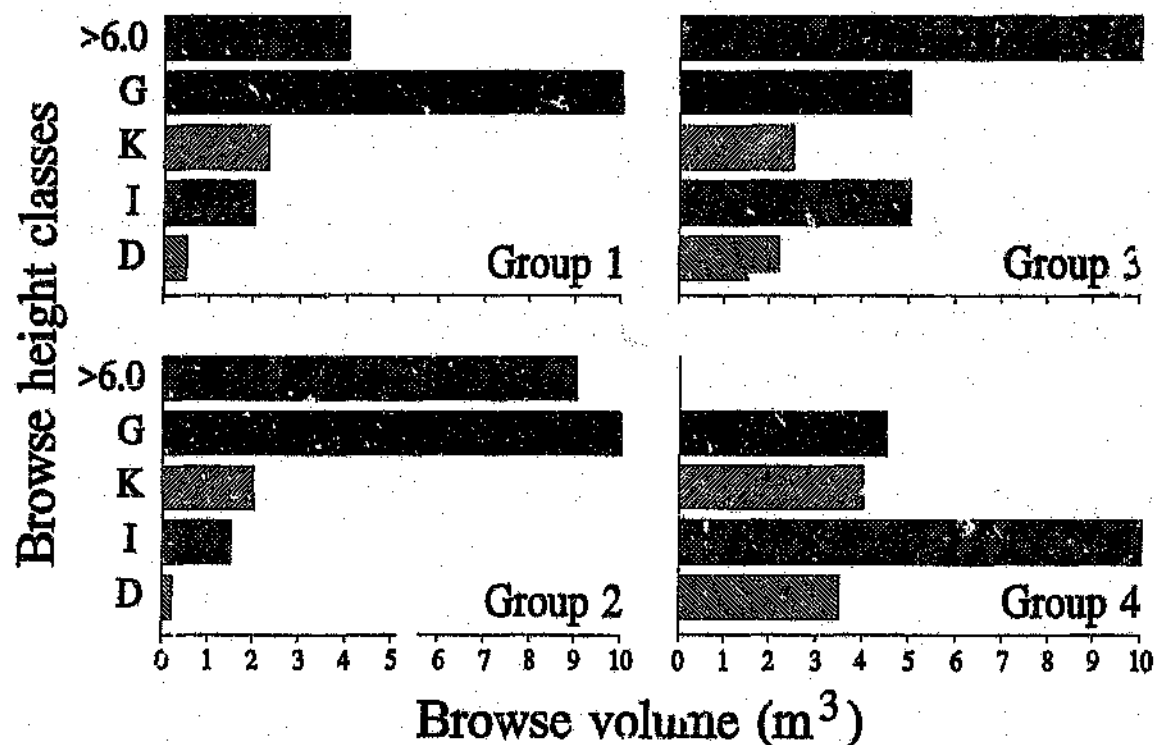


Figure 6.2.2 Four characteristic browse volume distribution profiles (group 1 - 4) formulated from a subjective comparison of the browse volume distribution profiles at each site. Sites were organised into groups irrespective of the total amount of browse available at each site. The browse classes were (D) 0 to 0.5 m (duiker), (I) 0.5 to 1.5 m (impala), (K) 1.5 to 2.5 m (kudu), (G) 2.5 to 6.0 m (giraffe) and (> 6.0) browse above 6.0 m that was too high for browsing.

Group 1 communities had most of the browse concentrated in the 2.5 to 6.0 m ('giraffe') browse height classes. Most of the communities in this group had a relatively low amount of browse above 6.0 m ($< 10\ 000\ m_3$).

Group 2 communities had most of the browse located above 2.5 m with similar amounts in the 'giraffe' and '> 6.0 m' browse height classes. All the communities had relatively small amount of browse below 2.5 m and the distribution of browse in the 'impala' (0.5 to 1.5 m) and 'duiker' (< 0.5 m) height classes was similar to that for the group 1 communities.

Group 3 communities had a large concentration of browse volume above 2.5 m. The browse in the 'impala' height class was comparatively well represented in these communities in comparison with the communities of groups 1 and 2.

Group 4 communities had most browse located below 2.5 m with the 'duiker' and 'impala' classes being most prominent.

A biplot of the DCA of browse volume distribution indicated a gradient in distribution profiles that was related to PAM (Fig. 6.2.3). The first DCA axis was negatively correlated with PAM ($r=-0.65$, $df=17$, $P<0.01$) but not correlated with AN ($r=-0.015$, $df=17$, $P>0.1$) indicating that PAM had an overriding effect on the browse distribution. The '> 6.0 m' and 'giraffe' classes were associated with high PAM and the 'impala' and 'duiker' classes with low PAM. Thus, there was a gradient of communities with browse volume mainly above 2.5 m to those with browse volume mainly below 2.5 m with a decrease in PAM.

The relationship between the four subjective browse volume groups and the PAM gradient was clear illustrated on the PAM-AN plane (Fig. 6.2.4). Sites with the most browse volume above 2.5 m and especially in the '> 6.0' m height class occurred in the mid reaches of the plane. The similarity in the browse volume distribution profiles of communities 2, 3 and 18, was unexpected since these communities differed with regard to the other structural features. The grouping of these communities illustrated the lack of an AN influence on browse volume distribution since there was a large difference in AN

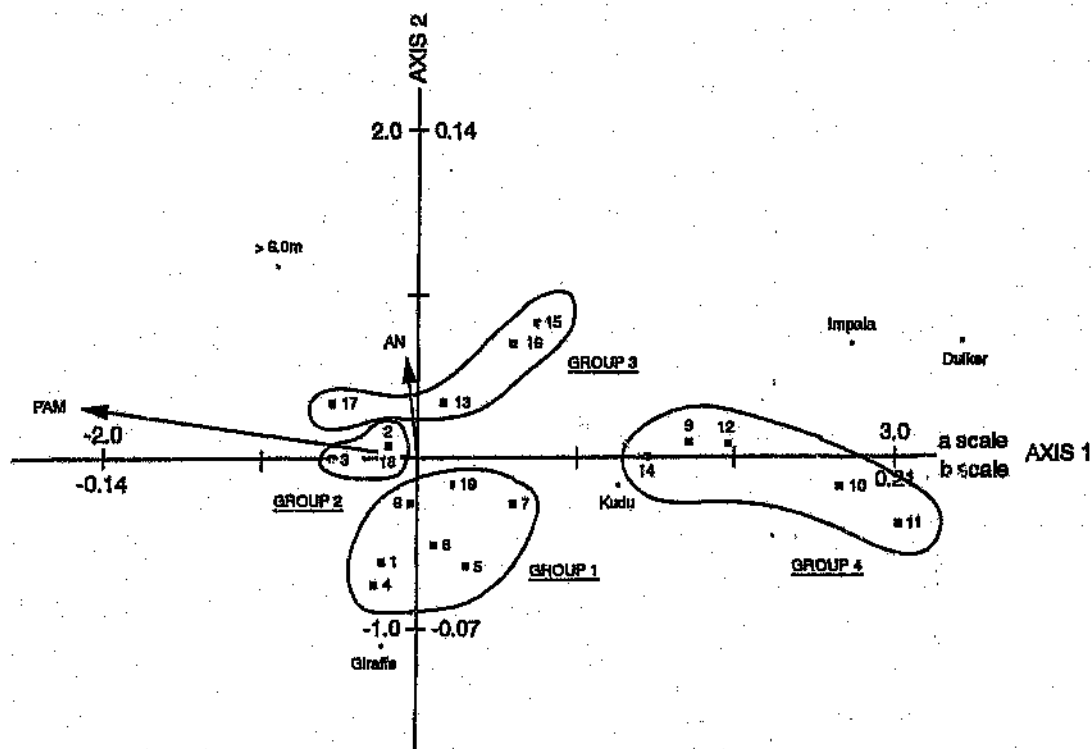


Figure 6.2.3 Plot of sites (■), browse classes (●) and environmental variables (arrows) in relation to the first two axes of the detrended correspondence analysis. The eigenvalues of the first two axes were 0.33 and 0.13 respectively. PAM and AN were represented by the number of Gdays per annum and the A horizon total nitrogen content (mg/kg), respectively. The *a* scale applies to the sites and browse classes and the *b* scale to the environmental variables. The scale of the arrow representing PAM is X 2. The groups of sites indicated are those based on a comparison of the browse volume distribution profiles at each site (Fig 6.2.2).

between them.

6.2.3 WOODY PLANT STRUCTURAL CLASSIFICATION

Neither the ordination or classification of all the woody plant structural features together produced structural gradients or groups that were related to the PAM and AN gradients.

The ordination and classification of tall and short heights and canopy covers grouped all the communities together except for communities 10 and 11. The eigenvalues of the first three DCA axes were low, 0.08, 0.02 and 0.01, indicating that structural gradients were not pronounced. The first DCA axis was correlated with PAM ($r=-0.64$, $df=17$, $P<0.01$).

No relationship between structure and AN ($r=-0.17$, $df=17$, $P>0.1$) was apparent.

The *a priori* structural classification systems of Pratt *et al* (1966), Edwards (1983), Bredenkamp & Theron (1985) and Grunblatt *et al* (1989), applied to the woody plant communities, did not produce clearly defined gradients of

structural types in relation to PAM. There was some trend in that the drier sites were mainly classified as bushland or shrubland with short, open woodland whereas the moister sites were mainly classified as woodland with a sparse shrub layer. No clear trends in structural types were apparent on the PAM-AN plane for either AN as TotN (Fig. 6.2.5 a) or AN as percentage clay (Fig. 6.2.5 b). These results again indicated that there were a range of structural types for similar conditions of PAM and AN.

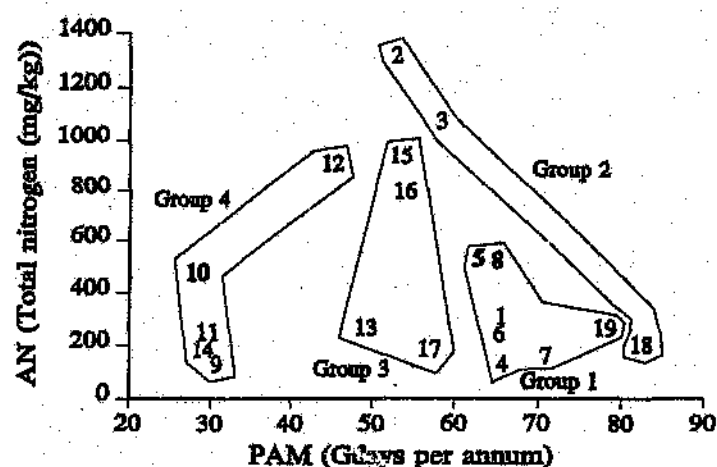


Figure 6.2.4 Patterns of browse volume distribution on the PAM - AN plane. The sites are grouped according to the four characteristic browse volume distribution profiles (Fig 6.2.2).

6.3 HERBACEOUS VEGETATION RESULTS

6.3.1 GRAMINOID COMMUNITY STRUCTURE IN RELATION TO PAM AND AN

Graminoid density was not significantly correlated with either PAM ($r=0.26$, $df=17$, $P>0.1$) or AN ($P>0.1$, $df=17$) and high and low densities occurred in all regions of the PAM-AN plane (Fig. 6.3.1 a).

Grass basal area was significantly positively correlated with PAM ($r=0.55$, $df=17$, $P<0.05$) indicating that there was an increase in basal area with an increase in soil moisture availability. Although the highest basal areas occurred in the high PAM - low AN region of the PAM-AN plane (Fig. 6.3.1 b), there was no significant correlation between basal area

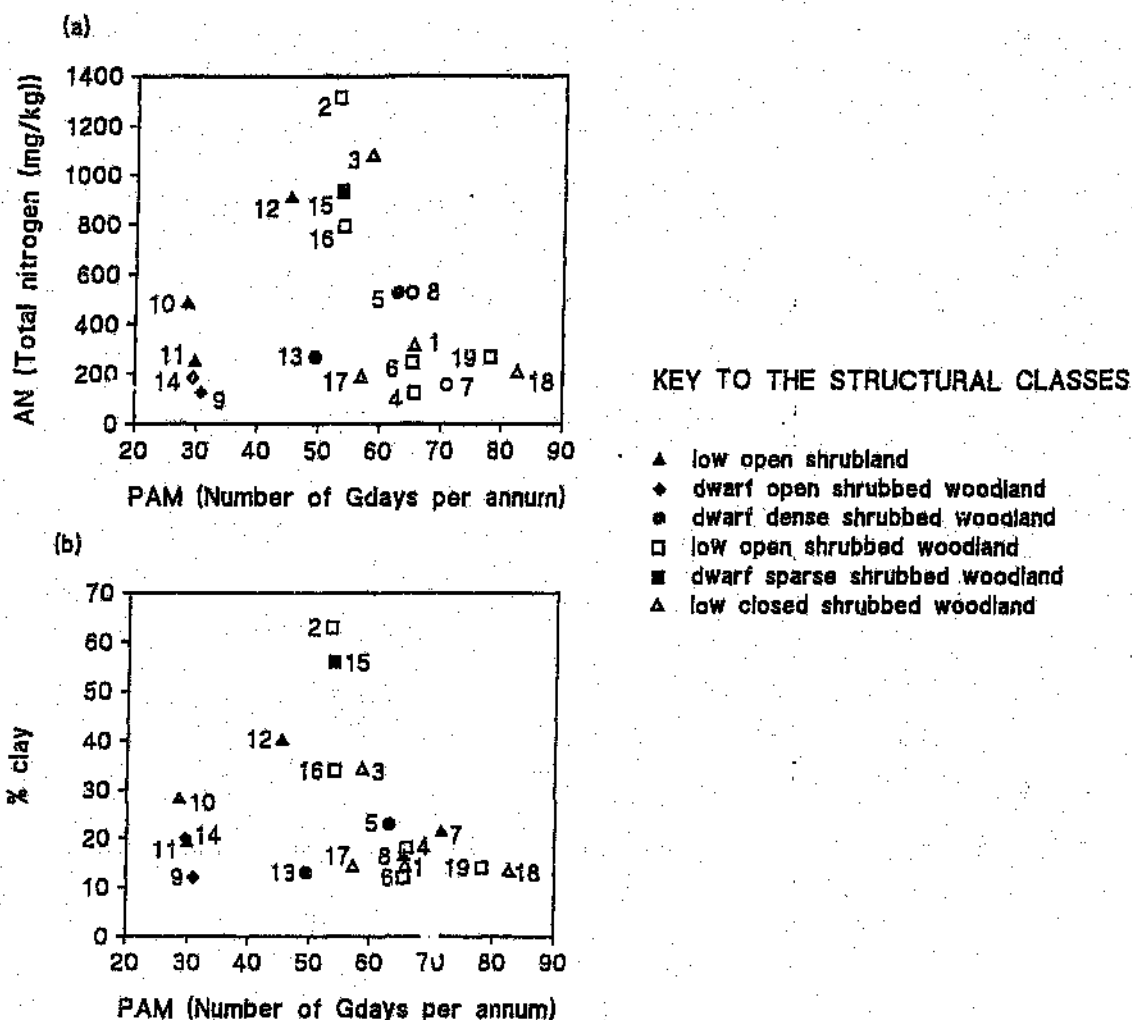


Figure 6.2.5 The structural classification of the sites based on the *a priori* classification system suggested by Grunblatt, Ottichilo and Sinange (1989). The AN axis was indexed by (a) total nitrogen content (mg/kg) and (b) percentage clay content of the A horizon, respectively.

and AN ($P > 0.1$, $df = 17$).

The grass volume index (basal area $\times$ height) was positively correlated with PAM ($r = 0.53$, $df = 14$, $P < 0.05$) and communities with the highest grass biomass occurred in the high PAM region of the PAM-AN plane. Communities with a low grass volume index occurred at the more arid sites (Fig. 6.3.1 c). There was no trend in grass volume index with AN ($P > 0.1$, $df = 14$) (Fig. 6.3.1 c).

Mean height ($r = 0.46$, $df = 14$, $P < 0.1$) and mean maximum height ($r = 0.54$, $df = 14$,

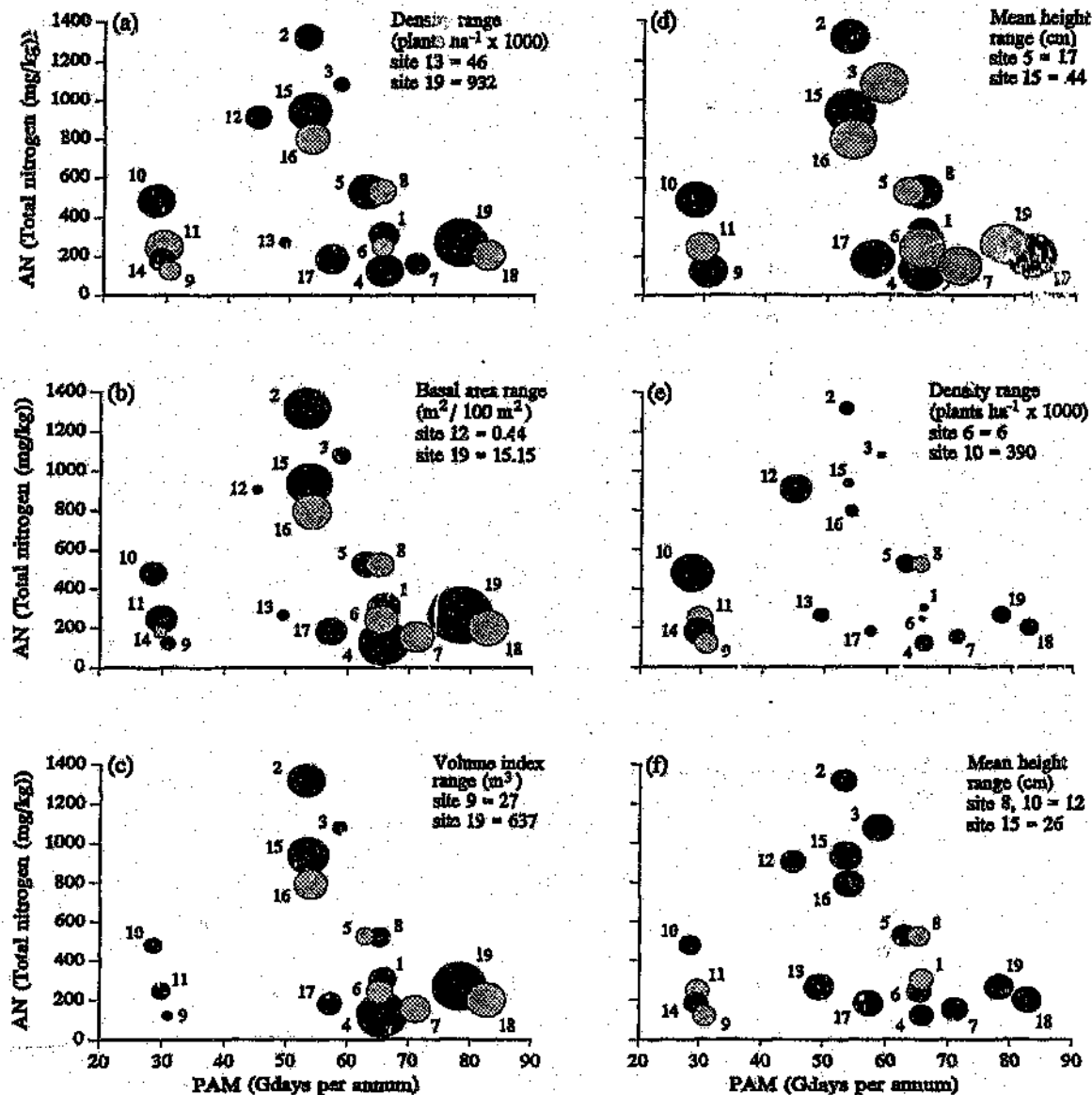


Figure 6.3.1 Trends in graminoid community (a) density, (b) basal area, (c) volume index and (d) mean height and in forb community (e) density and (f) mean height on the PAM-AN plane. PAM is indexed as the mean number of Gdays per annum and AN as the total nitrogen content of the A horizon in mg/kg of soil. The circles indicate the value of each structural variable at each site. The graminoid structural values are contained in Appendix 5 and the forb structural values in Appendix 7. Site numbers are as given in Table 2.1.

$P < 0.05$) were correlated with PAM indicating that the tallest grass communities occurred at the moist sites. There was no significant correlation of grass height with AN ($P > 0.1$, $df = 14$) but the tallest communities occurred on dystrophic soils (Fig. 6.3.1 d).

A range of grass structural features occurred within each region on the PAM-AN plane. Communities positioned in close proximity to one another on the plane, e.g. communities 5 and 8 and 1 and 6 were structurally different (Fig. 6.3.1 a-d). These results indicated that sites with similar conditions of PAM and AN did not consistently have similar structural features. Of the two environmental variables considered, PAM seemed to have the primary effect on grass community structure.

6.3.2 GRAMINOID STRUCTURAL CLASSIFICATION

Neither the ordination or classification of all the grass structural features produced interpretable structural gradients or groups. The DCA axes were not correlated with either PAM or AN and the TWINSpan groupings were not ecologically meaningful.

None of the *a priori* structural classification systems of Pratt *et al* (1977), Edwards (1983) and Grunblatt *et al* (1989) applied to the grass communities produced clearly defined gradients of structural types in relation to PAM. No clear trends in structural types were apparent on the PAM-AN plane for either AN as TotN or AN as percentage clay.

6.3.3 FORB COMMUNITY STRUCTURE IN RELATION TO PAM AND AN

Forb density was significantly negatively correlated with PAM ($r=-0.62$, $df=17$, $P<0.01$) indicating that there was a higher density of forbs in drier areas. There was no relationship between forb density and AN ($P>0.1$, $df=17$) (Fig. 6.3.1 e).

Forb mean height was not correlated with either PAM ($r=0.32$, $df=17$, $P>0.1$) or AN ($P>0.1$, $df=17$). Tall and short forb communities occurred in all regions of the PAM-AN plane (Fig. 6.3.1 f).

6.3.4 BEGINNING AND END OF SEASON HERBACEOUS STRUCTURE

A comparison of the structural features of the herbaceous communities sampled at the

beginning and end of the growing season indicated that there were significant changes in graminoid and forb community structure over time (Fig. 6.3.2).

The density of grass plants in community 2 increased in contrast to a substantial decrease in density in community 3 and a slight decrease in community 1 (Fig. 6.3.2 a). Grass basal area decreased in all communities (Fig. 6.3.2 b) and both communities 1 and 3 had substantially less grass biomass at the end of the season. The average height of the grass communities at all the sites increased over time (Fig. 6.3.2 c & d). The grass volume index decreased substantially in communities 1 and 3 (Fig. 6.3.2 e).

In contrast to the seasonal changes in grass density, forb density was higher in community 1 and lower in community 2 at the end of the growing season (Fig. 6.3.3 a). The average height of the forb communities at both sites increased during the growing season although only slightly in community 1 (Fig. 6.3.3 b).

These results indicated that time of sampling is an important factor when considering herbaceous community structural characteristics.

6.4 STRUCTURAL RELATIONSHIPS OF THE THREE COMPONENTS OF THE VEGETATION

6.4.1 WOODY PLANT AND GRAMINOID COMMUNITIES

There was no relationship between the amounts of woody and grass biomass over the range of sites sampled ($r=-0.05$, $df=7$, $P>0.1$). The woody to grass biomass ratio was not significantly correlated with PAM ($r=-0.27$, $df=17$, $P>0.1$) or AN ($r=-0.06$, $df=17$, $P>0.1$) (Fig. 6.4.1 a). Similarly, there was no trend in woody to grass biomass ratio with soil texture as percentage sand ($r=0.24$, $df=17$, $P>0.1$) (Fig. 6.4.1 b) or as percentage clay ($r=-0.17$, $df=17$, $P>0.1$).

