THE VARIATION OF ECOPHYSIOLOGICAL TRAITS OF SAVANNA PLANTS, IN RELATION TO INDICES OF PLANT AVAILABLE MOISTURE AND NUTRIENTS

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ABSTRACT

The present study was undertaken, within the South African savannas, to provide insight into a functional classification of savanna plants using ecophysiological characters. The primary objective of this study was to investigate the variation of these traits throughout the savanna, and to relate this variation to plant available moisture and