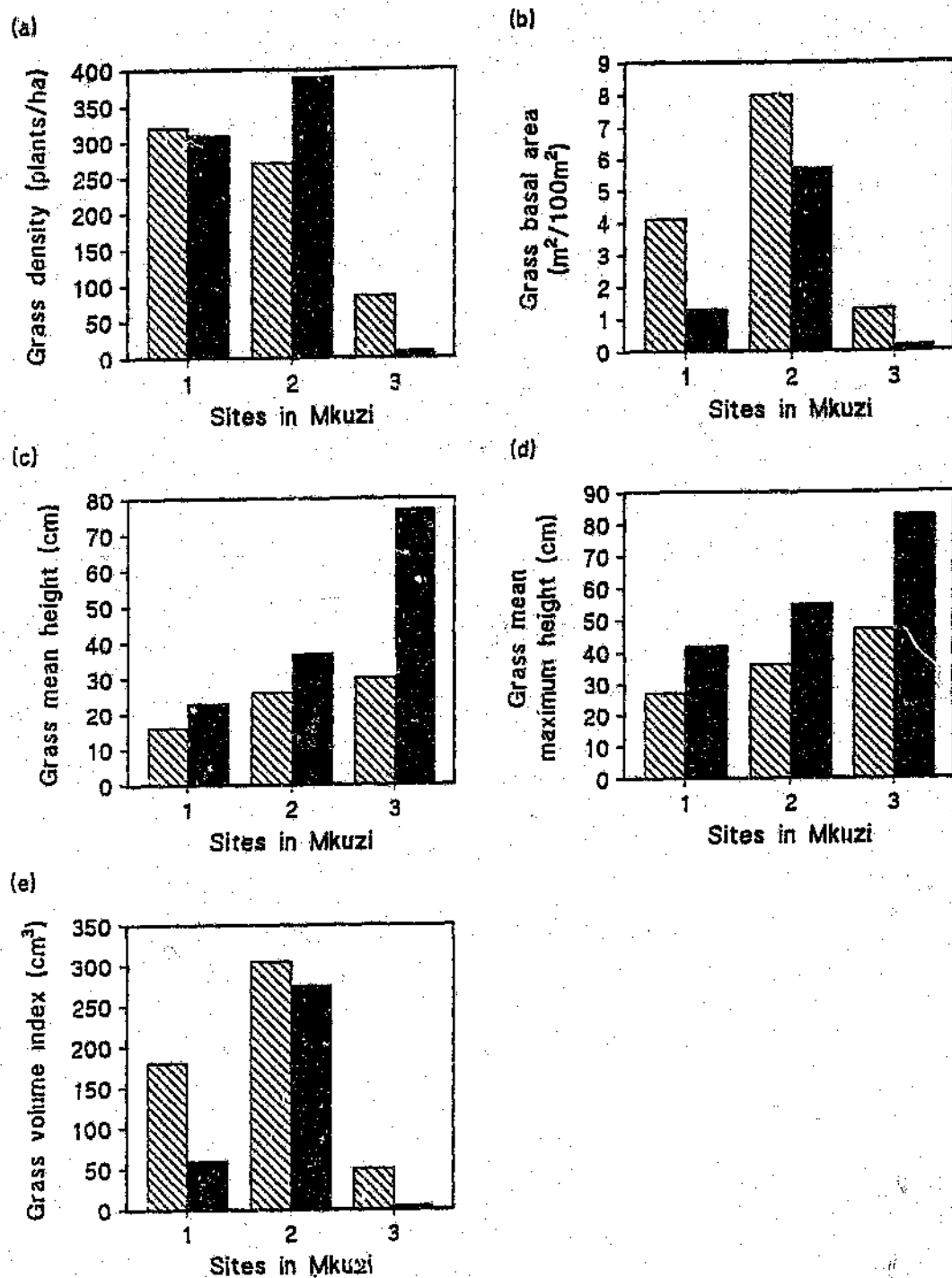


Figure 6.3.2 Comparison of the beginning (hatched bar) and end (solid bar) of season graminoid community (a) density, (b) basal area, (c) mean height, (d) mean maximum height and (e) volume index at sites 1, 2 and 3 in Mkuzi.

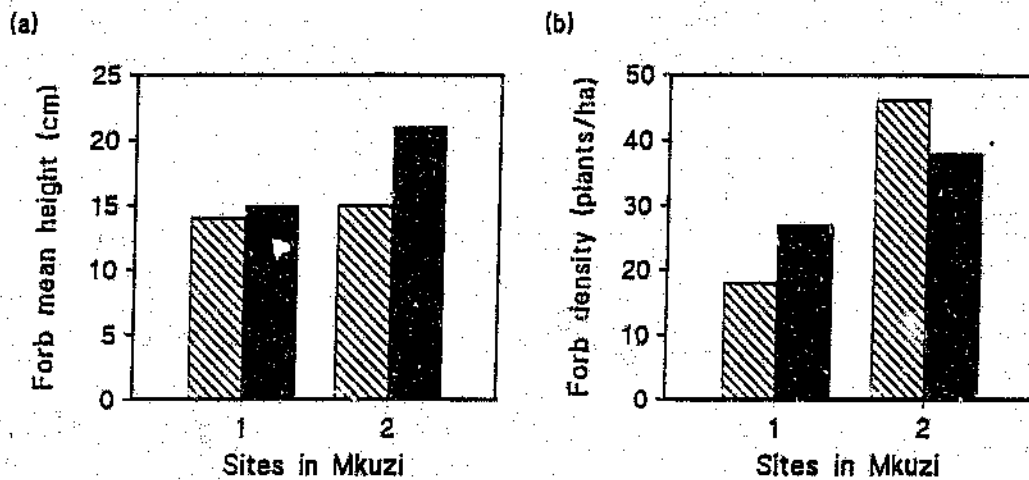


Figure 6.3.3 Comparison of the beginning (hatched bar) and end (solid bar) of season forb community (a) density and (b) mean height at sites 1 and 2 in Mkuzi.

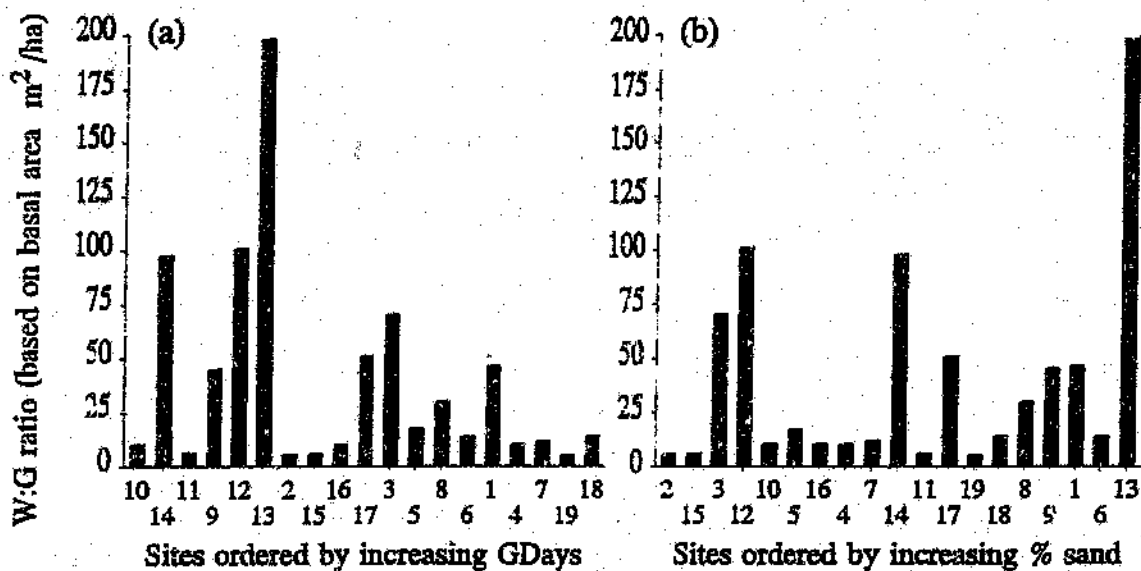


Figure 6.4.1 The woody to grass biomass ratio along the (a) PAM gradient and (b) the soil texture gradient.

6.4.2 GRAMINOID AND FORB COMMUNITIES

There was no relationship between grass and forb density over the range of sites sampled ($r=0.09$, $df=17$, $P>0.1$).

6.5 DISCUSSION

6.5.1 COMMUNITY STRUCTURE IN RELATION TO PAM AND AN GRADIENTS

The results of this study indicted that PAM had a primary influence on the structure of both the woody plant and graminoid communities. The influence of PAM on plant height has been observed in other studies. A positive correlation between tree height and precipitation was found in two semi-arid savanna areas in southern Africa (van der Meulen & van Gils 1983) and mean grass height was found to decrease with a decrease in PAM in the Serengeti grasslands (McNaughton 1983). Cole (1982) states that the variation in height and spacing of savanna vegetation is controlled by PAM. A positive correlation between the heights of both the woody plant and graminoid communities in this study supported this hypothesis, but a lack of any correlation of woody plant and graminoid density with PAM suggested that available moisture did not influence the spacing of the vegetation in a predictable way. The positive correlation between both woody plant and graminoid basal area and PAM supported the hypothesis that there is a general positive correlation between rainfall and plant biomass in savannas (Bell 1982).

There were no trends in community structure along the AN gradient although structural variation in relation to nutrient availability has been recorded in savannas. The influence of AN on vegetation structure has been observed in cerrado vegetation in Brazil where a positive relationship was found between the density and height of woody vegetation and certain soil properties (Lopes & Cox 1977). Edaphic factors are known to influence vegetation structure in southern African savannas, for example, the structure of *Colophospermum mopane* communities in the far northern Transvaal (O'Connor 1992) and in the Kruger National Park (Fraser *et al* 1987).

6.5.2 VARIATION ON THE PAM-AN PLANE

Although it appears that neither the woody plant or grassoid community structure varied predictably on the PAM-AN plane, a multiple linear regression model needs to be fitted to the data to support this conclusion. Even though there were no apparent trends with AN, a multiple linear regression of the form $y = \text{PAM} + \text{AN} + \text{PAM} \times \text{AN}$ would indicate if there was a significant interaction term or if the overall model was significant. This would enable the identification of structural variation that was a consequence of the combined effects of PAM and AN.

The results of this study indicated that there were a range of structural types for similar conditions of PAM and AN. This result was not unexpected since both arid and moist savannas have structural forms ranging from open treeless grasslands to closed canopy stratified woodlands (Huntley 1982). Belsky & Amundson (1990, submitted) state that a wide variety of community types existed within the east African savanna biome, changing along rainfall, topographic and edaphic gradients.

Models for the prediction of variation in savanna structure have been developed. On the basis of rainfall and soil texture, Walker & Noy-Meir (1982) predicted a change from grassland to savanna to woodland i.e. an increase in woodiness with an increase in rainfall. Bell (1984) predicted the structure of savannas under different conditions of PAM and AN. Open woodlands were predicted to occur in dry areas on fertile soils with a dominance of trees and shrubs and tall grasses under moist, dystrophic conditions. A low density of woody plants in arid, infertile areas and the occurrence of woodland under moist, eutrophic conditions was predicted. The structural variation of the savanna communities sampled in this study do not clearly reflect these predictions.

6.5.3 THE INFLUENCE OF OTHER DETERMINANTS ON SAVANNA STRUCTURE

The effects of the secondary determinants of herbivory and fire on savanna structure need to be considered in an explanation of savanna structural variation. These determinants are

hypothesised to be more important than PAM for influencing the structure of east African savannas (Belsky 1991). Rutherford (1979) found that the vegetation in the Nylsvley study area had a lower species basal area than in similar communities elsewhere and attributed this to the more frequent occurrence of fire at the Nylsvley site. Belsky (1984) has recorded a reduction in mean tree height in the Serengeti National Park as a consequence of browsing. Structural changes of the herbaceous communities of savannas in response to herbivory and fire are well documented (O'Connor 1985). Changes in graminoid density, tuft circumference and height and increases in forb density have been recorded in herbaceous communities in the eastern Transvaal lowveld in response to grazing (O'Connor & Pickett 1992).

6.5.4 STRUCTURAL RELATIONSHIPS OF THE DIFFERENT COMPONENTS OF THE VEGETATION

The variation in woody to grass biomass ratio recorded in this study did not support the current hypotheses that woody to grass biomass ratio is higher in moist than in arid savannas (Frost *et al* 1986), and that increasing tree dominance occurs with increasing rainfall (Walter 1971).

6.6 CONCLUSION

The structural variation of the woody plant and graminoid communities was primarily related to the PAM gradient. There were no trends with AN. There were no apparent predictable structural trends on the PAM-AN plane but this conclusion needs to be supported by the results of a multiple linear regression. A range of structural types occurred under similar conditions of PAM and AN. The effects of herbivory and fire on the structure of savanna communities need to be considered. The difference between the beginning and end of season herbaceous community structure suggested that sampling time was important and was likely to have influenced the variation in structural features recorded for the range of sites sampled.

7.0 FUNCTIONAL TRENDS AND CLASSIFICATION

7.1 INTRODUCTION

The functional approach to the classification of vegetation is not new (Knight & Loucks 1969). The basis of this approach is that plants under a similar set of environmental conditions have morphological and physiological characteristics in common and can be grouped on the basis of these (Grime 1985). If functional features are chosen that are known to represent environmental adaptations then the functional approach should provide a classification of vegetation that is more ecologically meaningful than that based on floristics alone (Knight & Loucks 1969, Werger & Sprangers 1982).

Although the functional approach has been used in different vegetation types (Knight 1965, Werger & Sprangers (1982), Friedel, Bastin & Griffin 1988, Montalvo *et al* 1991), the savanna vegetation of southern Africa has as yet not been classified on a functional basis. Existing classifications of savannas are predominantly floristic and do not provide much information about function. It is hypothesised that a general functional classification of savannas would provide a basis for predictive modelling of vegetation change. The rationale for using a functional approach and a review of studies where this approach has been employed in other vegetation types are presented in section 1.3 of chapter 1.

The aim of this chapter is to determine how the savanna communities are functionally related to one another and to the availability of water and nutrients. This chapter partly addresses study objectives 2 and 3.

The woody plant and graminoid components of the vegetation were analysed separately. Trends in individual functional features were considered in relation to the PAM and AN gradients. Functional classifications of the woody plant and graminoid communities were derived by ordination and classification of all the functional features. The woody plant and graminoid functional groups were compared and the functional classifications were compared with the floristic classifications derived in chapter 5. The results of the latter comparison

are presented in this chapter but discussed in chapter 8.

Plant available moisture was indexed as the number of Gdays per annum derived using the soil water balance model. Unless otherwise stated, AN was indexed by the total nitrogen content of the A horizon (mg/kg). The details of these indices are contained in chapters 3 and 4 respectively.

The methods of data collection and analysis of the functional features are discussed in section 2.3 and 2.4 of chapter 2. The woody plant and graminoid functional features are listed in Table 2.2 and Table 2.3 and the corresponding functional scores for each species are contained in Appendix 4 and Appendix 6. The sites are referred to by number as in Table 2.1.

7.2 RESULTS: WOODY VEGETATION

7.2.1 FUNCTIONAL TRENDS IN RELATION TO PAM AND AN GRADIENTS

7.2.1.1 Leaf duration

Deciduousness was weakly positively correlated with PAM ($r=0.42$, $df=17$, $P<0.1$) although most woody communities were more than 80 % deciduous. Evergreenness was negatively correlated with PAM ($r=-0.47$, $df=17$, $P<0.05$). These results indicated that woody communities in high PAM areas were predominantly deciduous and that there was a greater occurrence of evergreenness in the low PAM areas (Fig. 7.2.1 a).

7.2.1.2 Leaf type

The occurrence of compound leaves was positively correlated ($r=0.50$, $df=17$, $P<0.05$), and the occurrence of simple leaves, negatively correlated ($r=-0.50$, $df=17$, $P<0.05$) with AN. Communities with a high percentage basal area with simple leaves occurred predominantly in the low AN region of the PAM-AN plane (Fig. 7.2.1 b). Although there

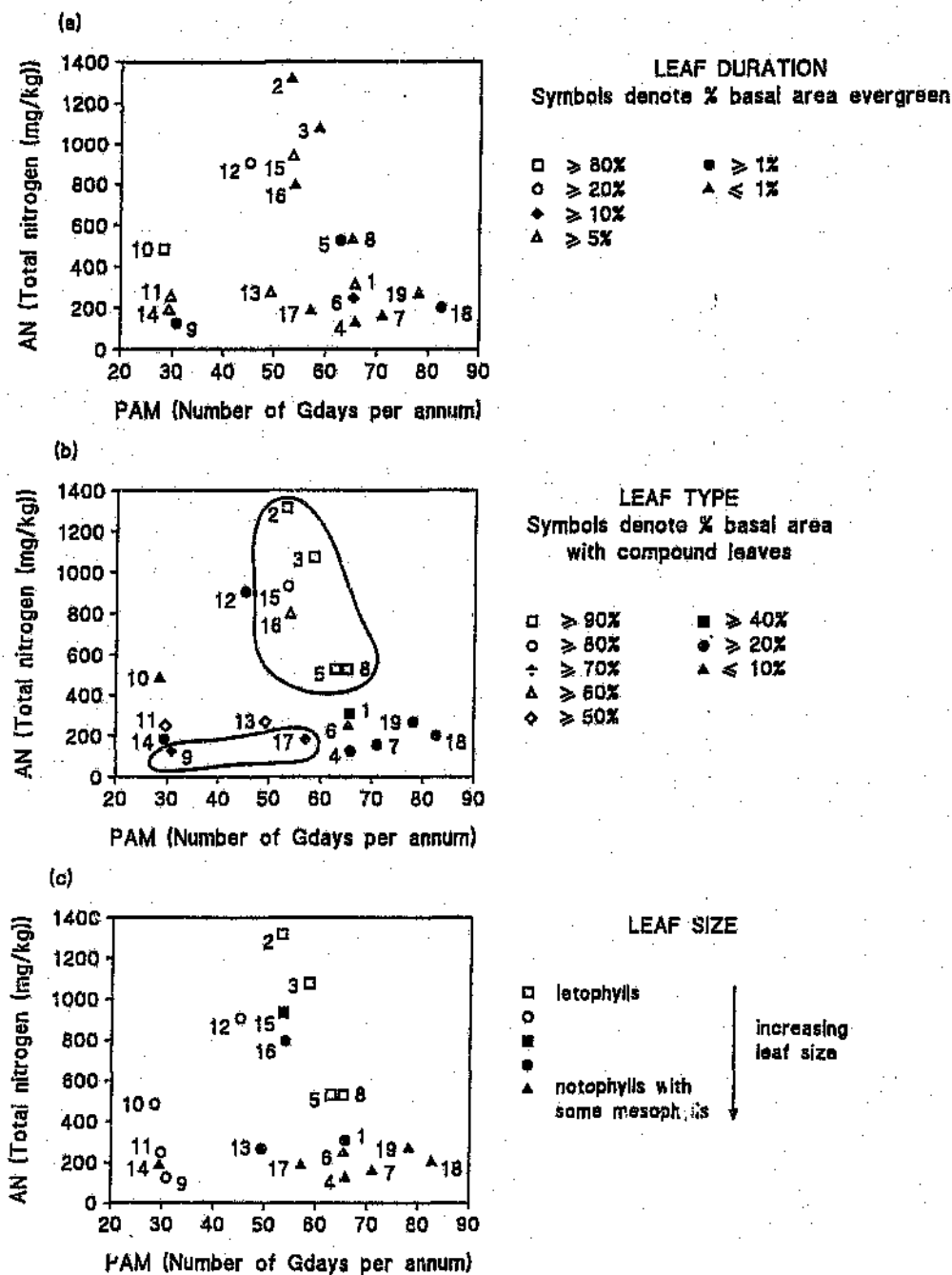


Fig. 7.2.1 Trends in woody plant community (a) leaf duration, (b) leaf type and (c) leaf size on the PAM-AN plane. Unless otherwise stated, the trends were identified by ordination and classification of % basal area data. The functional classes are listed Table 2.2. The symbols indicate the predominant trait or traits in each community.

were no significant correlations of leaf type and PAM ($r=0.06$, $df=17$, $P>0.1$), the communities at the arid end of the PAM gradient had a relatively low occurrence of compound leaves ($< 58\%$ of the basal area). The arid community 9 was an exception, however (Fig. 7.2.1 b).

7.2.1.3 Leaf size

The occurrence of small leaves (leptophylls) was positively correlated with AN ($r=0.47$, $df=17$, $P<0.05$) but not correlated with PAM ($r=0.14$, $df=17$, $P>0.1$). The occurrence of intermediate sized leaves (microphylls) was weakly negatively correlated with PAM ($r=-0.43$, $df=17$, $P<0.1$) only. The occurrence of large leaves (notophylls and mesophylls) was negatively correlated with AN ($r=-0.57$, $df=17$, $P<0.05$) and positively correlated with PAM ($r=0.50$, $df=17$, $P<0.05$). Large leafed woody plant communities occurred predominantly in the high PAM - low AN region of the PAM-AN plane (Fig. 7.2.1 c). Although the occurrence of small leaves (leptophylls and nanophylls) was not correlated with PAM, there was a predominance of nanophyllous and microphyllous leaves in four of the six arid communities and an associated absence of notophylls and mesophylls.

7.2.1.4 Spinescence

Spinescence was related to soil fertility. The percentage of the woody biomass that was unarmed was negatively correlated with AN ($r=-0.54$, $df=17$, $P<0.05$) and the highly spinescent communities occurred on fertile soils ($r=0.50$, $df=17$, $P<0.05$). Communities that were predominantly unarmed or slightly spinescent occurred mainly in the low AN region of the PAM-AN plane (Fig. 7.2.2 a). The spinescent nature of the low AN communities 9 and 11 was related to the abundance of *Acacia* spp. at these sites. Spinescence was unrelated to the PAM gradient.

7.2.1.5 Palatability

There were no predictable trends in palatability, expressed on a percentage basal area basis, with either PAM ($r=0.17$, $df=17$, $P>0.1$) or AN ($r=0.17$, $df=17$, $P>0.1$). Woody

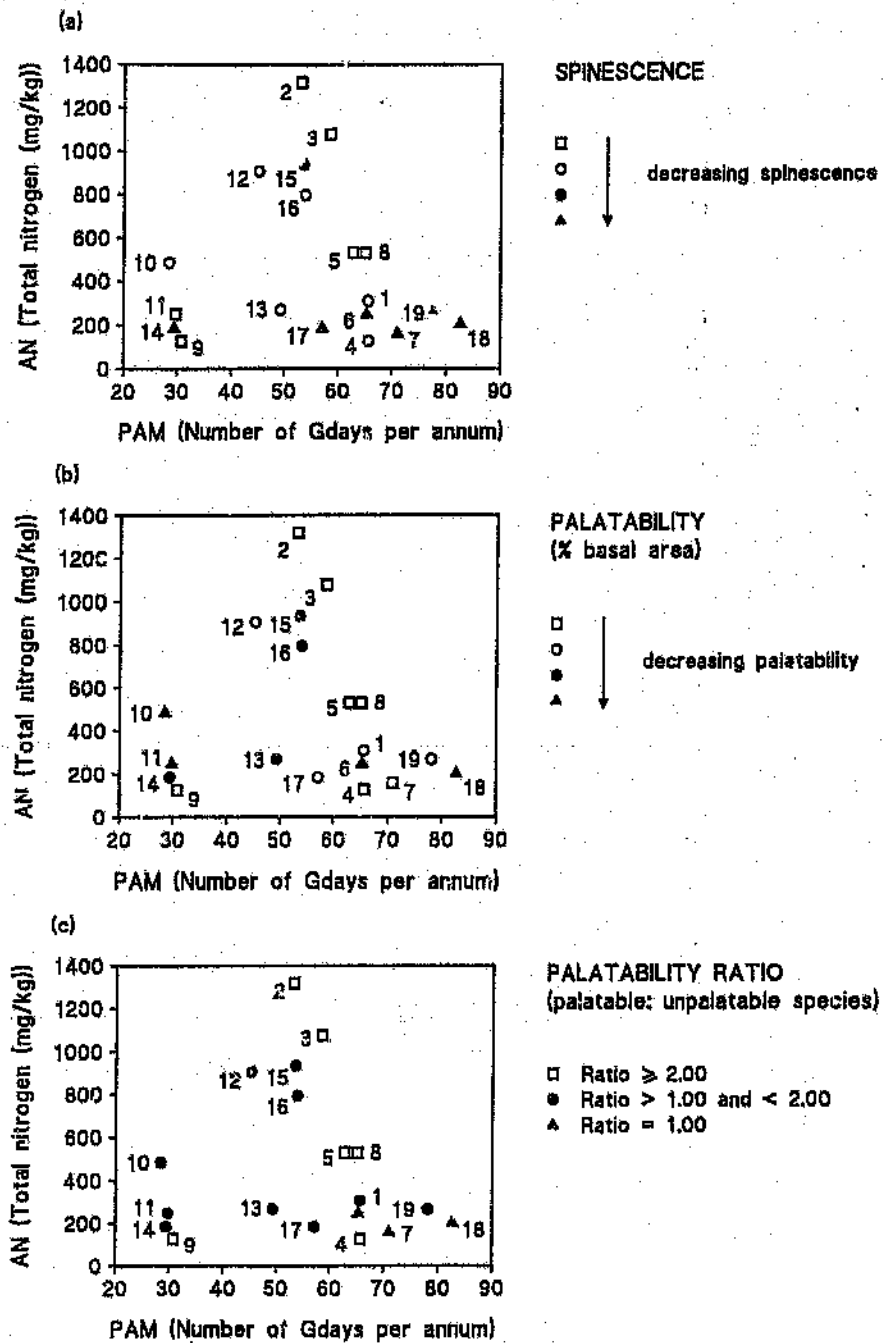


Figure 7.2.2 Trends in woody plant community (a) spinescence and (b and c) palatability on the PAM-AN plane. Unless otherwise stated, the trends were identified by ordination and classification of % basal area data. The functional classes are listed in Table 2.2. The symbols indicate the predominant trait or traits in each community.

communities with high, intermediate and low palatabilities occurred in all regions of the PAM-AN plane (Fig. 7.2.2 b). The ratio of the number of palatable to unpalatable species ranged from 1.0 to 6.0 indicating that there were the same number or more palatable than unpalatable species in all the communities. Communities with relatively low ratios occurred predominantly in the high PAM - low AN region of the PAM-AN plane (Fig. 7.2.2 c).

7.2.2 FUNCTIONAL CLASSIFICATION OF THE WOODY VEGETATION

The eigenvalues of the first 3 axes of the DCA of phenology, leaf type, leaf size, spinescence and palatability were 0.2, 0.07 and 0.03 respectively (Fig. 7.2.3). The cumulative percentage variance accounted for by the first two axes of the functional feature - environment biplot was 42.8 and 66.5% and hence the first two axes were considered an adequate representation of the functional and environmental variables (Fig. 7.2.3).

The first DCA axis was positively correlated with AN ($r=0.45$, $df=17$, $P<0.1$) but not correlated with PAM ($r=-0.01$, $df=17$, $P>0.1$) (Fig. 7.2.3). The second DCA axis was negatively correlated with PAM ($r=-0.49$, $df=17$, $P<0.05$) but not correlated with AN ($r=-0.11$, $df=17$, $P>0.1$).

The first axis described an available nutrient gradient. Communities at the fertile end of the gradient were characterised by leptophyllous, compound leaves. These communities were predominantly deciduous and palatable and had intermediate to very high spinescence (Fig. 7.2.3). Communities at the infertile end of the gradient were characterised by notophyllous and mesophyllous, simple leaves. These communities were predominantly partially palatable or unpalatable and were characterised by unarmed or slightly spinescent species (Fig. 7.2.3).

The second axis described a plant available moisture gradient. The arid end of the gradient was characterised by the occurrence of nanophyllous and microphyllous leaves and the occurrence of evergreen species (Fig. 7.2.3). The moist end of the PAM gradient was characterised by the occurrence of notophyllous and mesophyllous leaves, partial palatability and semi-deciduousness (Fig. 7.2.3).

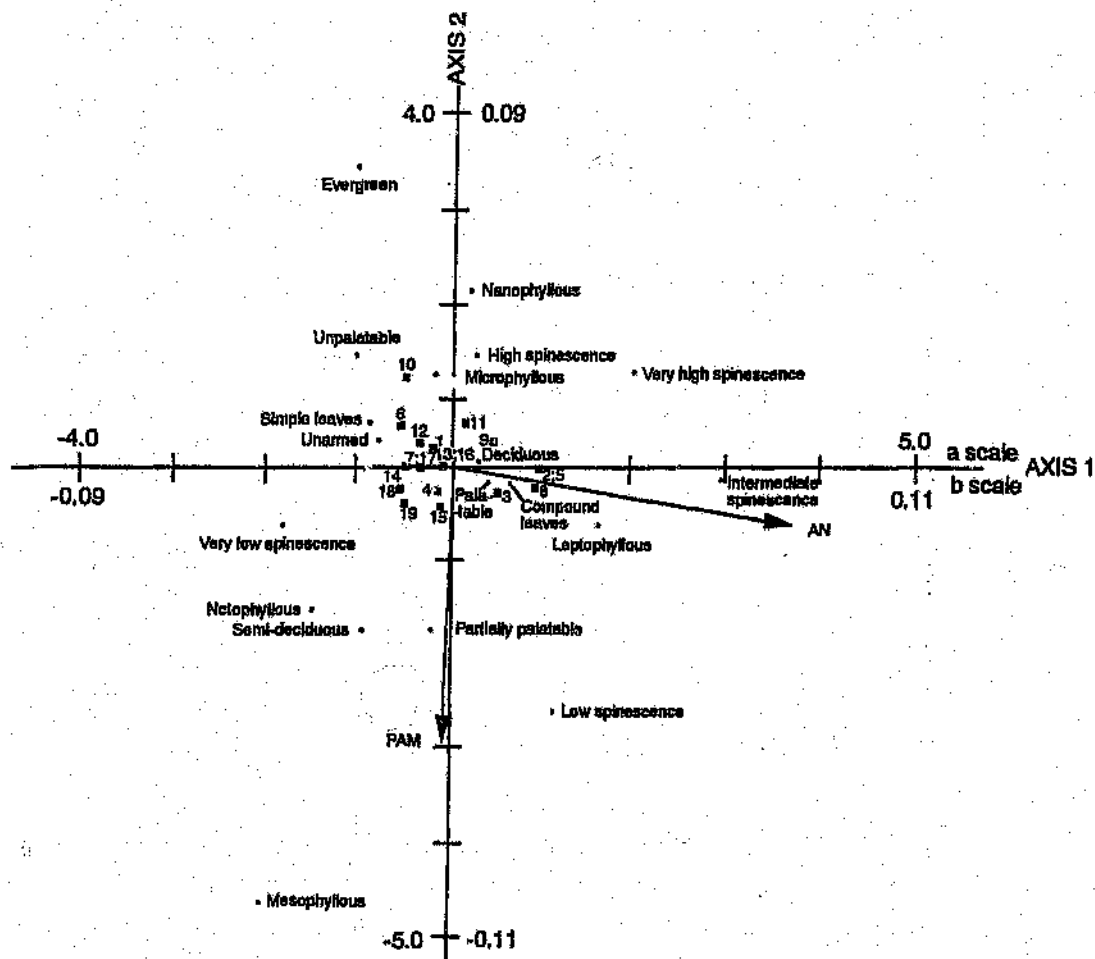


Figure 7.2.3 Plot of sites (■) and woody functional features (●) of phenology, leaf type, leaf size, spinescence and palatability, and environmental variables (arrows) in relation to the first two DCA axes. PAM and AN are the number of Gdays per annum and the A horizon total nitrogen content (mg/kg) respectively. The a scale applies to the sites and species and the b scale to the environmental variables. The scale of the arrows is X 2. The functional attributes and classes are listed in Table 2.2.

The woody plant communities were divided into four groups or types on the basis of the results of the ordination and classification of the functional variables (Fig. 7.2.4). Functional group 1 communities occurred on high AN soils (Fig. 7.2.4) and were characterised by species that had leptophyllous, compound leaves, and that were deciduous, palatable and highly spinescent. The functional features of this group reflected the predominance of *Acacia* spp. at these sites. Functional group 2 communities, in the low PAM and AN region of the PAM-AN plane (Fig. 7.2.4), had similar functional features to those of group 1, except that the sites in group 2 had slightly larger leaves (nanophylls and microphylls) and more evergreen species. Functional group 3 communities were spread over a range of low to

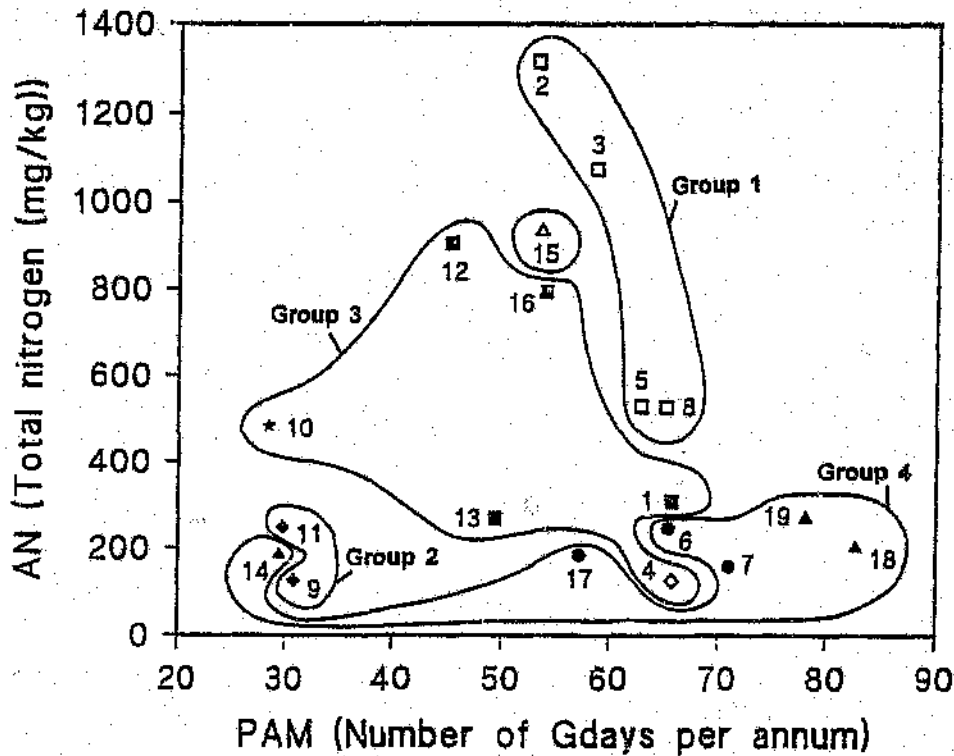


Figure 7.2.4 Woody plant functional types (group 1 to 4) on the PAM-AN plane. The sites were grouped according to the hierarchical classification of the woody functional attributes (Table 2.2). The lines indicate the groupings after TWINSpan division 4. The symbols represent the groupings after the final division of TWINSpan (division 10). Site numbers are as given in Table 2.1.

intermediate PAM and AN (Fig. 7.2.4). These communities were characterised by microphyllous and notophyllous, simple leaved species that were unarmed or slightly spinescent and partially palatable or unpalatable. Functional Group 4 communities occurred in the high PAM - low AN region of the PAM-AN plane (Fig. 7.2.4) and had species with notophyllous and mesophyllous, simple leaves. As for group 3, these communities had species that were predominantly unarmed or slightly spinescent and partially palatable or unpalatable. With the exception of site 14, all the communities in this group occurred in the high PAM - low AN region of the PAM-AN plane (Fig. 7.2.4).

Of the six communities in functional type 3, communities 4 and 10 were separated out as unique after the final division of TWINSpan (Fig. 7.2.4). Site 10 had a high occurrence of biomass that was unpalatable and evergreen, and this was related to the dominance of *Tarchonanthus camphoratus* at this site. Community 4 had functional features characteristic

of both functional types 1 and 4.

Community 15 was included with the functional type 4 communities after TWINSpan division two but was separated from them by division four to form a unique functional type (Fig. 7.2.4). Community 15 had functional features that were characteristic of both functional types 3 and 4. Although community 15 occurred on a relatively fertile soil, it was characterised by a low occurrence of spinescent, palatable species in comparison with communities that had a similar condition of PAM and AN. Only 19 % of the woody plant basal area in community 15 was spinescent in comparison with 42 % in community 16 and 94 % in community 3.

Although functional similarities of the woody plant communities enabled the derivation of functional groups or types in relation to PAM and AN, the results indicated that woody plant communities with similar moisture and nutrient conditions did not have consistently similar functional features. The arid *Colophospermum mopane* community, 14, had very similar conditions of PAM and AN to the *Acacia* spp. communities 9 and 11 but had functional features that were similar to the moist *Terminalia* and *Combretum* communities 18 and 19. Communities 1, 4 and 6 also had similar conditions of PAM and AN but were functionally different.

7.3 RESULTS: HERBACEOUS VEGETATION

7.3.1 FUNCTIONAL TRENDS IN RELATION TO PAM AND AN GRADIENTS

7.3.1.1 Phenology

There was no predictable trend in graminoid phenology with either PAM or AN. All communities except community 14 had more than 80 percent of the biomass composed of perennial species and most had more than 90 percent perennial. The greatest percentage basal area of annuals occurred in two of the moist communities, 1 (11.4 %) and 17 (4.8 %).

7.3.1.2 Physiology

There was no significant trend in the percentage of malate forming species with PAM ($r=0.06$, $df=17$, $P>0.1$) or AN ($r=-0.35$, $df=17$, $P>0.1$), but a comparison of the ratio of malate (M) to aspartate (A) formers in the dystrophic *Burkea africana* community 6 and the eutrophic *Acacia* spp. community 8 at Nylsvley suggested a relationship between grass physiology and nutrient availability. Although these sites had very similar values of PAM, the M/A ratio was 40:60 % on the low nutrient soil and 20:80 % on the fertile soil (Fig. 7.3.1 a). All communities in the high PAM - low AN region of the plane had M/A ratios of $40 (\pm 3) : 60 (\pm 3)$ % and the high AN communities 2, 3, 5 and 8 had more than 80 % aspartate formers (Fig. 7.3.1 a). The other high AN communities (12, 15 and 16) had more than 60 % aspartate formers except for community 10 which had an M/A ratio of 44.4:55.6 % (Fig. 7.3.1 a). These results suggested a higher occurrence of malate forming species on low AN soils. There were no predictable trends with PAM and AN in the occurrence of malate or aspartate formers on a percentage basal area basis, and the biomass at most communities was dominated by aspartate formers.

7.3.1.3 Growth form

The occurrence of tufted species was negatively correlated with PAM ($r=-0.65$, $df=17$, $P<0.01$), indicating that there was a predominance of tufted species in the low PAM communities. The first axis of a DCA of growth form types was negatively correlated with PAM ($r=-0.46$, $df=17$, $P<0.05$). The trend with PAM was apparent on the PAM-AN plane where low PAM communities were predominantly tufted and high PAM communities predominantly tufted-rhizomatous (Fig. 7.3.1 b). There was a mixture of growth forms in most of the communities in the mid-reaches of the PAM gradient (Fig. 7.3.1 b). Growth form was not significantly correlated with AN.

7.3.1.4 Mode of reproduction

There were no trends in mode of reproduction with PAM and AN and most communities had a relatively high occurrence of species that could reproduce both vegetatively and sexually.

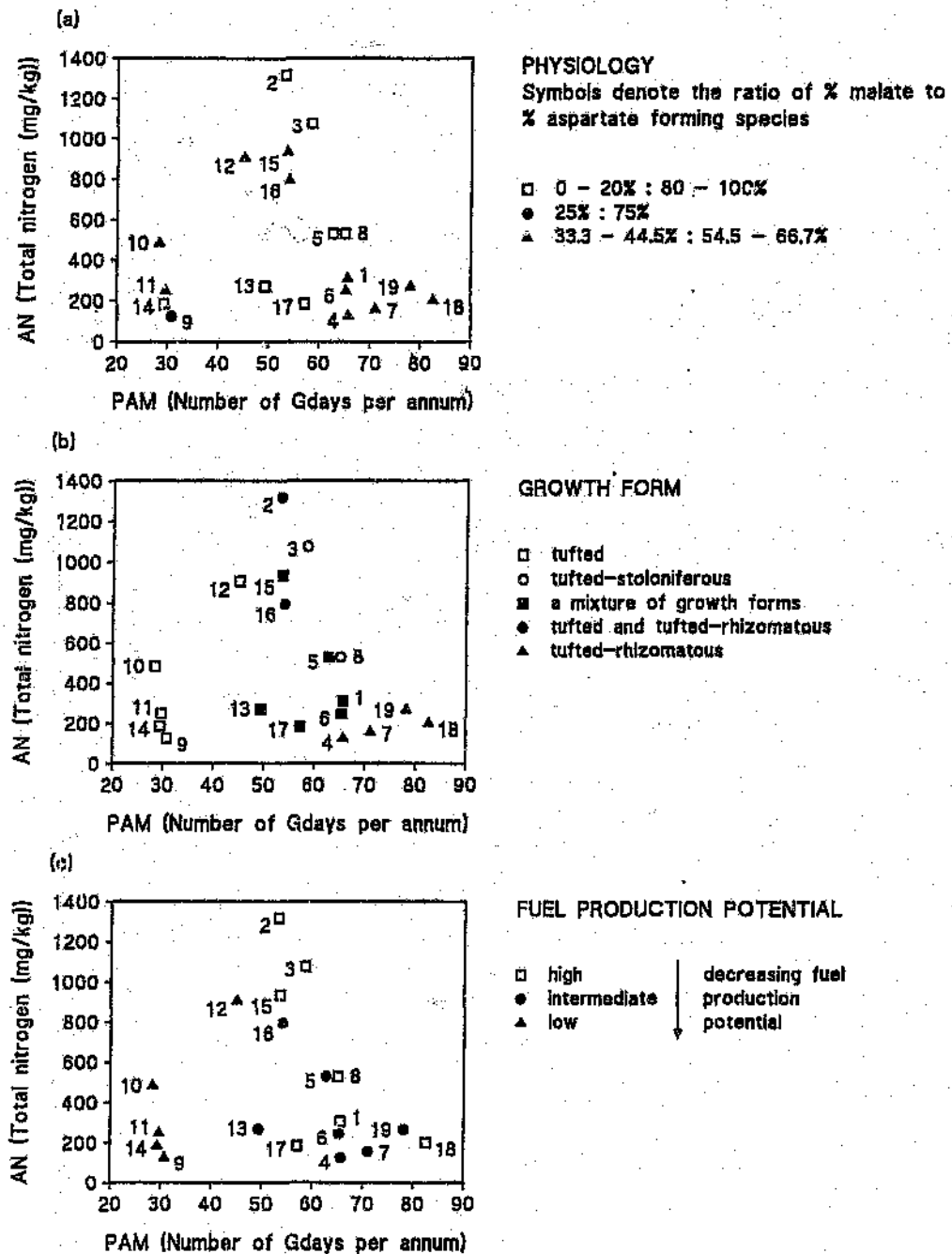


Figure 7.3.1 Trends in graminoid community (a) physiology, (b) growth form and (c) fuel production potential on the PAM-AN plane. Unless otherwise stated, the trends were identified by ordination and classification of % basal area data. The functional classes are listed in Table 2.3. The symbols indicate the predominant trait or traits in each community.

Only communities 2, 4, 7, 13 and 19 had more than 50 % basal area composed of obligate sexual reproducers.

7.3.1.5 Fuel production potential

Low fuel production potential, (the sum of production potential classes 1 and 2 in Table 2.3), was negatively correlated with PAM ($r=-0.61$, $df=17$, $P<0.01$) while the occurrence of high fuel production potential (the sum of classes 6, 7, 8 and 9) was weakly positively correlated with both PAM ($r=0.417$, $df=17$, $P<0.1$) and AN ($r=0.422$, $df=17$, $P<0.1$). The first axis of a DCA of the nine fuel production potential classes was positively correlated with PAM ($r=0.60$, $df=17$, $P<0.01$). These results indicated that there was a predominance of biomass with a low fuel production potential at the low PAM sites and where PAM was not limiting, the fuel production potential was influenced by the availability of nutrients (Fig. 7.3.1 c).

7.3.1.6 Successional status

The occurrence of late successional species was positively correlated with PAM ($r=0.56$, $df=17$, $P<0.05$) but not correlated with AN ($r=0.37$, $df=17$, $P>0.1$). The occurrence of mid-successional species was negatively correlated with PAM ($r=-0.47$, $df=17$, $P<0.05$) and AN ($r=-0.58$, $df=17$, $P<0.05$) while the occurrence of early successional species was unrelated to either environmental gradient. Species with late successional status occurred in the moist communities and although mid-successional species occurred in all the communities (except community 3) (Fig. 7.3.2 a), they increased in abundance with a decrease in PAM and AN. The first axis of a DCA of successional status was weakly positively correlated with AN ($r=0.43$, $df=17$, $P<0.1$) and, with the exception of community 10, all the high AN communities had a relatively high abundance of late successional species (Fig. 7.3.2 a).

7.3.1.7 Grazing response

The occurrence of species that declined with over utilisation (decreaser species) was positively correlated with PAM ($r=0.52$, $df=17$, $P<0.05$) and the occurrence of species that

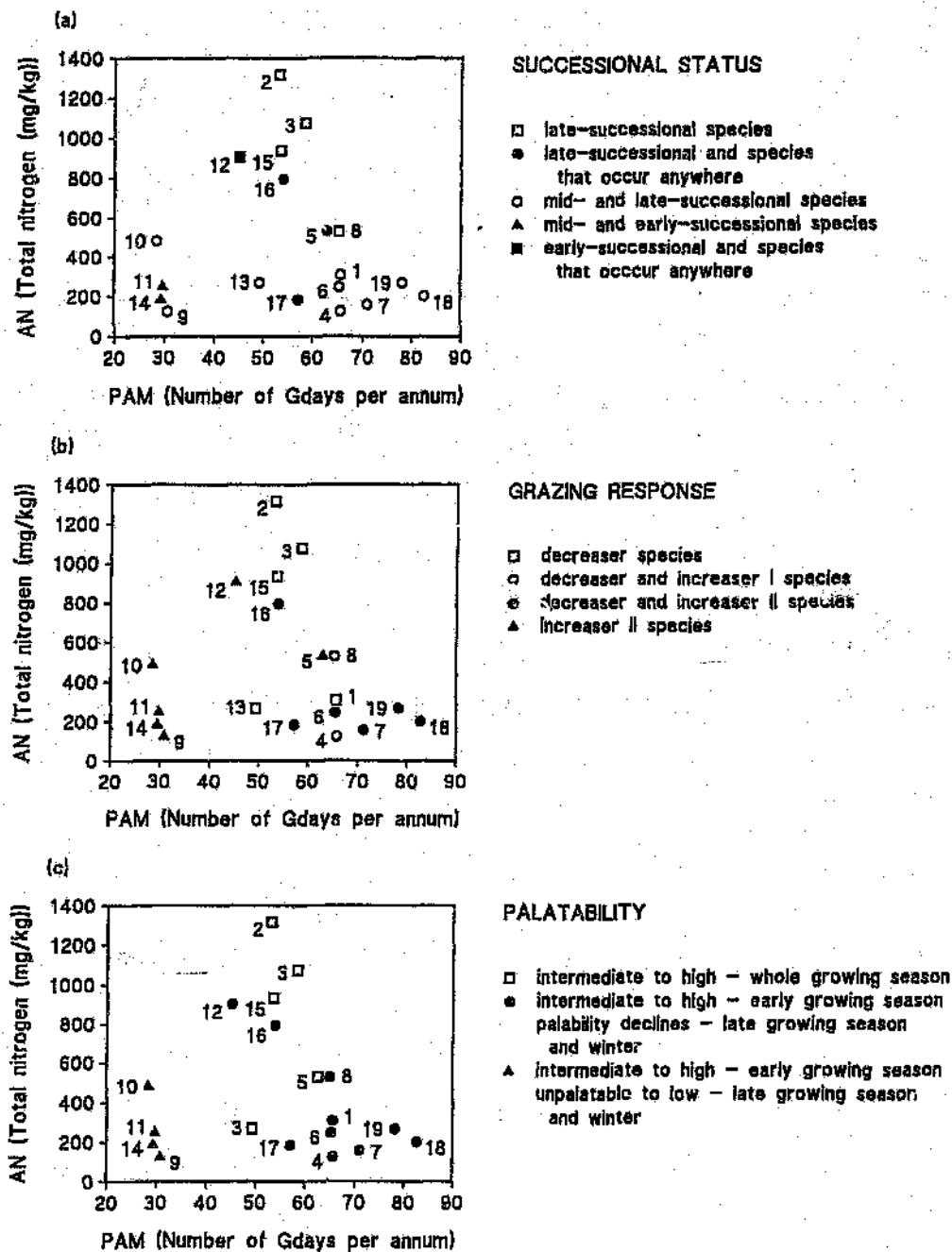


Figure 7.3.2 Trends in graminoid community (a) successional status, (b) grazing response and (c) palatability on the PAM-AN plane. Unless otherwise stated, the trends were identified by ordination and classification of % basal area data. The functional classes are listed in Table 2.3. The symbols indicate the predominant trait or traits in each community.

increased with over utilisation (increaser II species) was negatively correlated with PAM ($r=-0.74$, $df=17$, $P<0.001$). These results indicated that there was a higher relative basal area of increaser two species in the more arid communities (Fig.7.3.2 b). The grazing response of the grasses was not related to AN.

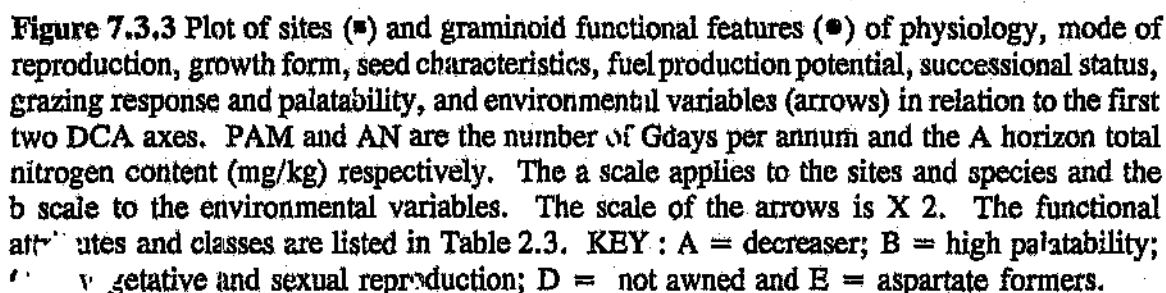
7.3.1.8 Palatability

The occurrence of highly palatable biomass during the early part of the growing season was weakly correlated with AN ($r=0.43$, $df=17$, $P<0.1$), suggesting that soil fertility has an important influence on grass palatability at this stage in the growing season. The occurrence of low palatability biomass in the early season was negatively correlated with PAM ($r=-0.55$, $df=17$, $P<0.05$), suggesting that there were more low palatability species at the drier sites. The occurrence of highly palatable species in the late and winter stages was positively correlated with PAM ($r=0.55$, $df=17$, $P<0.05$) and with AN ($r=0.50$, $df=17$, $P<0.05$), suggesting an interaction of the effects of PAM and AN on palatability of the graminoid layer. The results indicated that the palatability of the graminoid layer at the more arid sites declined dramatically over the growing season in comparison with the change at the more moist sites. Where PAM was not limiting, palatability was high on the fertile sites (Fig. 7.3.2 c).

7.3.2 FUNCTIONAL CLASSIFICATION OF THE GRAMINOID VEGETATION

The eigenvalues of the first 3 axes of the DCA of physiology, growth form, mode of reproduction, fuel production potential, successional status, grazing response, palatability and seed characteristics were 0.09, 0.05 and 0.04 respectively (Fig. 7.3.3). The cumulative percentage variance accounted for by the first two axes of the functional variable - environment biplot was 37.8 and 69.8% and hence the first two axes were considered an adequate representation of the functional and environmental variables (Fig. 7.3.3).

The first DCA axis was negatively correlated with PAM ($r=-0.57$, $df=17$, $P<0.05$) but not correlated with AN ($r=-0.04$, $df=17$, $P>0.1$) (Fig. 7.3.3). The second DCA axis was positively correlated with AN ($r=0.64$, $df=17$, $P<0.01$) but not correlated with PAM



The first axis described a plant available moisture gradient. Communities at the arid end of the gradient were characterised by tufted grasses that had a low fuel production potential (classes 1 and 2) and that were of early and mid-successional status (Fig. 7.3.3). Species with low palatability, and species with increaser II status were common. Grasses in these communities produced many small and medium sized seeds and the occurrence of plumed

and barbed seeds was restricted to these more arid sites (Fig. 7.3.3).

Communities at the moist end of the gradient were characterised by tufted-rhizomatous species and species that could exhibit all growth forms such as *Digitaria eriantha* (Fig. 7.3.3). Fuel production potential in these moist communities was high (classes 6 and 7) and species with intermediate to high palatability and decreaser status were common. There was a high occurrence of species with late-successional status and a low production of large, awned seeds (Fig. 7.3.3).

The high fertility communities were characterised by species that were stoloniferous or stoloniferous-rhizomatous or tufted-stoloniferous (Fig. 7.3.3) and could reproduce vegetatively or sexually. There was a predominance of aspartate formers, decreaser species and species with a high palatability. Fuel production potential was high in these communities. Although late-successional status species were common, species that could occur across the successional spectrum were also present (Fig. 7.3.3).

Communities at the infertile end of the AN gradient had a predominance of mid-successional status species and a low to intermediate fuel production potential. Palatability was low and unpalatable species occurred predominantly in the low AN communities. Increaser I species, malate formers, and species with vegetative reproduction were common (Fig. 7.3.3).

The graminoid plant communities were divided into four groups or types on the basis of the results of the ordination and classification of the functional variables (Fig. 7.3.4). Functional group 1 communities occurred at the low AN region of the PAM-AN plane (Fig. 7.3.4) and were characterised by tufted, increaser II, early and mid-successional species that had a low fuel production potential and a low palatability. Functional group 2 communities occurred on high AN soils (Fig. 7.3.4) and had a number of different growth forms, decreaser species, late-successional status, intermediate to high fuel production potential and high palatability. Functional group 3 was characterised by a mixture of functional features that occurred in the other groups. This group contained both low and high AN communities and was located in an intermediate position along the PAM gradient (Fig. 7.3.4). Functional group 4 communities, which were moist and dystrophic (Fig. 7.3.4), were characterised by tufted-

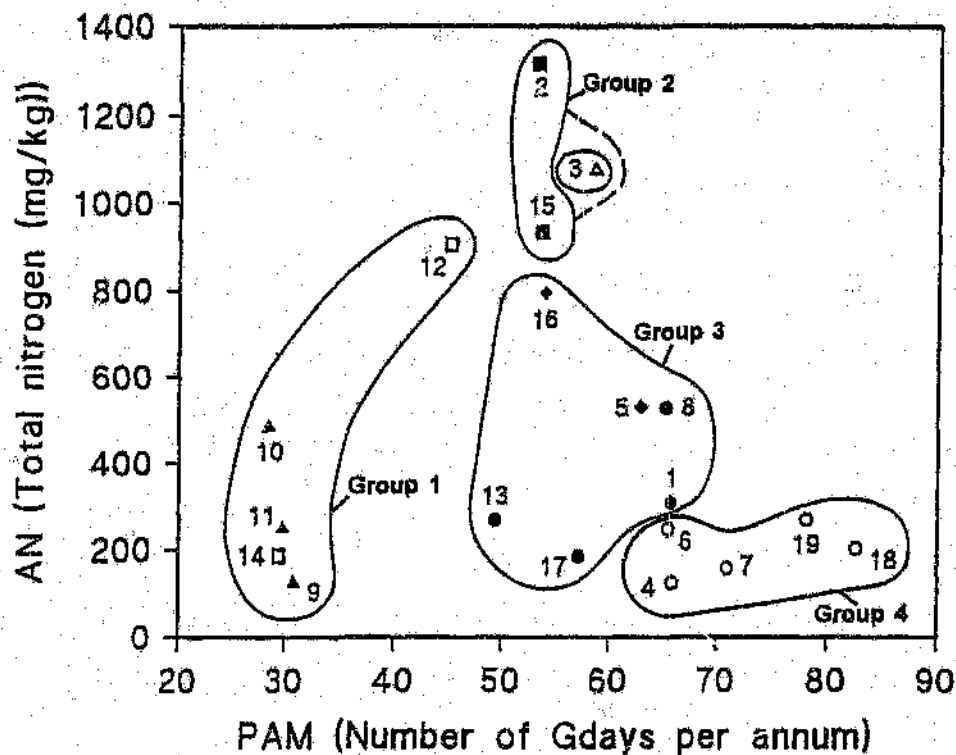


Figure 7.3.4 Graminoid functional types (group 1 to 4) on the PAM-AN plane. The sites were grouped according to the hierarchical classification of the graminoid functional attributes (Table 2.3). The lines indicate the groupings after TWINSpan division 4. The symbols represent the groupings after the final division of TWINSpan (division 6). Site numbers are as given in Table 2.1.

rhizomatous, decreaser and increaser I, mid- to late-successional species that had an intermediate to high fuel production potential and low to intermediate palatability (Fig. 7.3.4).

Community 3 was included in group 2 on the basis of the ordination results (Fig. 7.3.3) although it was classified as a unique community (Fig. 7.3.4). The uniqueness of community 3 is thought to be related to the fact that there was a low functional diversity at this site. Community 3 was characterised by 100% of the biomass being aspartate formers, decreaser species, of late-successional status, with a high fuel production potential (class 6), and more than 95% with a high palatability throughout the growing season and a tufted-stoloniferous growth form. The other fertile communities had a higher functional diversity and the community 3 functional features occurred predominantly, but not exclusively at these sites.

The subdivision of functional group 1 may be a biogeographical phenomenon since communities 9, 10 and 11 occurred in the north-eastern Cape while communities 12 and 14 were located in the far northern Transvaal.

The subdivision of functional group 3 into two groups of communities 5 and 16 and communities 1, 8, 13 and 17 may be related to a difference in available nutrients although communities 5 and 8 had a similar AN status.

Although functional similarities of the graminoid communities enabled the derivation of functional groups in relation to PAM and AN, the results indicated that graminoid plant communities with similar moisture and nutrient conditions did not have consistently similar functional features. Communities 1 and 6, and 15 and 16 had similar conditions of PAM and AN but were functionally different.

7.4 COMPARISON OF WOOD AND GRAMINOID FUNCTIONAL CLASSIFICATIONS

There was a low degree of similarity in the way in which the woody plant and graminoid communities were classified into functional groups. The woody plants were divided into nine functional types (Fig. 7.2.4) in comparison with seven functional types of the graminoid layer (Fig. 7.3.4). Although there were some similarities in the four woody plant and four graminoid functional groups, only communities 9 and 11, 1 and 13, 6 and 7 and 18 and 19 had similar woody plant and similar graminoid communities as reflected by the final TWINSpan division.

The lack of similarity was attributed to the fact that the functional features of the woody plants were primarily related to differences in AN while the graminoid functional groups primarily reflected the PAM gradient. This suggests that the woody and graminoid components of the vegetation were not related functionally in the same way to PAM and AN. In community 14, for example, the graminoid functional features reflected the low PAM status of the site but the woody plant component had functional features that were

characteristic of high PAM environments. Communities 5 and 8 had similar woody functional features but those of the graminoid layer were different. Similarly, the graminoid components of communities 4, 10 and 15, which were classified as unique on the basis of their woody functional features, were functionally similar to other communities.

An important conclusion that emerges from a comparison of these classifications is that they both mapped reasonably well onto the PAM-AN plane, indicating that it may be useful as an overall framework for the functional classification of savanna types. These results indicate that it is necessary to consider the woody plant and graminoid components of savannas as separate functional groups. Different models would have to be developed for each of these components for the prediction of change in savanna function in response to changes in PAM and AN.

It must be born in mind, however, that the nature of the functional features used to derive the classifications will have influenced the functional types derived and the relationships of these to PAM and AN.

7.5 COMPARISON OF FLORISTIC AND FUNCTIONAL CLASSIFICATIONS

7.5.1 WOODY VEGETATION

The major difference between the woody floristic and functional classifications was that the floristic groupings were primarily related to PAM (Fig. 5.2.1) while the functional groupings reflected the AN gradient (Fig. 7.2.3). The importance of AN was also reflected in the floristic classification of the woody plant communities based on the higher taxonomic level of selected subfamilies.

There were seven final floristic groups (Fig. 7.5.1 a) in comparison with eight functional groups (Fig. 7.2.4). This suggested that classifying the communities on a functional basis did not reduce a large number of floristic types into a smaller number of functional types.

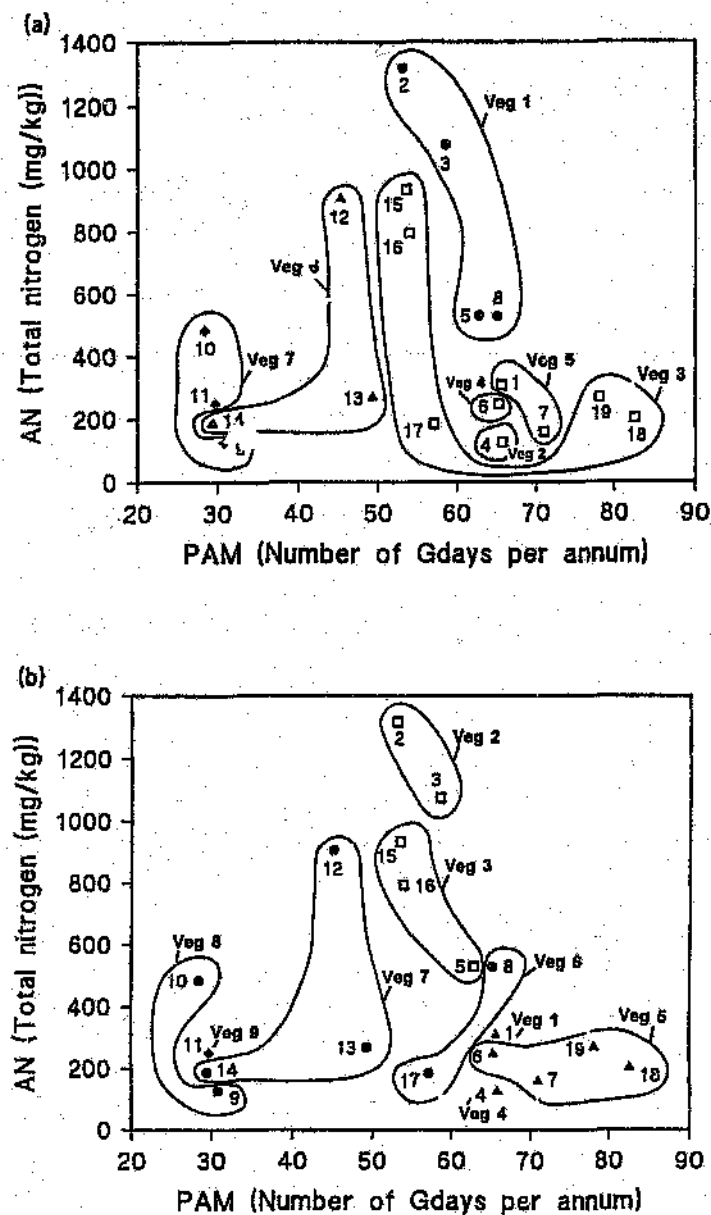


Figure 7.5.1 The floristic groupings of the (a) woody plant and (b) graminoid communities as derived in chapter 5. The lines in fig. (a) indicate the seven woody plant floristic types (veg 1 to 7) and the lines in fig. (b) indicate the nine graminoid floristic types (veg 1 to 9).

A comparison of the floristic and structural classifications indicated that there were communities that were floristically and functionally similar, such as the eutrophic communities 2, 3, 5 and 8, the arid communities 9 and 11 and the moist, dystrophic communities 18 and 19. There were communities that were floristically different but functionally similar such as the *Burkea africana* community (6) at Nylsvley, the *Combretum*

spp. community (7) at Nylsvley and the *Sclerocarya* - *Terminalia* community (17) in Timbavati. There were also communities that were floristically similar but functionally different such as the arid *Colophospermum mopane* community (14) that was related floristically to the other far northern Transvaal communities (12 and 13) but functionally to the high PAM, Pretoriuskop communities (18 and 19).

The floristic groups in part reflected the geographical separation of the savanna regions since the Rooipoort, far northern Transvaal and eastern Transvaal Lowveld sites were grouped according to region, irrespective of differences in PAM and AN. The functional classification did not reflect these regional groupings and communities were combined into functional types irrespective of their geographical location, for example, functional type 3 included communities from Rooipoort, the far northern Transvaal, the eastern Transvaal Lowveld and Mkuzi.

A common feature of both the floristic and functional classifications was that communities in similar positions on the PAM-AN plane were not always floristically or functionally similar.

7.5.2 GRAMINOID VEGETATION

Both the graminoid floristic (Fig. 5.2.5) and functional (Fig. 7.3.3) classifications were primarily related to PAM with the AN gradient of secondary importance. The primary importance of PAM was also reflected in the floristic classifications based on the higher taxonomic levels of subfamily and tribe.

There were nine final floristic groups (Fig. 7.5.1 b) in comparison with seven functional groups (Fig. 7.3.4). This suggested that the functional classification of the communities did reduce the floristic types into a smaller number of functional types. This was especially obvious for communities 1, 4 and 11 which were floristically distinct from but functionally similar to other communities.

A comparison of the floristic and structural classifications indicated that there were

communities that were floristically and functionally similar, such as the eutrophic communities 5 and 16, the arid communities 9 and 10 and the moist, dystrophic communities 6, 7, 18 and 19. There were communities that were floristically different but functionally similar such as community 11 which was functionally related to communities 9 and 10 and community 1 which was functionally related to communities 8, 13 and 17. There were also communities that were floristically similar but functionally different such as communities 2 and 3 and 15 and 16. With the exception of community 13, the arid sites were distinct floristically and functionally.

A common feature of both the floristic and functional classifications was that communities in similar positions on the PAM-AN plane were not always floristically or functionally similar.

7.6 DISCUSSION

7.6. WOODY VEGETATION

7.6.1.1 Leaf duration

The high occurrence of deciduousness in all communities in this study was not unexpected since most African savanna woody plants are semi-deciduous or deciduous (Frost *et al* 1986). The temporal pattern of leaf production and loss in response to the seasonal availability of water in savannas is considered an important characteristic of the water relations of savanna trees (Goldstein and Sarmiento 1987). Drought-deciduousness has been observed to increase as precipitation decreases (Schulze *et al* 1987) and this may account for the trend in deciduousness with PAM found in this study. The observation that trees and shrubs in arid savannas tend to be more distinctly deciduous than in moist savannas (Huntley 1982), suggests that the duration of PAM has an important influence on the way in which deciduous species function. It is likely that any one species would exhibit a plasticity of timing of leaf loss over a range of PAM.

Deciduousness is also related to the occurrence of fire during the dry season since leaf loss prior to the time of burning enables plants to avoid loss of photosynthate by damage to leaf material (Bate and Gunton 1982, Frost 1984). Since fire is infrequent in arid savannas but is a regular phenomenon in moist savannas (Huntley 1984), deciduousness in moist savannas may be fire rather than drought related.

Savanna evergreen species survive drought conditions without the loss of photosynthetic tissue. This was observed in the droughted far northern Transvaal communities (12, 13 and 14), where evergreen species such as *Boscia albitrunca* were fully leafed while the deciduous woody plants such as the *Grewia* and *Acacia* spp. were shedding their leaves. Although evergreenness is an adaptation for nutrient conservation (Goldstein and Sarmiento 1987), the retention of leaves during the dry season means that evergreen species are susceptible to tissue loss by fire. The higher occurrence of evergreenness in the low PAM communities in this study may be due to the absence of very hot and regular fires at these arid sites (Huntley 1984).

7.6.1.2 Leaf features

Many theories have been advanced to account for the adaptive significance of tree leaf size, relating to the regulation of leaf temperature, to water-use efficiency and to nutrient economy (Huntley 1982).

The trend in the occurrence of large leaves with PAM observed in this study can be explained on the basis of thermal regulation and water relations. Leaf size, shape, type and surface characteristics have an important influence on the leaf energy balance since both water vapour and heat transport are affected by the aerodynamic properties of leaves. The aerodynamic properties of small leaves enable them to stay closer to air temperature than larger leaves, even when stomata are closed. Thus a high occurrence of small leaves is expected in environments where stomata are closed for part of the day due to water stress caused by drought or high evaporative demand (Solbrig 1987, Schulze, Robichaux, Grace, Rundel & Ehleringer 1987). Larger leafed savanna species are considered to be less drought tolerant than those with smaller leaves (Huntley 1982, Goldstein and Sarmiento 1987) and

hence are expected to occur in moister areas.

The lack of any trend in leaf type with PAM is interesting since current theories consider compound leaves an adaptation for coping with water stress.

The significant trend in leaf size and type with AN in this study suggests that there is some adaptive advantage of having small leaves in fertile environments or large leaves in infertile environments. There is as yet, however, no convincing theory to explain the functional relationship of leaf size and soil fertility (Scholes, M.C. pers. comm.).

Leaf size may have co-evolved with spinescence in response to herbivory of palatable species because spinescence is most effective as a defence strategy in combination with small leaves (Dunham 1980b). This would not account for the occurrence of unpalatable and unarmed species with small leaves, however. Because small leaves have a lower shading effect than large ones, a tree with small leaves can have a greater number of layers of leaves in a given height interval for the same amount of light (Orians and Solbrig 1977). This may mean that the small leafed species have an increased photosynthetic surface relative to large leafed species and hence can maximise the use of freely available resources. Large leaves may be less susceptible to nutrient loss by leaching than small leaves and hence would be important for the nutrient economy of woody plants in resource poor environments. Plants growing in low resource environments have reduced growth potentials and long-lived tissues as a means of reducing resource demands (Chapin, Bloom, Field & Waring 1987). Thus, large leaves may in some way be related to low growth rates and leaf longevity. The adaptive significance of leaf size in Mediterranean environments has been explained using both nutrient deficiency and heat stress arguments (Cowling & Campbell 1983).

7.6.1.3 Palatability and Spinescence

Palatability was expected to be positively related to soil fertility since the production of plant metabolic constituents (protein and soluble carbohydrate) is strongly influenced by soil nutrient availability (Bell 1982). Bell (1982) suggested that the food quality of savanna plants is determined by the ratio of metabolic (M) to structural carbohydrate (S) constituents where

high M/S ratios are indicative of good quality food. Unpalatable species have chemical deterrents or low nutrient contents or high lignin and fibre contents that make the leaves tough. (Owen-Smith and Cooper 1987).

A comparison of the palatabilities of the low AN community (6) and the high AN community (8) indicated that the expected palatability - soil fertility trend occurred at Nylsvley, as recorded by Owen-Smith and Cooper (1987), but was not reflected over the entire range of sites sampled. A possible explanation for the lack of a trend in palatability with AN was related to the fact that certain species such as *Acacia burkei*, *A. erioloba*, *A. mellifera*, *A. tortilis*, *Combretum apiculatum*, *C. molle*, *Dichrostachys cinerea*, *Grewia flavescens*, *Sclerocarya birrea* and *Ziziphus mucronata* occurred abundantly on low fertility soils but were considered to be highly acceptable to browsers (Owen-Smith and Novellie 1982, Owen-Smith and Cooper 1987).

The rough palatability estimate used in this study, based on data collected from the literature rather than from observations at each site, must be interpreted with some caution. This is because the acceptability of any one plant species to herbivores can vary spatially and temporally with soil type, growth stage, growth season, the type of browsers present and the availability and acceptability of co-occurring plant species (Pellew 1984, Cooper, Owen-Smith & Bryant 1988, Owen-Smith and Cooper 1988). Research has shown that even species such as *Ochna pulchra* and *Euclea natalensis* that are classed as unpalatable are eaten at certain times (Owen-Smith and Cooper 1988).

The positive relationship between the occurrence of spinescence and AN observed in this study supports the hypothesis that woody plant anti-herbivore defence strategies are related to soil fertility. Structural defences were expected to be common on eutrophic soils and chemical defences common on dystrophic soils.

Milton (1991) found that spinescence was weakly related to soil-nutrient status at a regional scale in southern Africa and that nutrient-rich habitats in arid areas were more spinescent than the surrounding dry plains. Owen-Smith and Cooper (1987) found that plants with chemical defences were common on infertile soils and plants with structural defences on

nutrient rich soils at Nylsvley.

Both the nature and quantity of plant defences are determined by resource availability (Coley *et al* 1985). Low resource environments have plants with slow growth rates and high levels of defence while high resource environments have plants with faster growth rates and lower defence levels. Slower growers have higher defences because as the potential growth rate becomes more limited by resource availability, the replacement of resources lost to herbivores becomes more costly (Bell 1982, Chapin *et al* 1987).

The structural defences of palatable plants on fertile soils are thought to have evolved in response to high herbivory of these species (Huntley 1982, Cumming 1982, Milton 1991) since spinescent species have some of the highest crude protein and lowest fibre contents recorded (Pellew 1984, Cooper and Owen-Smith 1986). Structural defences do not completely protect palatable plants from herbivory but they reduce foliage losses by restricting the eating rates of herbivores below the levels that might otherwise occur (Cooper and Owen-Smith 1986). Plant thorns and spines restrict bite sizes to single leaves or leaf clusters and the combination of small leaves and spinescence appears to offer the greatest protection from browsers (Dunham 1980b, Cooper and Owen-Smith 1986). The varying forms of spinescence differ in their effectiveness against different sizes and feeding techniques of browsers (Cooper and Owen-Smith 1986).

7.6.2 GRAMINOID VEGETATION

7.6.2.1 Phenology

Although a predominance of perennial species was expected at all the sites, the occurrence of annual and facultatively perennial species was expected to be negatively related to PAM. More annuals were expected in the drier communities because plants with this phenology are able to survive unfavourable climatic periods as seeds and then germinate and grow in response to effective rainfall. The lack of any relationship between phenology and PAM may be because annuals only become important in extremely arid environments, at rainfalls less than the minimum rainfall sampled in this study. McNaughton (1983) found that perennial

plants dominated in 16 out of 17 Serengeti grassland communities sampled over a rainfall gradient of approximately 400 to approximately 1000 mm per annum.

7.6.2.2 Physiology

A relationship between the occurrence of malate and aspartate forming species and PAM was expected since malate formers have been shown to become more abundant with increasing rainfall, while aspartate formers showed the opposite tendency (Ellis *et al* 1980). From a preliminary investigation of 7 savanna sites, Huntley (1982) predicted a high ratio of aspartate to malate forming species in arid areas and a low ratio in moist areas.

The results of this study did not show the expected relationship between grass physiology and PAM but there was a weak trend between grass physiology and AN with more aspartate formers on fertile soils. This trend supported the results of the physiological studies of Tew, Grossman, Fair & Cresswell (1974), which suggested a link between grass photosynthetic type and soil nitrogen content. Tew *et al* (1974) found that aspartate formers were associated with soils of high nitrogen content and malate formers on low nitrogen soils. A relatively low leaf tissue N content has been recorded in malate forming grass species such as *Hyparrhenia rufa* (Medina 1987). Tew *et al* (1974), however, postulate that it is the level of reduced nitrogen rather than total nitrogen that is the effective edaphic control.

A possible explanation for the lack of a trend with AN may be that the apparent ecological association between mesic environments and malate formers (mostly Panicoideae) and arid environments and aspartate formers (mostly Chlorideae) breaks down with regard to the Arundinoideae, especially the *Aristida* spp., which are malate formers but have a high occurrence in dry regions (Gibbs Russell *et al* 1990). Another reason may be that the trend with PAM was masked by the lumping of NAD-ME and PEP-CK aspartate formers into one functional group. Ellis *et al* (1980) have found that within the aspartate forming group, the NAD-ME type dominated in areas of very low precipitation (less than 200 mm/ann.) while the PEP-CK type formed a group intermediate between the NAD-ME and the malate formers. Malate and PEP-CK forming species have been found to exhibit many anatomical similarities (Ellis *et al* 1980).

7.6.2.3 Growth form

Graminoid growth form has important functional implications because it influences the acceptability of grasses to grazers (O'Reagain and Mentis 1989), enables grasses to survive herbivory and fire (Stuart-Hill and Mentis 1982, Danckwerts & Stuart-Hill 1987, O'Connor 1991), facilitates competition for resources (Goldstein & Sarmiento 1987) and influences the recruitment potential of grasses.

The results of this study suggested that the occurrence of stoloniferous and rhizomatous growth forms was related to PAM since species at the arid sites were predominantly tufted. This may be because a tufted growth form has an adaptive advantage for survival in low PAM habitats or that stoloniferous and rhizomatous growth forms have an adaptive advantage for survival in moist habitats or that species in arid areas reproduce mainly by seed and hence lack vegetative growth features. Clump forming grasses are characteristic of dry prairies (Knight 1965). Clonal reproduction of herbaceous perennials in a Mediterranean grassland was found to be more effective in an environment with a less pronounced summer water deficit (Montalvo *et al* 1991).

Stolons and rhizomes are important adaptive mechanisms that enable grasses to survive herbivory and fire (Stuart-Hill & Mentis 1982), both of which are expected to be of a higher frequency and intensity in moist than in arid savannas. These vegetative structures facilitate the storage of photosynthate which can be used for the regeneration of new plant tissue after defoliation by grazing or burning. Grasses with low or decumbent growth forms have a greater chance of escaping herbivory since they are less accessible to herbivores than taller and more upright forms (Danckwerts & Stuart-Hill 1987). Species such as *Urochloa mosambicensis* exhibit growth form plasticity in response to herbivory which enables these species to tolerate heavy grazing (O'Connor & Pickett 1992). Fire is expected to be more detrimental to erect than to basal grass species (Silva, Raventos & Caswell 1990, in press).

Growth form is also related to the ability of a graminoid species to compete for resources such as light and space. The availability of these resources is more limited in moist than in arid environments (Stuart-Hill & Mentis 1982). Consequently growth forms that provide a

competitive advantage for resource accumulation would be favoured in moist areas. A stoloniferous or rhizomatous growth form may provide such an advantage.

Stolons and rhizomes enable graminoids to propagate by vegetative growth. The maintenance of grass populations depends in part on the availability of vegetative or sexual propagules for recolonising gaps caused by drought and grazing (O'Connor & Pickett 1992).

7.6.2.4 Fuel production potential

The observed trend in fuel production potential in relation to PAM and AN was expected since species characteristic of high PAM and AN environments have a high biomass production potential. The infrequent occurrence of fire in arid environments (Huntley 1984) is related to the low availability of fuel in the herbaceous layer as observed in this study. Research in the Kruger National Park has shown that fires will not spread when the fuel load is less than 2000 kg/ha and this fuel load was related to communities with a low to very low fuel score (Trollope & Potgieter 1985). One problem with these results is that the estimation of fuel production potential is subjective and estimates the inherent or genetic potential of each species rather than the actual production in relation to conditions of PAM and AN (Trollope *et al* 1989).

7.6.2.5 Grazing response

A consideration of the responses of species to grazing is an important way of assessing veld condition for monitoring sustained forage production and susceptibility of the veld to erosion (Trollope *et al* 1989). Although grazing response is directly related to disturbance, PAM (in combination with fire regime) has been found to influence the responses of grasses to utilisation. Trollope *et al* (1989) hypothesise that rainfall is an underlying control on the response of veld in the Kruger National Park to herbivory and fire. High rainfall in the Lowveld Sour Bushveld areas of the Park is thought to facilitate the development of predominantly unpalatable increaser I communities in the absence of burning. Trollope *et al* (1989) suggest that these increaser I communities represent the climatic climax on these soils and that the decreaser stage observed in other landscapes is the climatic climax because

the lower annual rainfall of these areas limits further succession.

The greater occurrence of increaser II species in arid communities and decreaser species in moist communities in this study may be because increaser II species are better adapted to survive in more harsh environments. These results also suggest that arid rangeland is less suitable for grazing and more susceptible to degradation by overgrazing than moist rangeland.

7.6.2.6 Palatability

The acceptability of grasses to grazers is influenced by several factors including the time of season (Georgiadis & McNaughton 1990), the availability of other species, the occurrence of plant antiherbivore defences (Stuart-Hill & Mentis 1982) and grass growth form (O'Reagain and Mentis 1989).

The observed trends in palatability with AN in this study were expected since grasses growing on fertile soils have been shown to have high metabolic to structural carbohydrate ratios and hence to be highly acceptable to grazers (Bell 1982). Plant structure also influences acceptability to grazers and cattle were found to prefer species that were leafy and non-stemmy (O'Reagain & Mentis 1989). The acceptability of grass species to grazers changes seasonally as a result of seasonal changes in crude protein levels and in plant structure (O'Reagain & Mentis 1990, Georgiadis & McNaughton 1990).

Chemical antiherbivore defences occur in some grass species such as *Cymbopogon excavatus* and *Elionurus muticus* (Stuart-Hill and Mentis 1982). Chemical protection may be due to toxicity or to compounds such as fibre and lignin that reduce the digestibility of the plant material. This latter form of defence occurs in species such as *Eragrostis curvula*. Grasses also have physical features that provide protection from herbivory. Such physical features include high leaf tensile strength, hairiness and stemmyness. Stemmyiness is viewed as a defence mechanism analogous to spinescence in woody species since it reduces herbivore bite size and feeding rates (O'Reagain & Mentis 1989). As discussed for the woody plant species, graminoid species with chemical defences are most common on dystrophic soils.

A common way of describing the palatability of the herbaceous layer in south African savannas in relation to PAM and AN is by the identification of 'sweet' veld and 'sour' veld. Sweetveld is considered to occur in arid areas on fertile soils while sourveld occurs in moist dystrophic environments (Scholes 1991). Sweetveld contains palatable species such as *Panicum maximum*, *Digitaria* spp., and *Cenchrus ciliaris*, while species such as *Hyparrhenia hirta*, *Diheteropogon amplexans* and *Pogonarthria squarrosa* (Gertenbach 1983) occur in sourveld. Huntley (1982) states that moist savannas characteristically produce herbage of high bulk and low nutritive value.

7.7 CONCLUSION

The functional variation of the woody plant component was related to the availability of nutrients while that of the graminoid layer was primarily related to plant available moisture. The woody plant and graminoid communities were not grouped functionally in the same way, suggesting the need for the development of separate models for the prediction of functional change in response to changes in PAM and AN. Woody plant and graminoid communities with similar conditions of PAM and AN did not have consistently similar functional characteristics but both classifications mapped well onto the PAM-AN plane suggesting that it may provide a suitable overall framework for the classification of savannas on a functional basis.

8.0 DISCUSSION

8.1 INTRODUCTION

The aim of this study was to test the prediction that savanna communities with similar conditions of plant available moisture (PAM) and available nutrients (AN) have similar structural and functional features. The objectives were (1) to develop ecologically meaningful indices of PAM and AN, (2) to classify the sampled savanna types floristically, structurally and functionally and to relate these classifications to PAM and AN and to one another, and (3) to relate the findings of this study to current hypotheses about PAM and AN related floristic, structural and functional trends in savannas.

This chapter discusses the results of this study in the light of the aim and objectives. The first section discusses issues relating to the indices of PAM and AN. The second section considers the classification of the savanna types in relation to PAM and AN. The third section considers the comparison of the floristic and functional classifications. Finally, the implications of the results of this study for future research are discussed.

8.2 PAM AND AN INDICES

Because PAM and AN are considered to be the primary determinants of savanna structure and function, the PAM-AN plane has been proposed as a suitable framework for the comparison of savannas on a structural-functional basis (Frost *et al* 1986). The potential of this approach hinges on the development of satisfactory indices of PAM and AN for the quantification of the PAM-AN plane (Solbrig 1990). There has been much debate within the forum of the RSSD programme about how these indices should be derived and several approaches to the development of PAM and AN indices have been suggested (Frost *et al* 1986, Solbrig *et al* 1988). There is general consensus that the indices should be biologically meaningful, as simple as possible to calculate and should be transportable both spatially and temporally. In developing suitable indices there must inevitably be a trade-off between increasing complexity of the index and the availability of the necessary climate and soil data.

The effort-to-information ratio of the index must be assessed. The issue of spatial scale must also be taken into account and it may be that different indices are needed for intra- and inter-continental comparisons. The development of biologically meaningful indices is a difficult task because it requires a simple measure of the complex ways in which plants respond to the availability of water and nutrients, both of which are difficult to index in natural environments.

The PAM index used in this study is biologically meaningful. It reflects the duration of the growing season based on the temporal dynamics of soil water potential in each of a number of soil horizons. It is important to have an index that reflects seasonality because all savanna regions are characterised by a marked seasonal effect (Walker 1985). The water balance model used to derive this index includes the modifying effects of soil properties on the water budget. Soil property differences at the community scale have been shown to have a marked influence on PAM (Knoop & Walker 1985).

In terms of the effort-to-information ratio, the soil water balance model approach to indexing PAM yields a detailed index with a high degree of information. The data required for this level of detail such as the depth, bulk density, stone content, organic carbon content and soil water holding capacity of each soil horizon, however, mean that the effort component is also high. The results of this study show that the PAM index derived from the soil water balance model provides a suitable basis for the comparison of savannas at the community level, the scale at which savannas are managed. However, the usefulness of this index must be balanced against the data and computational requirements of the soil water balance model, both of which may limit its applicability as a general PAM index.

A number of different approaches to the development of AN indices were tried. These approaches encompassed various degrees of complexity and the indices derived varied in their effort-to-information ratio. An important aspect of the assessment of the indices was how easily they could be altered to include additional soils. The reference indices had a high effort component but they were considered to be biologically meaningful since they reflected nutrient availability in terms of soil-plant interactions. The effort required to determine these indices limits their potential for the quantification of the PAM-AN plane but the results of

this study indicate that they provide a suitable means for assessing the usefulness of other indices that are easier to derive. The single factor indices had a relatively low effort-to-information ratio and correlated well with the reference indices. The results of this study indicated that the single indices based on nitrogen availability, soil texture and percentage organic carbon are potentially useful for the quantification of the PAM-AN plane because they are simple to derive and ecologically meaningful. Of these, total nitrogen in the A horizon was used as the main AN index in this study because it is easy to measure, provides an index without complicated calculations, relates well to the reference indices and is a limiting nutrient in savanna systems (Medina 1987, San José *et al* 1991).

For the purposes of this study, PAM and AN indices were sought that best reflected the average conditions of water availability and soil fertility at the community level. An average index of this nature does not take into account spatial and temporal variations in PAM and AN at scales above and below the community level that affect the structure and function of savannas communities. The seasonal dynamics of nutrient availability and the spatial (patch scale) patterns of nutrient distribution that occur within savanna communities (Kellman 1979, Bate & Gunton 1982) were not reflected in these AN indices. These temporal and spatial patterns have been shown to influence savanna structure and function (Walker & Knoop 1987, Georgiadis & McNaughton 1990). Events at larger scales such as droughts and floods may have an influence on savanna structure and function for long periods thereafter (Tinley 1982).

The fact that PAM and AN do not vary independently of one another, because water availability influences nutrient availability, has been a concern within the RSSD forum (Solbrig 1990) because it means that the axes of the PAM-AN plane are not orthogonal. The results of this study indicate that although orthogonality of the axes may be desirable, it may not be necessary for the purposes for which the PAM-AN plane is to be used. Variations in the floristic and functional characteristics of the communities mapped well onto the PAM-AN plane used in this study. The indices of Gdays per annum and total nitrogen in the A horizon were not correlated.

8.3 FLORISTIC, STRUCTURAL AND FUNCTIONAL CLASSIFICATION

The results of this study indicated the importance of the primary determinants of PAM and AN for the composition, structure and function of South African savanna communities. The results of the floristic classification of both the woody plant and graminoid communities supported the conclusion that water is the major environmental determinant of species composition in savannas (Huntley and Walker 1982). The observed primary influence of PAM and secondary influence of AN on species composition has been hypothesised (Bell 1982, Tinley 1982).

The structure of the woody plant and graminoid communities was primarily related to PAM as suggested by Cole (1982). There was a range of structural types in all regions of the PAM-AN plane as has been observed in other African savannas (Belsky & Amundson 1990, submitted).

The functional trends in the graminoid communities were predominantly related to PAM but the woody functional features trended predominantly with AN. The apparent primary influence of PAM on the functioning of the graminoid layer is interesting since soil nutrient content has been shown to be very important functionally in the graminoid layer (Olsvig-Whittaker & Morris 1982, Theron, Morris & van Rooyen 1984). The influence of AN on, for example, grass palatability is marked within communities at the patch scale and the importance of this determinant in this study may have been masked by the average AN index derived for the community level of resolution.

The woody plant and graminoid components of eleven of the nineteen communities were not grouped into functional types in the same way. This lack of functional similarity between vegetation components of the same communities has been observed in Wisconsin forest vegetation (Knight & Loucks 1969). There was a considerable variation in the predominant understorey plant functional features between stands dominated by the same tree species in this forest vegetation. Knight & Loucks (1969) suggested that functional features of the understorey vegetation could be used to interpret environmental influences that were not apparent from the arboreal vegetation.

The apparent difference in the importance of the primary determinants on the function of the graminoid and woody plant communities indicates that separate models will need to be developed for these two components of the vegetation for predictive purposes. Separate models for predictive purposes would take into account the fact that woody plants and grasses respond to changes in the primary determinants at different spatial and temporal scales. The herbaceous layer of semi-arid savannas, for example, changes rapidly in response to annual rainfall variability (O'Connor 1985).

A common feature of both the woody plant and graminoid functional classifications was that sites with similar conditions of PAM and AN did not have consistently similar functional characteristics. Except in extreme conditions it is unlikely that plant communities under similar conditions will be composed of exclusively similar strategies (Grime 1985).

A word of caution is needed about the way in which the functional data were collected. A large portion of the functional data, such as estimates of palatability, leaf size and grazing response were collected from the literature. These estimates therefore reflected the genetic potential of each species rather than site specific information. Many of the features were applied indirectly through species identification and this method does not take into account the effects and implications of plant plasticity. Species may vary in adaptation depending on genotype and habitat of the individual plant (Knight 1965). Refined field observations are necessary to incorporate intra-species variation into a structural-functional classification. If the structural and functional features are assessed in the field, the effects of plasticity will be accounted for. There are two other problems associated with this approach. Firstly, there is a paucity of data in the literature on a number of life history attributes, especially of woody plant species. Secondly, the data of features that exhibit a seasonal variability such as flowering time cannot be extrapolated from one area to another with a high degree of confidence. Consequently site specific records of these features over the medium to long term are required. The 'snap-shot' approach to sampling in this study (approximately one week per site), precluded the observation of seasonal changes.

A relatively small number of functional attributes were used to define the woody plant functional types in this study in comparison with the number used in other studies. The

woody plant communities were classified on the basis of five functional attributes with a total of nineteen attribute classes. Werger and Sprangers (1982) used 62 structural-physiognomic characteristics and Knight and Loucks (1969) used 29 features. Montalvo *et al* (1991) concluded from a comparison of communities using non-taxonomic attributes that the number of attributes influences the extent of possible inferences that can be drawn from the resulting classification. The choice and number of functional features used has been found to influence the classification derived (Webb *et al* 1976, Werger and Sprangers 1982). Leishman and Westoby (1992) used a large number of traits in order to prevent the classification from being dominated by preconceptions as to which traits are best correlated with others or are most important in themselves. Montalvo *et al* (1991) used a high number of attributes in order to obtain a broad characterisation of each species without the *a priori* assumption that some attributes are more important than others. It is suggested, therefore, that a larger number of functional features be considered in future functional classifications of savanna vegetation. The collection of site-specific functional data, as suggested above, may serve to overcome the problem of paucity of data on functional attributes that was experienced in this study.

8.4 COMPARISON OF FLORISTIC AND FUNCTIONAL CLASSIFICATIONS

A high degree of similarity was not observed between the woody plant and graminoid floristic and functional classifications in this study although similarities between taxonomic and structural-functional classifications have been observed in elsewhere. Knight (1965) compared a structural-functional index derived for Wisconsin prairie vegetation with a compositional index derived for the same vegetation and found a close relationship between the two indices. Werger and Sprangers (1982) compared floristic and structural-physiognomic classifications of a dry semi-evergreen forest and thicket vegetation of south-eastern India. They found the classifications to be very similar in their main groupings and concluded that the use of structural-physiognomic criteria allows a detailed and ecologically significant classification of vegetation. Montalvo *et al* (1991) found correspondence between classifications based on species composition and on morpho-functional traits in Mediterranean grasslands. A common feature of these studies is that data were sampled within one geographical area in each case and a lack of a high degree of correspondence between the

floristic and functional classifications of the savanna communities in this study may be related to the fact that communities were sampled over a wide geographical area.

In this study the floristic groupings reflected the geographical separation of the communities sampled while communities from different geographical locations were grouped together functionally. Studies of the convergence of ecosystem structures under similar climates have shown that the selective forces of the environment can overrule the importance of taxonomic relationships or phylogeny in the evolution of structural-physiognomic characters (Werger and Sprangers 1982, Cowling and Campbell 1983). The convergence of form and function under similar evolutionary pressures is the underlying hypothesis of the structural-functional classification approach. It is on the basis of this that functional classifications are considered to be more ecologically meaningful than floristic ones. Montalvo *et al* (1991) consider that in Mediterranean grassland vegetation, species composition facilitates differentiation between grasslands from different localities and suggest that this is due to a variation in the distribution and abundance of the species related to more local types of peculiarities such as differences in species migrations and establishment. They consider that a non-taxonomic classification expresses the influence of environmental variability on these systems in a more gradual way. Knight and Loucks (1969) consider the question of ecological equivalence and suggest that emphasis on taxonomic differences can cover very real ecological similarities. The observation in this study that the woody plant and graminoid communities were grouped into floristic types in a more similar way than into functional types supports the idea that species composition reflects biogeographical separation while functional features reflect plant responses to environmental conditions.

The results of this study indicate that convergence of form and function irrespective of taxonomic relationships should enable the comparison of floristically different but structurally and/or functionally similar savanna communities. This is especially important for inter-continental comparisons for the classification of the savannas of the world proposed by the RSSD research effort (Frost *et al* 1986). A structural-functional index derived for Wisconsin prairie vegetation is considered to have the potential for application to grasslands with similar environments around the world, irrespective of species differences (Knight 1965). Knight (1965) contrasts this with a compositional index, developed for the same vegetation, that can

only be used where the same indicator species are found. Knight and Loucks (1969) suggested that the structural-functional coordinates derived in their study of Wisconsin forest vegetation could be applied to temperate upland forest vegetation of Europe, Asia and North America, all with different species composition but similar ecological conditions.

One of the main differences between the floristic and functional classifications of the woody plant communities was that the floristic types, based on species composition, were primarily related to PAM while the functional types reflected differences in AN. The functional / floristic convergence of the woody plants appears to be higher at the familial level, however, since the occurrence of the selected families (Mimosoideae, Caesalpinoideae and Combretaceae) was also primarily related to the AN gradient. The classifications of the graminoid communities on the basis of species composition, tribes, subfamilies and functional features were all primarily related to the PAM gradient.

It must be born in mind that the range of functional attributes used will have influenced the functional types derived and consequently the comparison of the floristic and functional classifications. The functional classifications derived in this study are not considered to be definitive and only represent a first attempt at classifying South African savannas on a functional basis. If a different suite of woody plant functional traits, such as those relating to fire response had been used, the influence of PAM may have been found to be more functionally important.

8.5 IMPLICATIONS FOR FUTURE RESEARCH

This study suggests that there is potential for using the PAM-AN plane as an overall framework for the functional classification of savannas. The following issues need to be considered with respect to any future research.

The predictive potential of the devised woody plant and graminoid functional classifications in the plane of PAM and AN needs to be tested. This can be done in two ways. The first is by positioning the savanna type on the PAM-AN plane on the basis of its structural and

functional characteristics and then determining if the predicted PAM and AN values correspond with the actual values measured at the site. The second way is by using actual measures of PAM and AN to predict the structural and functional characteristics of a savanna type and then determining if the predicted structural and functional characteristics correspond with the actual structural and/or functional characteristics measured at the site. The ultimate utility of a functional classification will only be demonstrated after thorough testing has shown that the classification does have predictive value and that it is transportable both spatially and temporally (Noble 1988).

At a recent RSSD meeting the inclusion of temperature as a third axis on the PAM-AN plane was suggested (Solbrig 1990). Although the influence of temperature on savanna structure and function was not investigated in this study, similarities in mean monthly temperatures and in the seasonal variation of temperature for all these South African savannas suggest that temperature may not be an important determinant. Further investigation, as a determinant is needed before a conclusion can be drawn. A temperature may be important for a classification of savannas from different continents.

In using the PAM-AN plane idea for predictions of vegetation dynamics it is suggested that different classifications may be required depending on the purpose of the predictive model. A consideration of the dynamics of vegetation structure and function in response to fire, for example, would require a classification with a different set of features from one that predicted vegetation change in response to herbivory. The functional classification developed by Friedel *et al* (1988) is an example of a classification specifically for the purposes of management of arid rangelands. Functional attributes should be selected according to their relevance for management purposes. Noble (1988) considers that it is unlikely that a definite set of functional classifications will be developed until specific applications are required.

An important consideration in the use of the PAM-AN plane is how to take into account the problem that the current floristic, structural and functional conditions of the vegetation may be reflecting the direct effects of land use rather than the average conditions of PAM and AN. The classifications derived in this study were based on vegetation subjected only to natural disturbances. The potential direct effects of the secondary determinants and especially human

influence on the structure and function of savannas on the basis of PAM and AN needs to be considered. These determinants are hypothesised to be more important than PAM for influencing the structure of East African savannas (Belsky 1991).

The development and use of a structural-functional index for savannas as developed by Knight (1965) for prairie vegetation and by Knight & Loucks for forest vegetation could be investigated. Such an index might prove useful for the comparison of savanna vegetation on an inter-continental basis.

8.6 CONCLUSIONS

There are six main conclusions from the results of this study.

1. The PAM and AN indices derived in this study were ecologically meaningful and suitable for the quantification of the PAM-AN plane. The PAM index (number of growth days per annum) derived by the soil water balance model was considered to be detailed enough for use at the community level. Ten AN indices were considered worth using on the PAM-AN plane namely (1) mean score of experts' ratings, (2) shoot production, (3) total nitrogen, (4) nitrogen mineralisation rate, (5) percentage clay, (6) percentage organic carbon, (7) percentage base saturation, (8) N-P, (9) N-P-K, and (10) eigenvalues of N,P,K. The AN index used in this study (total nitrogen content mg/kg in the A horizon) was considered to account for floristic, structural and functional variation of the vegetation on the basis of soil fertility.
2. The floristic variation of the savanna vegetation was related to the primary determinants of PAM and AN. Plant available moisture had a primary effect on the species composition of the savanna communities sampled and on the distribution of graminoid subfamilies and tribes. The effect of available nutrients was less pronounced, but still significant and was strong on tree composition at the family level.
3. The woody plant and graminoid components at each site were not always classified into

the same floristic types but there was a degree of correlation indicating that these components do not act entirely independently in response to conditions of PAM and AN.

4. The structural variation of the woody plant and graminoid communities was primarily related to the PAM gradient and there were no trends with soil fertility. There were no apparent predictable structural trends on the PAM-AN plane but this conclusion needs to be supported by the results of a multiple linear regression. A range of structural types occurred under similar conditions of PAM and AN. The effects of herbivory and fire on the structure of savanna communities need to be considered.
5. The functional trends of the savanna communities were related to the primary determinants of PAM and AN. The functional variation of the woody plant component was related to the availability of nutrients while that of the graminoid layer was primarily related to plant available moisture. The woody plant and graminoid communities were not grouped functionally in the same way, suggesting the need for the development of separate models for the prediction of functional change in response to changes in PAM and AN.
6. Woody plant and graminoid communities with similar conditions of PAM and AN did not have consistently similar functional characteristics but both classifications mapped well onto the PAM-AN plane suggesting that it may provide a suitable overall framework for the classification of savannas on a functional basis. The predictive potential of the derived functional classification models in the plane of PAM and AN needs to be assessed.

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APPENDIX 1.

Details about the weather stations from which the monthly and daily climate data were collected.

(a) Mean monthly rainfall and maximum and minimum temperatures

<u>Area</u>	<u>Name and number of station</u>		<u>Number of years of records</u>	
			<u>Rainfall</u>	<u>Temperature</u>
Mkuzi	Mkuzi Game Reserve	375366	8	8
Nylsvley	Nylsvley Nature Reserve	590307	12	12
Rooipoort	Kimberley Airport	290468	90	53
Langjan	Mara Agric. Station	721725	33	33
Messina	Macuville	809706	33	51
Lower Sabie	Skukuza	596657	33	77
Timbavati	Satara	639214	11	6
Pretoriuskop	Pretoriuskop	556295	25	25

(b) Daily rainfall

<u>Area</u>	<u>Name and number of station</u>		<u>Latitude</u>	<u>Longitude</u>
Mkuzi	Mkuzi Game Reserve	375366	37° 36"	32° 13"
Nylsvley	Nylsvley Nature Reserve	590307	24° 37"	28° 41"
Rooipoort	Caerwinning	289302	28° 32"	24° 11"
Langjan	Omloop	764710	22° 50"	29° 24"
Messina	Goeree	809285	22° 15"	29° 40"
Lower Sabie	Krokodilbrug	557712	25° 22"	31° 54"
Timbavati	Tshokwane	596647	24° 47"	31° 52"
Pretoriuskop	Gutshwa-NAF	556289	25° 19"	31° 10"

(c) Approximate distance and direction of the daily rainfall simulation weather stations from each site.

<u>Site</u>	<u>Distance and Direction</u>	<u>Site</u>	<u>Distance and Direction</u>
1	2 km S	11	16 km NW
2	6 km N	12	19 km E
3	16 km NNW	13	19 km E
4	9 km N	14	36 km WSW
5	8 km W	15	11 km S
6	5 km NW	16	59 km SE
7	5 km NW	17	60 km ESE
8	4 km NNE	18	20 km SW
9	16 km NW	19	25 km WSW
10	16 km NW		

APPENDIX 2.

Woody plant species composition and structural data recorded at each site. Full species names are listed in Appendix 4. Family names are listed in Appendix 3. The rare species at each site are indicated with an asterisk. Totals exclude values for rare species.

(a) Mkuzi 1

	Family	Density (#/ha)	Basal area (m ² /ha)	Mean height (m)	Canopy cover (%)	Browse volume (m ³)
	acac burk	17	113	6.770	6.2	67.03
	albi forb	17	8	0.140	6.0	4.74
*	ancy mont	24	4	0.160	3.0	0.91
*	brac disc	10	29	0.001	0.3	0.02
*	capp tran	7	59	0.010	0.4	0.04
	cari bisp	3	401	0.020	0.2	0.25
*	cass aeth	8	29	0.010	0.5	0.05
	catu spin	24	8	0.020	3.8	0.45
	codd rudi	24	90	0.120	1.3	0.65
	comb moll	9	252	1.420	4.0	12.52
	comm negl	5	46	0.141	2.7	1.71
	dich sine	17	4	0.040	3.0	0.75
	ehre rigi	4	57	0.040	0.2	0.01
	eucl cris	11	37	0.941	2.4	0.19
	eucl divi	11	160	0.050	1.1	0.87
	eucl nata	11	151	0.050	1.1	0.98
	euge cape	18	544	0.040	0.2	0.15
	grew hexa	29	4	0.001	1.1	0.05
*	grew mico	29	33	0.320	2.2	1.99
	grew occi	29	973	0.430	0.3	1.91
*	mayt moss	8	57	0.020	0.3	0.36
	ochn nata	19	90	0.070	0.8	1.10
	rhys guen	1	120	0.360	1.9	3.10
*	scho brac	6	4	0.800	8.0	5.77
	sola birr	1	13	1.310	7.2	9.46
	stry mada	14	122	2.160	1.7	3.30
	term seri	9	46	0.280	4.1	2.24
*	tree spec	4	4	0.430	10.0	2.61
	zizi mucr	23	198	2.650	3.6	27.94
TOTALS		3437	17.053	2.5	139.40	43156.0

(b) Mkuzi 2

	Family	Density (#/ha)	Basal area (m ² /ha)	Mean height (m)	Canopy cover (%)	Browse volume (m ³)
	acac gran	17	3	0.100	4.4	1.20
	acac nigr	17	127	2.150	4.1	10.46
	acac nilo	17	305	1.070	1.6	8.61
	acac tort	17	127	0.560	0.6	4.76
	bosc shru	7	32	0.011	0.9	0.17
	dich cine	17	101	0.021	0.8	0.66
*	doyv long	13	6	0.001	1.1	0.07
	ehre rigi	4	13	0.001	0.5	0.02
	eucl undu	11	19	0.001	0.7	0.16
*	grew spec	29	6	0.001	0.8	0.01
	mayt sene	8	20	0.002	1.0	0.09
*	rhoi trid	31	6	0.001	0.7	0.02
	zizi mucr	23	16	0.011	2.0	0.26
TOTALS		763	3.927	1.5	26.39	7048.5

(c) Mkuzi 3

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)	
	acac nilo	17	5	0.130	3.9	1.08	207.8
	acac tort	17	49	2.191	5.1	26.33	5396.7
	acac xant	17	95	6.230	9.3	70.61	44883.0
*	azin tetr	25	10	0.001	0.0	0.01	0.3
	capp tome	7	45	0.010	0.5	0.14	7.9
	carr bisp	3	3	0.001	0.7	0.01	0.6
*	cord spec	4	3	0.001	0.1	0.00	0.1
	dich sine	17	30	0.060	2.3	1.80	317.8
	dois lyci	11	17	0.061	1.6	0.07	8.1
	domb rotu	28	7	0.270	4.0	1.16	455.1
*	doyv rham	13	3	0.001	0.5	0.00	0.1
	ehre rigi	4	209	0.080	0.8	0.55	58.3
	eucl undu	11	3	0.001	1.0	0.00	0.2
	grew occi	29	17	0.001	1.0	0.03	2.0
*	grew spec	29	7	0.001	0.9	0.05	4.6
	mayt sene	8	118	0.060	0.7	0.44	49.5
	scla birr	1	3	0.120	6.3	0.90	337.9
*	spir afri	12	1	0.050	7.5	0.68	374.6
*	tric emet	16	1	0.030	4.5	0.25	49.6
	zizi mucr	23	6	0.081	3.6	1.38	775.5
TOTALS		607	9.296	2.9	104.50	52500.1	

(d) Mkuzi 4

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume
		(#/ha)	(m ² /ha)	(m)	(%)	(m ³)
acac burk	17	2	0.330	9.0	2.10	1048.8
acac nigr	17	376	0.460	0.8	2.03	958.4
acac nilo	17	62	0.010	0.2	0.09	2.1
acac tort	17	95	0.050	0.9	0.17	19.3
albi forb	17	33	0.041	1.5	0.16	34.6
comb apic	9	925	6.420	3.8	36.91	12532.2
dich sine	17	426	0.310	0.7	1.38	186.3
eucl cris	11	31	0.001	0.1	0.00	0.0
grew subs	29	3	0.100	3.8	0.48	119.0
mayt sene	8	62	0.010	0.2	0.03	0.7
ozor obov	1	25	0.291	3.2	1.58	431.5
scla birr	1	10	0.550	5.8	3.15	1192.3
zizi mucr	23	2	0.210	4.5	1.79	447.8
TOTALS		2052	8.783	2.6	49.87	16973.0

(e) Mkuzi 5

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)
* acac leud	17	1	0.020	3.5	0.48	143.1
acac nigr	17	1	0.030	3.5	0.50	74.6
acac nilo	17	152	0.570	1.4	4.62	699.6
* acac sene	17	20	0.010	0.5	0.13	5.0
acac tort	17	267	4.590	2.9	49.28	7332.6
* azim tetr	25	5	0.001	0.7	0.13	9.0
cada nata	7	20	0.060	1.0	0.57	111.3
capp tome	7	96	0.020	0.7	0.56	38.5
ari blasp	3	5	0.001	0.3	0.02	0.5
dich sine	17	76	0.010	0.5	0.22	9.8
ehra rigi	4	5	0.001	0.6	0.01	0.3
eucl undu	11	20	0.001	0.9	0.09	6.0
* goss herb	15	10	0.001	0.4	0.07	1.9
lyci acut	27	20	0.010	0.6	0.04	1.8
mayt sene	8	30	0.001	0.7	0.06	2.3
rhus quen	1	15	0.001	0.9	0.06	3.7
* sida iner	26	2	0.160	4.5	1.03	359.3
TOTALS		707	5.295	1.2	56.03	8281.0

(f) Nylsvley 6

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)
acac burk	17	4	0.001	1.8	0.13	21.1
burk afri	6	179	2.830	3.8	14.36	5076.0
comb zeyh	9	7	0.240	6.0	1.95	813.9
dich sine	17	21	0.001	0.4	0.05	2.9
domb rotu	28	16	0.031	2.1	0.38	89.6
grew flve	29	102	0.150	1.9	2.61	578.5
* lann disc	1	15	0.111	2.2	0.53	263.9
* lyci spec	27	2	0.010	2.5	0.03	4.3
ochn pulc	18	322	0.530	0.8	1.04	190.7
* ozar pani	1	4	0.001	1.3	0.03	3.4
stry pung	14	63	0.640	2.8	2.09	635.7
tarm seri	9	35	0.510	6.3	5.56	2030.7
* vite nomb	30	9	0.001	0.3	0.01	0.3
TOTALS		749	4.933	2.9	28.17	9439.1

(g) Nylsvley 7

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
*	acac caff	17	85	0.020	0.9	0.11	19.3
	comb apic	9	1461	1.380	2.5	12.47	3292.5
	comb moll	9	1904	1.990	2.0	8.54	1546.0
	comb zeyh	9	10	0.270	4.4	1.51	709.0
	dich sine	17	257	0.030	1.2	0.71	93.7
*	dipl cond	3	42	0.010	0.2	0.13	2.8
	eucl divi	11	42	0.040	1.8	0.50	88.3
	eucl line	11	42	0.001	0.7	0.08	1.6
*	gard spat	24	5	0.050	3.3	0.56	165.2
	grew bico	29	2	0.010	3.0	0.17	30.4
*	mayt poly	8	125	0.020	0.8	0.33	18.9
	mund seri	21	2	0.001	5.5	0.36	89.4
	ochn pulc	19	44	0.020	1.6	0.07	15.0
*	ozar pani	1	2	0.030	4.5	0.22	65.3
*	pave zeyh	24	167	0.050	0.5	0.05	14.1
	pelt afri	6	10	0.240	4.3	1.32	324.6
*	rhus lept	1	2	0.010	3.5	0.10	25.4
	term seri	9	5	0.010	3.1	0.27	46.6
	vite rehman	30	1083	0.830	1.7	6.79	811.1
TOTALS		4862	4.822	2.1	32.79	7052.2	

(h) Nylsvley 8

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
	acac nigr	17	2	0.001	0.6	0.01	0.4
	acac nilo	17	20	4.791	4.5	5.34	1482.2
	acac sieb	17	28	0.001	0.4	0.13	5.6
	acac tort	17	115	2.810	3.4	24.03	7134.9
	comb here	9	2	0.001	0.5	0.00	0.1
	dich sine	17	74	0.210	1.2	1.82	309.3
	domb rotu	28	3	0.030	4.5	0.23	81.8
	ehre rigi	4	4	0.001	0.3	0.00	0.0
	grew flve	29	31	0.011	0.9	0.23	33.2
	grew micr	29	9	0.051	2.8	0.68	179.9
*	lipp java	30	2	0.001	0.7	0.01	0.2
	rhus guen	1	3	0.031	1.9	0.19	55.8
	scla birr	1	2	0.500	10.8	3.13	2446.0
	zizi mucr	23	20	0.041	1.0	0.43	96.7
TOTALS		313	8.479	2.5	36.22	11825.9	

(i) Rooipoort 9

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)	
	acac erio	17	111	1.360	3.6	8.20	1884.82
	acac mell	17	240	1.400	2.4	16.07	3691.59
	bosc albi	7	25	0.120	1.5	0.62	136.11
	ehre rigi	4	34	0.211	2.2	0.57	128.46
	grew flav	29	379	0.560	1.2	8.32	1052.24
	lyci hirs	27	7	0.002	1.9	0.21	33.60
*	rhus lanc	1	6	0.001	0.8	0.05	3.79
	zizi mucr	23	8	0.011	2.1	0.37	82.62
TOTALS		804	3.664	2.1	34.36	7009.44	

(j) Rooipoort 10

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)	
	acac erio	17	3	0.001	0.5	0.00	0.2
	acac mell	17	8	0.010	0.7	0.14	16.1
	acac tort	17	31	0.010	0.7	0.7	41.6
	ehri rigi	4	5	0.001	0.7	0.01	1.0
	grew flav	29	123	0.300	1.3	4.49	737.0
	lyci cine	27	3	0.001	1.3	0.01	0.6
*	rhus lanc	1	3	0.001	0.7	0.00	0.2
	rhus undu	1	100	0.040	0.8	0.30	31.2
	tarc camp	10	298	2.250	2.0	16.95	3666.5
	zizi mucr	23	44	0.070	1.8	1.14	235.4
TOTALS		615	2.683	1.1	23.33	4729.6	

(k) Rooipoort 11

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)
acac mell	17	898	0.820	0.8	15.16	1551.6
acac tort	17	244	0.190	0.8	3.83	468.8
bosc albi	7	31	0.060	0.7	0.32	26.9
ehre rigi	4	8	0.001	0.2	0.01	0.2
grew flav	29	496	0.730	1.0	8.77	924.1
lyci cine	27	126	0.100	0.8	1.10	97.1
tarc camp	10	79	0.090	1.1	1.23	155.5
zizi mucr	23	8	0.010	0.9	0.12	11.0
TOTALS		1890	2.001	0.8	30.54	3235.2

(1) Langjan 12

Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)	
acac erio	17	5	0.001	0.7	0.02	1.5
acac mell	17	23	0.020	1.1	0.40	62.1
acac tort	17	188	0.980	1.4	8.26	1472.0
bosc albi	7	22	1.030	2.9	3.39	864.5
bosc foet	7	14	0.191	1.1	0.43	77.1
comm pyro	5	5	0.010	0.8	0.06	4.4
dich sine	17	23	0.020	1.3	0.46	58.5
ehre rigi	4	10	0.001	0.7	0.04	2.5
grew flav	29	485	1.000	1.7	16.24	3082.1
grew flve	29	25	0.030	1.7	0.87	170.8
grew reti	29	38	0.110	1.4	1.21	248.7
grew vill	29	31	0.030	1.1	0.41	47.7
lyci cine	27	5	0.010	1.3	0.15	19.2
term prun	9	204	1.190	1.7	9.62	2298.4
TOTALS	1078	4.633	1.4	41.56	8409.6	

(m) Langjan 13

	Family	Density (#/ha)	Basal area (m2/ha)	Mean height (m)	Canopy cover (%)	Browse volume (m3)	
	acac burk	17	2	2.960	11.0	2.03	1519.7
	acac erio	17	3	0.400	9.3	1.93	1126.0
	acac tort	17	2	0.090	3.8	0.35	95.9
	albi forb	17	12	0.020	1.4	0.50	64.7
	bosc albi	7	14	1.030	4.7	2.99	889.5
*	cant cili	24	2	0.010	3.0	0.11	34.0
	catu spin	24	77	0.040	0.8	0.80	161.0
	comb apic	9	94	1.820	4.5	17.20	6029.1
	comm afri	5	138	0.071	0.9	1.43	163.6
	comm moll	5	14	0.041	2.2	0.17	34.7
	comm pyro	5	71	0.370	1.4	4.31	677.0
	dich sine	17	69	0.270	2.1	2.71	587.9
	eucl divi	11	30	0.010	0.6	0.09	6.0
	grew bico	29	7	0.090	2.8	1.18	344.4
	grew flav	29	125	0.480	1.7	5.39	1023.1
	grew flve	29	84	0.560	2.8	7.26	1867.0
	grew sp.	29	11	0.090	3.0	1.56	431.1
	grew reti	29	41	0.050	1.4	1.00	170.0
*	ozar pani	1	6	0.001	0.5	0.02	1.0
	plec arma	24	43	0.331	3.1	2.77	788.9
	scle birr	1	19	2.001	9.5	12.30	14756.6
	stry mada	14	50	0.120	2.0	0.84	200.6
*	xime amer	20	6	0.001	0.6	0.02	1.1
TOTALS		906	10.844	3.5	66.81	30936.8	

(n) Messina 14

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
*	acac sene	17	10	0.001	1.1	0.25	27.0
	bosc albi	7	36	0.290	2.2	1.25	244.9
	bosc foet	7	16	0.090	2.2	0.70	154.1
	colo mopa	6	314	2.940	2.8	20.11	6971.2
	comb apic	9	186	0.850	2.2	8.28	2753.8
	comm afri	5	16	0.480	4.4	2.57	714.3
	comm moll	5	20	0.650	3.8	5.90	1534.5
	dich cine	17	180	0.080	0.9	1.43	137.1
	grew bico	29	73	0.110	1.1	1.42	216.8
	grew flav	29	96	0.290	1.9	4.50	978.6
	grew hexa	29	41	0.040	0.0	0.66	58.3
	lyci cine	27	18	0.050	1.7	0.54	88.3
	scle birr	1	4	0.320	6.0	1.35	540.1
	term prun	9	680	0.700	0.8	6.81	1298.4
TOTALS		1680	6.890	2.3	55.52	15690.4	

(o) Lower Sabie 15

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
	acac gerr	17	123	0.260	2.7	1.94	593.5
	albi harv	17	665	0.680	1.7	6.49	1136.5
	bolu spec	21	10	0.910	3.4	0.97	651.1
	dalb mela	21	168	0.090	1.5	1.60	278.3
	dich cine	17	149	0.430	2.2	3.88	781.6
*	doyv caff	13	2	0.001	1.8	0.09	15.2
*	shre amoe	4	77	0.020	0.4	0.40	31.6
	grew hexa	29	2	0.010	1.8	0.04	7.2
	grew mont	29	2	0.001	2.5	0.07	17.4
	long capp	21	61	0.090	1.9	0.53	115.3
	mayt hete	8	52	0.200	2.3	1.11	242.8
	mayt sene	8	519	0.220	1.3	3.71	445.3
	ochn nata	19	2	0.001	2.5	0.05	4.9
	ormo tric	21	1466	0.250	0.5	1.62	77.2
	scle birr	1	31	0.790	6.0	3.51	3091.9
	secu viro	22	26	0.010	0.7	0.44	30.8
	zizi mucr	23	2	0.001	1.6	0.08	12.7
TOTALS		3277	3.943	2.2	26.04	7486.5	

(p) Timbavati 16

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
acac	exuv	17	29	0.011	1.9	0.29	49.7
acac	nigr	17	76	2.021	7.6	13.83	7304.1
bolu	spec	21	2	0.040	4.3	0.17	51.1
comb	apic	9	49	0.040	1.4	0.51	66.1
comb	here	9	24	0.080	2.7	0.81	211.5
comb	zeyh	9	6	0.020	2.5	0.26	65.0
comm	afri	5	70	0.020	0.5	0.19	9.8
dalb	mela	21	667	0.091	0.5	1.18	82.6
dich	cine	17	47	0.010	1.0	0.64	75.7
ehre	rigi	4	23	0.010	0.9	0.08	9.8
eucl	undu	11	12	0.001	0.9	0.07	3.2
grew	bico	29	45	0.120	2.0	1.31	286.0
grew	flve	29	47	0.070	1.0	1.02	172.5
grew	mont	29	251	0.840	2.4	13.75	3349.1
grew	subs	29	111	0.610	2.8	8.96	2838.4
ormo	tric	21	95	0.021	0.9	0.29	23.9
ozor	insi	1	2	0.010	3.8	0.17	62.2
sole	birr	1	15	1.000	8.7	5.45	3285.7
sacu	viro	22	47	0.030	1.3	0.79	133.7
zizi	mucr	23	18	0.011	2.1	0.50	94.1
TOTALS		1634	5.046	2.4	30.10	18112.9	

(q) Timbavati 17

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
	acac exuv	17	120	0.060	1.6	1.54	193.6
	acac gerr	17	6	0.010	2.5	0.27	67.6
	albi harv	17	58	0.140	1.2	0.74	113.0
	comb here	9	26	0.251	2.1	0.57	345.1
	comm afri	5	7	0.001	0.6	0.10	6.3
	dich cine	17	193	0.570	1.7	6.66	1281.2
*	dios mesp	11	6	2.820	15.0	4.08	4081.9
	ehre rigi	4	13	0.001	0.5	0.01	0.5
	eucl undu	11	24	0.031	2.3	0.56	124.3
	grew bico	29	13	0.001	0.4	0.04	1.5
	grew flav	29	6	0.020	2.3	0.49	85.1
	grew flve	29	19	0.100	1.7	0.86	212.3
	grew mont	29	20	0.020	1.2	0.37	45.5
	long capp	21	60	0.030	0.6	0.10	6.7
	mayt hata	8	13	0.011	2.2	0.17	23.4
	mund seri	21	47	0.010	0.6	0.10	5.6
	ormo tric	21	100	0.020	0.6	0.16	11.8
	scla birr	1	88	10.491	8.8	63.68	57162.8
*	spir afri	12	7	0.001	0.6	0.02	1.2
	stry mada	14	53	0.030	0.7	0.25	50.6
	term seri	9	598	3.880	3.8	42.36	18233.4
	zizi mucr	23	7	0.001	1.0	0.10	10.0
	TOTALS	1471	15.679	2.5	119.13	77980.3	

(r) Pretoriuskop 18

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume
		(#/ha)	(m2/ha)	(m)	(%)	(m3)
* anno sene	2	6	0.02	3.5	0.31	110.15
* ante veno	12	33	0.14	2.4	1.21	290.13
dich cine	17	2090	1.95	1.7	30.06	6987.6
dios lyci	11	67	0.01	0.6	0.16	9.79
mayt sene	8	172	0.11	1.0	1.33	183.83
mund seri	23	67	0.01	0.6	0.29	18.33
ochu nata	19	166	0.11	0.8	0.98	88.44
pelt afri	6	33	0.001	0.4	0.17	6.69
* rhus pyro	1	33	0.01	0.6	0.1	5.62
scle birr	1	67	0.01	0.3	0.08	2.63
stry mada	14	39	0.35	3.6	1.63	703.83
term brac	9	666	0.12	0.6	4.6	295.95
term seri	9	1295	5.6	5.0	77.41	38197.05
TOTALS		4662	8.271	1.5	116.71	46494.14

(s) Pretoriuskop 19

	Family	Density	Basal area	Mean height	Canopy cover	Browse volume	
		(#/ha)	(m2/ha)	(m)	(%)	(m3)	
	acac gerr	17	5	0.020	2.9	0.25	48.5
	albi harv	17	10	0.001	0.5	0.08	4.2
	comb apic	9	200	2.660	3.9	16.43	7672.6
	comb coll	9	43	0.471	3.7	4.67	1657.6
	comb here	9	2	0.040	6.0	0.32	112.5
	comb zeyh	9	61	0.511	3.5	4.79	1700.0
	dalb mela	21	195	0.030	0.4	0.52	26.4
	dich cine	17	204	0.260	1.7	4.63	740.5
	domb rotu	28	31	0.010	0.6	0.16	10.9
	grew mont	29	10	0.050	2.9	0.70	146.0
	mayt hete	8	51	0.010	0.6	0.24	15.6
	mayt sene	8	21	0.001	0.7	0.05	3.9
	mund seri	21	53	0.120	1.3	0.75	87.1
*	ozor insi	1	12	0.120	2.8	0.72	182.5
	pelt afri	6	10	0.010	0.8	0.13	9.6
*	rhus pent	1	10	0.001	1.4	0.03	4.1
	scle birr	1	51	1.250	4.4	5.89	2789.2
	stry mada	14	286	0.460	1.5	3.72	1026.6
	term brac	9	21	0.010	0.7	0.30	23.9
	term seri	9	252	0.710	2.6	6.94	1696.4
TOTALS		1506	6.704	2.2	50.57	17772.3	

APPENDIX 3.

The woody plant families recorded over the range of savanna floristic communities sampled. The families that were represented at each site are listed by number in Appendix 2 a-s.

1	Anacardiaceae	17	Mimosoideae
2	Annonaceae	18	Myrtaceae
3	Eupocynaceae	19	Ochnaceae
4	Boraginaceae	20	Olaceae
5	Burseraceae	21	Papilionoideae
6	Caesalpinoideae	22	Polygalaceae
7	Capparaceae	23	Rhamnaceae
8	Celastraceae	24	Rubiaceae
9	Combretaceae	25	Salvadoraceae
10	Compositae	26	Sapotaceae
11	Ebenaceae	27	Solanaceae
12	Euphorbiaceae	28	Sterculiaceae
13	Flacourtiaceae	29	Tiliaceae
14	Loganiaceae	30	Verbenaceae
15	Malvaceae	31	Vitaceae
16	Meliaceae		

APPENDIX 4.

Woody plant functional attributes of each species. The classes of each functional attribute are listed in Table 2.2. The code representing each functional class corresponds with that in Table 2.2. The asterisks denote rare species.

	Abbrev	Leaf dura	Spin	Leaf Type	Leaf Size	Pala	Grow Rate	Cold	Fire	Drou	Repr	Parts Eaten	Fruit Type
Acacia burkei	acac burk	1	6 t	1	2	1	3	2	0	1	0	0	1
* Acacia caffra	acac caff	1	3 t	1	1	1	1	1	0	0	0	0	1
Acacia erioloba	acac erio	1	6 t	1	1	1	2	1	0	1	0	1	2
Acacia exuvialis	acac exuv	1	4 t	1	1	1	0	0	0	0	0	0	1
Acacia gerrardii	acac gerr	1	4 t	1	1	1	1	1	0	0	1	1	1
Acacia grandicornuta	acac gran	1	4 t	1	1	1	1	2	0	0	0	1	1
* Acacia leudoritzii	acac leud	1	5 t	1	1	1	3	0	0	0	0	0	1
Acacia mellifera	acac mell	1	6 t	1	2	1	0	0	0	1	6	7	1
Acacia nigrescens	acac nigr	1	6 t	1	3	1	3	1	1	1	0	0	1
Acacia nilotica	acac nilo	1	4 t	1	1	1	3	1	0	0	0	0	2
* Acacia robusta	acac robu	1	4 t	1	1	1	1	1	0	0	0	0	1
Acacia sieberana	acac sieb	1	4 t	1	1	1	1	1	0	0	1	1	1
* Acacia senegal	acac sene	1	5 t	1	1	1	1	1	0	0	0	1	1
Acacia tortilis	acac tort	1	6 t	1	1	1	3	1	3	1	1	1	1
Acacia xanthophloea	acac xant	1	6 s	1	1	1	3	2	0	0	1	7	2
Albizzia forbsii	albi forb	1	1	1	1	1	3	2	0	1	0	0	2
Albizzia harveyi	albi harv	1	1	1	1	1	3	2	1	0	1	8	1
* Ancyranthos monteiroi	ancy mont	0	1	2	2	0	0	0	0	0	0	0	3
* Annona senegalensis	anno sene	1	1	2	3	1	1	2	1	0	2	1	3
* Antedasma venosum	ante veno	2	1	2	3	3	1	1	0	0	0	0	3
* Azima tetracantha	azim tetr	3	4 s	2	3	1	0	0	0	0	0	0	3
Bolusanthus speciosus	bolu spec	2	1	1	3	3	1	1	0	0	1	0	1
Boscia albitrunca	bosc albi	3	1	2	3	1	3	2	0	1	6	1	3
Boscia foetida	bosc foet	3	1	2	2	1	0	1	0	1	0	0	3
Boscia species	bosc sp.	2	1	2	2	1	0	0	0	1	0	0	5
* Brachylaena discolor	brac disc	3	1	2	3	3	1	0	0	0	0	0	6
Burkea africana	burk afri	1	1	1	3	3	3	1	2	0	3	0	2
Cadaba natalensis	cada nata	3	1	2	3	2	0	0	0	0	0	0	3
* Canthium cilliatum	cant cill	0	0	0	0	0	0	0	0	0	0	0	0
Capparis tomentosa	capp tome	2	4 t	2	3	1	0	0	0	0	0	0	3
* Capparis transvaalensis	capp tran	1	4 t	2	3	1	0	0	0	0	0	0	3

Appendix 4 continued...

Appendix 4 continued...

	Abbrev	Leaf dura	Spin Type	Leaf Size	Leaf Size	Pala	Grow Rate	Cold	Fire	Drou	Repr	Parts Eaten	Fruit Type
Carissa bispinosa	cari bisp	3	5 t	2	3	1	0	0	1	0	0	0	3
* Cassine aethiopica	cass aeth	1	1	2	5	2	0	0	0	0	0	1	3
Catunaregam spinosum	catu spin	2	4 s	2	3	3	0	0	0	1	0	0	5
Coddia rudis	codd rudi	1	1	2	3	1	0	0	2	0	0	0	5
Colophospermum mopane	colo mopa	1	1	2	4	3	1	2	1	1	1	1	2
Combretum apiculatum	comb apic	1	1	2	4	1	3	2	0	1	0	0	6
Combretum colinum	comb coli	1	1	2	5	1	3	2	1	2	0	0	6
Combretum hereroense	comb here	1	1	2	3	1	3	2	0	1	0	0	6
Combretum molle	comb moll	1	1	2	4	1	1	2	1	0	6	0	6
Combretum zeyheri	comb zeyh	1	1	2	4	1	3	2	1	0	0	0	6
Commiphora africana	comm afri	1	2 s	3	4	2	1	0	0	1	0	0	3
Commiphora mollis	comm moll	1	2 s	3	3	1	1	2	0	1	6	3	3
Commiphora neglecta	comm negl	1	2 s	3	3	2	1	2	0	1	6	1	3
Commiphora pyrocanthoides	comm pyro	1	2 s	3	4	2	0	0	0	1	0	0	3
* Cordia species	cord sp.	0	0	0	0	0	0	0	0	0	0	0	0
Dalbergia melanoxylon	dalb mela	2	2 s	1	3	2	3	2	0	0	1	3	2
Dichrostachys cinerea	dich cine	1	3 s	1	1	1	3	1	1	1	6	1	2
Diospyros lycioides	dios lyci	1	1	2	4	1	3	1	0	0	0	0	3
* Diospyros mespilliformes	dios mesp	2	1	2	4	2	1	2	0	0	0	1	3
* Diplorhynchus condylocarpon	dipl cond	1	1	2	5	0	1	0	1	0	0	0	5
Dombeya rotundifolia	domb rotu	1	1	2	4	3	1	1	0	0	0	0	5
* Doyvealis caffra	doyv caff	1	3 s	2	2	2	0	1	0	0	0	1	3
* Doyvealis longispina	doyv long	1	3 s	2	5	2	0	1	0	0	0	1	3
Doyvealis rhamnoides	doyv rham	1	3 s	2	3	2	0	1	0	0	0	1	3
* Ehretia amoena	ehre amoe	1	1	2	4	0	0	0	0	0	0	0	3
Ehretia rigida	ehre rigi	1	1	2	3	1	0	0	0	1	0	1	3
Euclea crispa	eucl cris	3	1	2	3	3	0	0	1	1	0	0	3
Euclea divinorum	eucl divi	3	1	2	3	3	3	1	0	1	0	1	3
Euclea linearis	eucl line	2	1	2	2	3	0	0	0	1	0	0	5
Euclea natalensis	eucl nata	3	1	2	3	3	0	0	2	1	0	0	3
Euclea schimperi	eucl schi	3	1	2	3	3	0	0	0	0	0	0	3
Euclea undulata	eucl undu	3	1	2	3	3	0	0	0	1	0	0	3
Eugenia capensis	euge cape	2	1	2	3	3	0	0	1	0	0	1	3
* Gardenia spatulifolia	gard spat	1	1	2	3	0	1	0	0	0	6	0	5
* Gossypium herbaceum	goss herb	0	0	0	0	0	0	0	0	0	0	0	0
Grewia bicolor	grew bico	1	1	2	3	1	0	0	0	1	0	1	3

Appendix 4 continued...

Appendix 4 continued...

	Abbrev	Leaf dura	Spin	Leaf Type	Leaf Size	Pala	Grow Rate	Cold	Fire	Drou	Repr	Parts Eaten	Fruit Type
Grewia flava	grew flav	1	1	2	3	3	0	0	0	1	0	1	3
Grewia flavescens	grew flve	1	1	2	4	1	0	0	0	1	0	1	3
Grewia hexamita	grew hexa	1	1	2	4	1	3	2	0	0	0	1	3
Grewia micrantha	grew micr	1	1	2	3	3	0	0	0	1	0	1	3
* Grewia microthyrsa	grew mico	1	1	2	3	2	0	0	0	0	0	1	3
Grewia monticola	grew mont	1	1	2	3	3	0	0	0	1	0	1	3
Grewia occidentalis	grew occi	1	1	2	3	1	0	0	0	0	0	1	3
Grewia retinervis	grew reti	1	1	2	3	2	0	0	0	1	0	0	3
Grewia species	grew sp.	1	1	2	3	2	0	0	0	1	0	0	3
Grewia subspathulata	grew subs	1	1	2	3	2	0	0	0	2	0	1	3
Grewia villosa	grew vill	1	1	2	4	3	0	0	2	1	0	1	3
Lannea discolor	lann disc	1	1	1	4	1	1	2	1	0	6	0	3
* Lippia javanica	lipp java	0	0	0	0	0	0	0	0	0	0	0	0
Lonchocarpus capassa	lcnc capa	2	1	3	5	1	3	2	1	0	6	1	2
Lycium acutifolium	luci acut	1	4 s	1	2	2	0	0	0	1	0	0	0
Lycium hirsutum	lyci hirs	1	4 s	1	2	2	0	0	0	1	0	0	0
Lycium cinereum	lyci cine	1	4 s	2	2	2	0	0	0	1	0	0	0
* Lycium species	lyci sp.	1	4 s	2	2	2	0	0	0	0	0	0	0
Maytenus heterophylla	mayt hete	3	4 s	2	3	1	3	0	0	1	1	1	4
* Maytenus mossambicensis	mayt moss	1	4 s	2	3	1	0	0	0	0	0	0	4
* Maytenus polyacantha	mayt poly	1	4 s	2	3	1	0	0	0	0	0	0	4
Maytenus senegalensis	mayt sene	2	4 s	2	4	1	0	0	1	0	0	0	4
Mundulea sericea	mund seri	2	1	3	3	3	3	0	0	1	1	0	1
* Ochna arborea	ochn arbo	3	1	2	3	3	0	0	0	0	0	0	4
Ochna natalita	ochn nata	3	1	2	4	3	3	2	1	0	0	0	5
Ochna pulchra	ochn pulc	1	1	2	3	3	3	2	1	0	0	0	5
Ormocarpum trichocarpum	ormo tric	2	1	1	2	3	0	0	0	0	0	0	1
* Ozoroa insignis v. ret	ozor insi	1	1	2	4	2	2	1	2	0	0	0	5
Ozoroa obovata	ozor obov	2	1	2	3	3	2	1	2	0	0	0	5
* Ozoroa paniculosa	ozor pani	2	1	2	4	2	2	1	2	0	0	0	5
Pavetta zeyheri	pave zeyh	1	1	2	2	1	0	0	0	0	0	0	0
Peltophorum africanum	pelt afri	1	1	1	1	3	1	1	0	0	6	6	2
Plectroniella armata	plec arma	2	3 s	2	3	0	0	0	0	1	0	0	3
* Rhoicissus tridentata	rhoi trid	0	0	0	0	0	0	0	0	0	0	0	0
Rhus gueinzii	rhus guen	2	2 s	3	3	1	0	0	0	0	0	0	3
* Rhus lancea	rhus lanc	1	1	3	3	1	1	0	0	0	6	0	3

Appendix 4 continued...

Appendix 4 continued...

	Abbrev	Leaf dura	Spin	Leaf Type	Leaf Size	Pala	Grow Rate	Cold	Fire	Drou	Repr	Parts Eaten	Fruit Type
* Rhus leptodictya	rhus lept	3	1	3	5	1	1	1	0	1	6	0	3
* Rhus pentheri	rhus pent	1	1	3	2	0	0	0	0	0	0	0	3
* Rhus pyroides	rhus pyro	1	1	3	3	1	0	0	0	0	0	0	3
Rhus undulata	rhus undu	3	2 s	2	2	3	0	0	0	1	0	0	3
* Schotia brachypetala	scho brac	2	1	1	3	2	3	1	0	0	0	0	1
Sclerocarya birrea	scler birr	1	1	1	3	1	1	2	0	1	6	1	3
Securidaca longipedunculata	secu long	1	2 s	2	3	1	0	0	0	0	4	0	5
Securinea virosa	secu viro	2	1	2	3	2	0	0	0	0	0	1	3
* Sideroxylon inerme	side iner	2	1	2	4	2	3	1	0	0	2	1	3
* Spirostachys africana	spir afri	1	1	2	3	2	3	1	0	0	0	0	5
Strychnos madagascariensis	stry mada	2	1	2	4	1	1	2	0	1	1	1	3
Strychnos pungens	stry pung	3	2 s	2	3	1	0	0	1	1	0	0	3
Tarchonanthus camphoratus	tarc camp	3	1	2	3	3	1	0	1	1	1	1	5
Terminalia brachystemma	term brac	1	1	2	5	3	0	0	1	1	0	0	6
Terminalia prunioides	term prun	2	2 s	2	3	1	3	2	0	1	0	0	6
Terminalia sericea	term seri	1	1	2	4	3	3	1	1	1	2	0	6
* Trichilia emetica	tric emet	3	1	1	5	3	1	2	0	0	6	0	5
* Vitex mombassae	vite romb	1	1	3	4	1	0	0	1	0	0	1	5
Vitex rehmannii	vite rehm	1	1	3	3	1	0	0	1	0	0	0	5
* Ximenia americana	xime amer	2	2 s	2	3	1	3	2	1	0	1	0	3
* Ximenia caffra	xime caff	2	2 s	2	3	1	3	2	0	0	1	0	3
Ziziphus mucronata	zizi mucr	1	6 t	2	3	1	1	1	0	1	0	1	3

APPENDIX 5.

Graminoid species composition and structural data recorded at each site. Full species names are listed in Appendix 6. The rare species at each site are indicated with an asterisk. Totals exclude values for rare species.

(a) Mkuzi 1

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris bipa	1590	0.037	0.22	0.80
Aris conj	11127	0.075	0.20	1.46
Aris stip	14307	0.415	0.28	16.82
* Brac nigr	6358	0.007	0.09	0.07
Dact aust	135117	0.229	0.09	5.00
Digi eria	19075	0.219	0.12	5.70
* Digi long	6358	0.005	0.13	0.07
* Erag curv	6358	0.187	0.27	8.35
Erag mogg	22255	0.053	0.15	0.84
Pani maxi	84249	2.808	0.28	141.58
Pero pate	11127	0.053	0.10	0.61
TOTALS	298847	3.889	0.18	172.81

(b) Mkuzi 2

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris bipa	9493	0.058	0.15	0.95
Cenc cili	1356	0.057	0.30	1.71
Digi dida	20341	0.516	0.14	11.51
Digi eria	5424	0.048	0.08	0.42
Erag supe	35259	1.163	0.28	32.53
Pani colo	48820	0.488	0.19	12.38
Pani deus	12205	0.779	0.37	31.98
Pani maxi	21698	0.246	0.29	7.87
Spor nite	4068	0.033	0.07	0.27
Them tria	101707	4.513	0.36	204.33
Uroc mosa	10849	0.047	0.14	0.69
TOTALS	271220	7.948	0.22	304.64

(c) Mkuzi 3

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Cenc cili	2156	0.008	0.47	0.19
Pani deus	3882	0.043	0.30	1.97
Pani maxi	80222	1.299	0.31	46.76
TOTALS	86260	1.350	0.36	48.92

(d) Mkuzi 4

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris bipa	11276	0.027	0.23	0.61
Andr gaya	85695	3.004	0.64	221.06
Chry serr	15786	0.363	0.33	12.16
Digi eria	60889	0.195	0.32	6.27
Dihe ampl	38773	0.52	0.46	28.39
* Erag spec	2255	0.004	0.22	0.10
Erag supe	4510	0.008	0.18	0.14
Eust pasp	27067	0.152	0.23	4.14
Hete cont	36082	1.902	0.46	112.43
Meli repe	11276	0.059	0.36	2.31
Pani maxi	6765	0.193	0.36	5.97
Them tria	105991	2.475	0.59	163.91
Tric gran	4510	0.012	0.16	0.16
Tric mona	22551	0.221	0.37	10.09
* Tris spec	13531	0.085	0.36	3.36
Uroc mosa	4510	0.001	0.26	0.04
TOTALS	435676	9.132	0.35	567.68

(e) Mkuzi 5

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris bipa	7422	0.009	0.13	0.10
Dact aust	145973	0.114	0.14	1.88
Digi agyr	27215	0.165	0.14	2.91
Digi eria	9896	0.044	0.12	0.58
Erag supe	4948	0.021	0.12	0.23
Pani colo	17319	0.048	0.14	0.67
Pani maxi	29689	0.213	0.19	4.51
* Pani spec	2474	0.024	0.10	0.24
Spor locl	163291	1.507	0.12	20.65
Spor nite	29689	0.132	0.07	0.98
Them tria	9896	0.544	0.45	29.36
Uroc mosa	39586	0.391	0.27	12.70
* Uroc tric	7422	0.089	0.14	1.28
TOTALS	484924	3.188	0.17	74.57

(f) Nylsvley 6

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris arge	5687	0.019	0.33	0.70
Aris conj	1625	0.019	0.32	0.52
Both inac	1625	0.024	0.46	1.08
Brac serr	1625	0.014	0.19	0.33
Digi eria	99125	1.855	0.22	41.76
Dihe ampl	812	0.029	0.54	1.54
Erag lehm	4062	0.106	0.27	3.84
Erag pall	24375	0.634	0.50	37.01
Hete cont	1625	0.336	0.48	21.11
Loud simp	1625	0.113	0.57	6.35
Meli repe	1625	0.061	0.34	1.97
Pani maxi	11375	0.134	0.25	3.90
Pero pate	3250	0.109	0.13	1.02
Seta spha	2437	0.274	0.45	12.93
Them tria	1625	0.154	0.80	12.28
TOTALS	162498	3.880	0.39	146.34

(g) Nylsvley 7

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
* Allo semi	1044	0.003	0.28	0.08
* Andr schi	2088	0.008	0.21	0.27
Aris conj	2088	0.054	0.37	2.70
* Aris diff	1044	0.001	0.20	0.03
Brac serr	5221	0.026	0.25	0.67
Digi eria	7309	0.04	0.18	0.68
Dihe ampl	36546	0.958	0.34	40.62
Elyo muti	5221	0.085	0.29	3.24
Erag race	6265	0.189	0.22	4.05
Hete cont	6265	0.205	0.38	9.11
Loud simp	26104	0.596	0.25	23.32
Meli nerv	6265	0.201	0.40	7.64
Pani colo	2088	0.009	0.31	0.29
Seta spha	51164	0.96	0.29	40.99
Them tria	46987	1.168	0.38	62.79
Tric gran	3132	0.004	0.36	0.19
TOTALS	204656	4.495	0.31	196.29

(h) Nylsley 8

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris conj	25940	0.054	0.26	1.77
Cenc cili	2358	0.004	0.52	0.21
Cyno dact	2358	0.002	0.30	0.06
Erag barb	74283	0.477	0.19	10.74
Erag pall	8254	0.305	0.41	17.09
Erag rigi	29477	0.081	0.19	1.93
Hete cont	7075	0.003	0.14	0.04
Pari maxi	53059	1.933	0.31	75.78
Schm papp	3537	0.006	0.29	0.19
Uroc mosa	29477	0.04	0.11	0.47
TOTALS	235819	2.904	0.27	108.28

(i) Roipoort 9

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris conj	3099	0.033	0.43	1.39
Erag lehm	82909	0.355	0.24	10.26
Erag pall	48041	0.301	0.30	11.09
Schm papp	20921	0.144	0.21	3.77
TOTALS	154970	0.833	0.30	26.51

(j) Roipoort 10

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris conj	53690	0.042	0.13	0.62
Aris stip	4474	0.001	0.03	0.03
Cymb plur	6711	0.677	0.43	13.17
Erag lehm	297532	1.105	0.18	28.11
Erag pall	6711	0.016	0.22	0.54
Erag supe	2237	0.011	0.26	0.30
Hete cont	2237	0.009	0.34	0.30
Pogo squa	42505	0.1	0.21	2.80
Schm papp	31319	0.837	0.21	24.42
TOTALS	447416	2.799	0.24	70.29

(k) Rocipoort 11

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris adsc	6796	0.005	0.13	0.08
Aris barb	45306	0.499	0.17	12.56
Aris conj	2265	0.003	0.22	0.06
Aris vest	22653	0.331	0.23	9.63
Cenc cili	4531	0.064	0.24	1.28
Enne scop	9061	0.033	0.25	0.88
Erag lehm	294492	1.92	0.16	37.05
Erag nind	15857	0.144	0.09	1.72
Erag obtu	33980	0.484	0.18	11.30
Hete cont	9061	0.269	0.29	7.71
Schm papp	2265	0.026	0.13	0.34
* Spor fimb	4531	0.023	0.15	0.38
* Uroc pani	2265	0.001	0.10	0.01
TOTALS	446267	3.777	0.19	82.61

(l) Langjan 12

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris conj	20898	0.033	0.10	0.51
Aris stip	17599	0.007	0.11	0.09
Cenc cili	15399	0.031	0.19	0.75
Enne cenc	93492	0.171	0.16	2.88
Hete cont	2200	0.001	0.06	0.00
Schm papp	1100	0.011	0.33	0.35
Trag bert	9899	0.009	0.04	0.07
Uroc mosa	48396	0.174	0.11	2.49
* Ques spec	10999	0.023	0.05	0.06
TOTALS	208983	0.437	0.13	7.14

(m) Langjan 13

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris conj	466	0.002	0.15	0.03
Digi eria	24467	0.316	0.02	0.30
Enne cenc	4893	0.014	0.06	0.06
Erag lehm	11185	0.143	0.02	0.13
* Erag tric	699	0.004	0.00	0.00
Pani maxi	3961	0.049	0.10	1.26
Schm papp	699	0.018	0.12	0.39
Uroc mosa	233	0.000	0.12	0.00
TOTALS	45904	0.542	0.08	2.17

(n) Messina 14

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris bipa	2171	0.001	0.16	0.01
Aris conj	162798	0.554	0.15	9.46
Digi eria	1085	0	0.10	0.00
Enne cenc	23877	0.064	0.16	0.95
Erag lehm	13024	0.046	0.18	0.87
Pani maxi	1085	0.025	0.24	0.60
Schm papp	1085	0	0.08	0.00
Trag bert	5427	0.009	0.07	0.04
Tric gran	3256	0.004	0.10	0.05
Uroc mosa	3256	0.005	0.09	0.05
TOTALS	217063	0.708	0.13	12.03

(o) Lower Sabie 15

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Both insc	76959	0.856	0.40	42.97
Digi eria	262943	2.910	0.38	128.72
Erag supe	6413	0.067	0.50	3.33
Eust papp	25653	0.216	0.37	8.20
Hete cont	16033	0.154	0.55	11.00
Pani colo	19240	0.136	0.39	6.54
Pani maxi	64132	0.546	0.51	34.71
Them tria	166744	2.673	0.47	150.20
Uroc mosa	3207	0.083	0.41	3.39
TOTALS	641323	7.651	0.44	389.06

(p) Timbavati 16

	Density (#/ha)	Basal Area (m2/100m2)	Mean height (m)	Vol. index (m3)
Aris adsc	7357	0.005	0.26	0.14
Aris bipa	1839	0.018	0.31	0.55
Aris conj	1839	0.005	0.25	0.13
Both insc	14715	0.135	0.37	5.41
Cenc cili	5518	0.061	0.52	3.01
Digi eria	25751	0.364	0.30	14.34
Enne scop	60698	0.733	0.31	26.84
Erag supe	7357	0.083	0.35	3.38
Fing afri	12875	0.49	0.33	26.68
Hete cont	62537	0.62	0.36	28.85
Pani colo	1829	0.059	0.40	2.34
Pani maxi	22072	0.743	0.54	58.14
Schm papp	34947	0.143	0.23	3.74
Spor nite	12875	0.092	0.15	1.29
Them tria	47823	0.71	0.39	35.25
Uroc mosa	47823	1.061	0.31	40.26
TOTALS	367865	5.322	0.34	250.35

(q) Timbavati 17

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris barb	1988	0.019	0.30	0.57
Aris conj	1988	0.001	0.24	0.03
Aris stip	23852	0.044	0.36	1.69
Digi eria	77518	0.275	0.22	6.56
Erag barb	13913	0.101	0.28	2.90
Erag lehm	23852	0.113	0.35	3.83
Erag pall	5963	0.031	0.27	0.81
Erag rigi	35777	0.224	0.40	9.15
Loud simp	3975	0.029	0.32	0.95
Pani colo	15901	0.089	0.33	3.42
Pani maxi	129196	2.106	0.35	84.23
Pero pate	15901	0.13	0.19	2.53
Pogo squa	5963	0.007	0.27	0.24
Schm papp	5963	0.058	0.21	0.92
Tric gran	5963	0.01	0.22	0.23
Tric mona	5963	0.039	0.34	1.37
Uroc mosa	23852	0.345	0.24	8.91
TOTALS	397526	3.621	0.29	128.34

(r) Pretoriuskop 18

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris bipa	2040	0.001	0.48	0.03
Both insc	4080	0.009	0.23	0.19
Cymb plur	4080	0.016	0.27	0.42
Cyno dact	16321	0.177	0.31	12.76
Digi eria	34681	0.099	0.27	2.61
Dihe ampl	85683	1.589	0.54	98.35
Erag rigi	4080	0.011	0.28	0.43
Erag supe	2040	0.079	0.39	3.06
Hete cont	20401	0.249	0.48	12.11
Hype diss	30601	1.006	0.82	85.76
* Hypp fili	8160	0.018	0.53	1.14
Loud simp	34681	0.414	0.35	13.69
Pani maxi	28561	0.417	0.57	23.95
Pero pate	12240	0.04	0.23	0.93
Pogo squa	4080	0.032	0.42	1.36
Schi sang	44882	1.399	0.46	67.48
Seta spha	38761	0.267	0.36	9.89
Spor stap	12240	0.114	0.21	2.36
* Erag spec	4080	0.059	0.63	3.56
* Trac spic	4080	0.287	0.72	21.35
Tric gran	6120	0.022	0.23	0.48
TOTALS	385572	5.941	0.38	335.86

(s) Pretoriuskop 19

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Vol. index (m ³)
Aris barb	9315	0.003	0.33	0.10
Aris bipa	9315	0.007	0.29	0.26
Digt eria	172330	1.589	0.25	47.59
Dike ampl	23288	0.672	0.46	46.24
Elyo muti	4658	0.095	0.49	4.63
Erag rigi	4658	0.063	0.70	4.39
Eete cont	130412	3.201	0.39	140.38
Hype diss	4658	0.009	0.21	0.20
Loud simp	139727	6.261	0.31	231.61
Pani maxi	18630	0.113	0.42	1.22
Pero pate	37261	0.126	0.21	3.32
Pogo aqua	79179	0.149	0.35	5.32
Schm papp	32603	0.221	0.22	5.78
Seta spha	260824	2.633	0.47	141.90
Tric gran	4658	0.006	0.20	0.12
TOTALS	931514	15.149	0.36	636.97

APPENDIX 6.

Graminoid functional attributes of each species. The classes of each functional attribute are listed in Table 2.3. The code representing each functional class corresponds with that in Table 2.3. The asterisks denote rare species.

Species name		phen	phys	gfor	repr	size	no.	disp	graz	pala			succ	fres	fuel	sfam	trib
										earl	late	wint					
* Alloteropsis semi-alata	allo semi	3	2	6	2	3	2	2	2	3	1	1	1	0	4	3	4
Andropogon gayanus	andr gaya	3	2	1	3	2	2	1	2	3	2	1	2	0	4	3	6
* Andropogon schirensis	andr schi	3	2	1	3	2	2	1	2	3	2	1	2	0	4	3	6
Aristida adscensionis	aris adsc	1	2	1	3	2	1	1	3	2	1	1	1	0	3	1	1
Aristida argentea	aris arge	3	2	1	3	2	1	1	2	2	1	1	1	0	3	1	1
Aristida barbicollis	aris barb	4	2	1	3	2	1	1	3	2	1	1	1	1	1	1	1
Aristida bipartita	aris bipa	3	2	1	3	2	1	1	3	2	1	1	1	0	1	1	1
Aristida conjesta	aris conj	4	2	1	3	2	1	1	3	2	1	1	2	0	1	1	1
* Aristida diffusa	aris diff	3	2	1	3	2	2	1	3	1	1	1	1	0	1	1	1
Aristida junciformis	aris junc	3	2	6	2	1	1	1	3	2	1	1	1	0	3	1	1
Aristida stipitata	aris stip	1	2	1	3	1	1	1	3	1	1	1	1	0	2	1	1
Aristida vestita	aris vest	3	2	1	3	1	1	1	3	1	1	1	2	0	2	1	1
Bothriochloa insculpta	both insc	3	2	5	2	2	1	1	3	3	2	1	2	2	7	3	6
* Brachiaria nigropedata	brac nigr	3	3	6	2	2	2	2	1	3	3	3	3	0	3	3	4
Brachiaria serrata	brac serr	3	3	6	2	2	2	2	1	3	3	3	3	0	3	3	4
Cenchrus ciliaris	cenc cili	3	3	7	2	2	2	4	1	3	3	2	3	0	6	3	4
Chloris gayana	chlo gaya	3	3	5	2	1	1	2	1	4	3	3	3	0	2	2	3
Chrysopogon serrulatus	chry serr	3	2	6	2	2	2	1	1	3	3	3	3	0	3	3	6
Cymbopogon excavatus	cymb exca	3	2	1	3	2	2	1	2	3	1	1	3	0	9	3	6
Cymbopogon plurinodis	cymb plur	3	2	1	3	2	2	1	2	4	2	1	3	1	9	3	6
Cynodon dactylon	cyno dact	3	3	4	2	1	2	2	3	4	4	4	1	0	1	2	3
Dactyloctenium australe	dact aust	3	3	2	2	1	3	1	3	4	4	4	2	0	3	2	3
Digitaria agropyrograpt	digi agyr	3	3	6	2	2	2	2	1	4	4	4	3	2	2	3	4
Digitaria didactyla	digi dida	3	3	5	2	2	2	2	1	3	2	2	2	0	2	3	4
Digitaria eriantha	digi eria	3	3	4	2	2	2	2	1	4	4	1	3	4	4	3	4
* Digitaria longiflora	digi long	4	3	5	2	1	1	2	2	2	2	1	1	0	2	3	4
Diheteropogon amplexans	dihe ampl	3	2	6	2	2	2	1	1	4	4	4	3	0	4	3	6
Echinochloa crus-galli	echl crus	1	3	5	1	1	1	2	0	3	3	3	1	0	3	3	4
Elyonurus muticus	elyo muti	3	2	1	3	1	2	2	3	3	1	1	1	2	6	3	6
Enneapogon cenchroides	enne cenc	3	3	1	3	1	2	4	3	2	2	2	1	0	2	2	2
Enneapogon scoparius	enne scop	3	3	1	3	1	2	4	5	1	1	1	4	0	2	2	2

Appendix 6 continued...

Appendix 6 continued...

Species name			phen	phys	gfor	repr	size	no.	disp	graz	pala			succ	fres	fuel	sfam	trib
											earl	late	wint					
Eragrostis barbinodis	erag	barb	3	3	5	2	1	3	2	3	4	3	3	2	0	2	2	3
* Eragrostis curvula	erag	curv	3	3	1	3	1	3	2	3	3	2	1	2	0	2	2	3
Eragrostis gummiflua	erag	gumm	3	3	1	3	1	1	2	0	1	1	1	2	0	2	2	3
Eragrostis lehmanniana	erag	lehm	3	3	1	2	1	1	2	3	4	3	3	2	0	2	2	3
Eragrostis moggii	erag	mogg	3	3	1	3	1	1	2	3	3	2	2	3	0	2	2	3
Eragrostis nindensis	erag	nind	3	3	1	3	1	1	2	3	3	3	2	2	0	2	2	3
Eragrostis obtusa	erag	obtu	3	3	1	2	1	1	2	3	4	3	2	1	0	2	2	3
Eragrostis pallens	erag	pall	3	3	5	2	1	1	2	2	2	1	1	2	2	6	2	3
Eragrostis racemosa	erag	race	3	3	1	3	1	1	2	3	3	3	3	1	0	2	2	3
Eragrostis rigidior	erag	rigi	3	3	1	2	1	1	2	3	3	2	1	2	1	2	2	3
Eragrostis superba	erag	supe	3	2	1	2	1	2	2	3	4	4	4	3	0	4	2	3
* Eragrostis trichophora	erag	tric	3	3	5	2	1	2	2	3	4	3	3	2	0	2	2	3
Eustachys paspaloides	eust	pasp	3	3	6	2	2	2	2	3	4	4	4	3	0	4	2	3
Fingerhuthia africana	finger	afri	3	3	6	2	1	2	2	1	2	2	2	2	0	3	2	3
Heteropogon contortus	hete	cont	3	2	6	3	3	3	1	3	3	3	3	2	1	4	3	6
Hyperthelia dissoluta	hype	diss	3	2	1	2	3	2	1	2	3	1	1	3	2	9	3	6
* Hypparrhenia filipendula	hypp	fili	3	2	6	2	3	1	1	2	4	2	1	3	2	8	3	6
Hypparrhenia hirta	hypp	hirt	3	2	6	2	3	1	1	2	4	2	2	3	0	8	3	6
Loudetia simplex	loud	simp	3	3	1	3	2	1	1	4	1	1	1	2	2	2	3	5
Melinis nerviglumis	meli	nerv	3	3	1	1	1	1	2	4	2	1	1	2	0	2	3	4
Melinis repens	meli	repe	4	3	1	1	1	1	2	3	2	1	1	1	2	2	3	4
Panicum coloratum	pani	colo	3	3	1	2	1	1	2	1	4	4	4	3	3	7	3	4
Panicum deustum	pani	deus	3	3	6	2	3	2	2	1	4	4	4	3	0	6	3	4
Panicum maximum	pani	maxi	3	3	5	2	1	1	2	1	4	4	4	3	0	6	3	4
Paspalum distichum	pasp	dist	3	3	4	2	1	2	2	0	0	0	0	0	0	1	3	4
Perotis patens	pero	pate	1	3	1	3	1	1	1	3	1	1	1	1	0	3	2	3
Pogonarthria squarrosa	pogo	squa	3	3	6	2	1	1	2	3	2	1	1	1	1	3	2	3
Sacciolepis curvata	sacc	curv	4	3	5	2	1	1	2	0	0	0	0	0	1	3	4	
Schizocarum sanguineum	schiz	sang	3	2	6	2	1	1	1	3	3	1	1	3	0	6	3	6
Schmidtia pappophoroides	schm	papp	3	3	5	2	3	1	4	3	3	3	3	3	2	3	2	2
Setaria incrassata	seta	incr	3	3	6	2	2	1	2	1	4	4	4	3	0	7	3	4
Setaria sphacelata	seta	spha	3	3	6	2	2	1	2	1	4	4	4	3	0	6	3	4
* Sporobolus fimbriatus	spor	fimb	3	3	6	2	1	1	2	3	3	3	3	2	4	6	2	3
Sporobolus ioclados	spor	iocl	3	3	4	2	1	1	2	3	3	3	3	3	0	2	2	3
Sporobolus nitens	spor	nite	3	3	4	2	1	1	2	3	3	3	3	3	0	2	2	3
Sporobolus stapfianus	spor	stap	3	3	1	3	1	1	2	3	2	2	2	2	0	2	2	3

Appendix 6 continued...

Appendix 6 continued...

Species name		phen	phys	gfor	repr	size	no.	disp	graz	pala			succ	fres	fuel	sfam	trib
											earl	late	wint				
Stipagrostis uniplumis	stip unip	3	2	6	2	2	2	1	1	3	3	3	3	0	2	1	1
Themeda triandra	them tria	3	2	6	3	3	3	1	1	4	4	4	3	1	7	3	6
* Trachypogon spicatus	trac spic	3	2	6	2	3	2	1	1	4	1	1	3	0	3	3	6
Tragus berteronianus	trag bert	4	3	1	3	2	1	3	3	1	1	1	1	2	1	2	3
Tricholeana monachne	tric mona	3	3	1	1	1	1	2	3	2	1	1	2	0	1	3	4
Trichoneura grandiglumis	tric gran	3	3	1	1	2	1	2	3	2	2	2	2	0	2	2	3
Urelytrum agropyroides	urel agro	3	2	1	1	2	2	1	2	2	1	1	2	0	4	3	6
Urochloa mosambicensis	uroc mosa	3	3	5	2	2	1	2	3	4	4	4	4	4	3	3	4
* Urochloa panicoides	uroc pani	1	3	1	3	2	1	2	3	2	2	2	1	0	1	3	4
* Urochloa trichopus	uroc tric	1	3	1	3	2	1	2	3	2	2	2	1	0	1	3	4

APPENDIX 7.

Forb structural data recorded at each site.

Sites	Density (#/ha)	Height (m)
1	18000	0.14
2	45643	0.15
3	11682	0.23
4	78516	0.13
5	84317	0.15
6	6108	0.16
7	52550	0.17
8	66183	0.12
9	109226	0.14
10	389801	0.12
11	149938	0.13
12	216326	0.16
13	54655	0.20
14	185979	0.15
15	25531	0.26
16	40547	0.23
17	33469	0.20
18	81125	0.20
19	74817	0.21

APPENDIX 8.

Graminoid species composition and graminoid and forb structural data recorded at the end of the growing season at three sites in Mkuzi. Full species names are given in Appendix 6.

(a) Mkuzi 1 (Repeat)

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Mass index (m ³)	Mean circ (m)	Mean basal area	Mean mass index
Aris bipa	6082	0.011	0.16	0.17	0.045	0.003	0.042
Aris conj	1520	0.001	0.40	0.04	0.030	0.001	0.044
Aris stip	9123	0.095	0.31	2.90	0.087	0.016	0.483
Erag mogg	10643	0.019	0.25	0.48	0.036	0.003	0.058
Erag pall	10643	0.044	0.42	2.24	0.059	0.006	0.320
Dact aust	156606	0.137	0.16	3.03	0.027	0.001	0.029
Digi eria	15204	0.032	0.12	0.39	0.047	0.003	0.039
Digi long	6082	0.013	0.13	0.21	0.045	0.003	0.051
Pani maxi	85145	0.987	0.40	50.38	0.083	0.018	0.900
Pero pate	3041	0.012	0.20	0.24	0.070	0.006	0.118
Totals	304089	1.351	0.24	60.06	0.048	0.007	0.300

(b) Mkuzi 2 (Repeat)

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Mass index (m ³)	Mean circ (m)	Mean basal area	Mean mass index
Aris bipa	1925	0.074	0.350	2.59	0.220	0.074	2.594
Cenc cili	1925	0.019	0.550	1.02	0.110	0.019	1.019
Digi dida	28868	0.434	0.164	7.56	0.110	0.029	0.504
Digi eria	44264	0.361	0.326	13.65	0.089	0.016	0.594
Erag supe	28868	0.438	0.399	18.00	0.117	0.029	1.200
Eust pasp	9623	0.032	0.392	1.23	0.058	0.006	0.246
Pani colo	69282	0.399	0.291	12.85	0.070	0.011	0.357
Pani deus	42339	0.598	0.366	24.89	0.110	0.027	1.131
Pani maxi	32717	1.044	0.470	61.84	0.156	0.061	3.638
Spor nite	1925	0.039	0.190	0.75	0.160	0.039	0.745
Them tria	121244	2.353	0.464	127.35	0.123	0.037	2.021
Uroc mosa	1925	0.001	0.250	0.02	0.020	0.001	0.015
Totals	384900	5.792	0.375	271.76	0.108	0.029	1.359

(c) Mkuzi 3 (Repeat)

	Density (#/ha)	Basal Area (m ² /100m ²)	Mean height (m)	Mass index (m ³)	Mean circ (m)	Mean basal area	Mean mass index
Pani maxi	6310	0.052	0.77	3.48	0.081	0.000	0.021
Pani deus	859	0.047	0.75	3.78	0.207	0.002	0.164
Cenc cili	261	0.005	0.83	0.49	0.140	0.001	0.071
Uroc mosa	37	0.000	0.75	0.02	0.090	0.000	0.018
Totals	7467	0.105	0.77	7.77	0.098	0.001	0.039

(d) Forbs

Sites	End of season sample	
	Density	Height
1	26371	0.15
2	38028	0.21

APPENDIX 9.

The information on A horizon soil chemical properties sent to the soils experts for their use in rating the soil fertility of the nineteen sites. Site numbers are as given in Table 2.1.

[illegible]

APPENDIX 10.

Soil structural properties at each site. Adepth and Bdepth refer to the depths of the A and B horizons respectively. Pdepth is the soil depth from the soil surface to the bottom of the B horizon.

Site	% stones	Adepth (cm)	Bdepth (cm)	Pdepth (cm)
1	0.00	29	67	96
2	11.00	20	30	50
3	0.00	44	60	104
4	90.00	31	81	112
5	0.60	26	87	113
6	0.03	17	83	100
7	69.00	20	10	30
8	0.80	25	75	100
9	0.02	20	80	100
10	3.00	64	64	128
11	7.00	37	17	54
12	10.00	28	12	40
13	0.70	30	70	100
14	11.00	38	92	130
15	1.00	24	26	50
16	1.00	39	10	49
17	10.00	14	49	63
18	5.00	28	71	99
19	10.00	30	28	58

APPENDIX 11.

B horizon soil properties (stone content corrected). Sites were divided into geological groups and ordered within each group according to percentage sand in the A horizon. Site numbers are as given in Table 2.1. Key to the geological parent material at each site: Kar sand = Karoo sandstone; Wat sand = Waterberg sandstone; Quat sand = Quaternary sands; Kala sand = Kalahari sands; Quar = Quartzite; Wat sand (+) = Waterberg sandstone + nutrient enrichment; Gran midl = Granite midlands; Gran upld = Granite uplands; Mar sand = Marine sandstone; Mud = Mudstone; Ande = Andesite; Fels = Felsite; Rhyo = Rhyolite; Tim gabb = Timbavati gabbro; Kar bas = Karoo basalt; Alluv = Alluvium; SR bas = Sabie River basalt; Bas = Basalt.

	(1) Acidic & nutrient poor					(2)						(3)			(4) Basic & nutrient rich				
Site	13	6	1	9	14	8	18	19	17	5	10	11	7	4	16	12	3	15	2
Geology	Kar sand	Wat sand	Quat sand	Kala sand	Quar	Wat sand	Gran midl	Gran upld	Gran upld	Mar sand	Mud	Ande	Fels	Rhyo	Tim gabb	Kar bas	Alluv	SR bas	Bas
Texture:																			
% sand	84	82	82	80	74	74	74	76	74	38	64	56	-	60	55	48	58	12	6
% silt	4	2	4	5	6	6	12	8	8	13	9	17	-	19	14	12	14	15	18
% clay	12	16	14	15	20	20	14	16	17	49	27	27	-	21	31	42	28	73	76
pH (1M KCl)	5.30	4.10	3.95	5.10	5.10	4.90	4.30	4.00	5.95	4.90	6.35	5.80	-	4.20	6.20	6.25	5.55	4.60	5.00
Cations (cmol(+)/kg)																			
Ca	2.06	0.72	5.05	2.13	9.64	3.28	0.68	1.80	2.85	8.31	25.36	21.68	-	0.13	33.59	37.09	11.25	22.20	20.81
Mg	2.67	0.53	1.84	0.91	2.30	0.90	0.55	0.82	0.82	4.08	2.33	5.02	-	0.15	3.12	2.67	2.67	5.90	5.47
K	0.53	0.52	0.59	0.57	0.57	0.66	0.47	0.54	0.56	0.85	0.77	0.73	-	0.07	0.71	0.89	0.75	0.91	0.94
Acidity (cmol(+)/kg)	0.12	0.49	0.55	0.06	0.04	0.02	0.21	0.54	0.05	0.07	0.12	0.09	-	0.81	0.22	0.33	0.05	0.17	0.10
Effective cation exchange capacity (cmol(+)/kg ¹)	5.29	2.26	8.03	3.67	12.56	4.86	2.08	3.90	4.28	11.29	26.58	27.52	-	1.15	37.63	40.96	15.00	29.18	27.32
Base saturation (cmol(+)/kg)	5.17	1.77	7.48	3.61	12.52	4.84	1.85	3.26	4.23	11.22	26.46	27.43	-	0.4	37.41	40.65	14.95	29.01	27.22
Phosphorus (mg/kg)	2.13	5.22	4.02	2.92	17.02	34.26	1.68	3.02	2.99	12.66	6.18	5.09	-	0.49	6.62	16.66	11.12	8.95	8.31

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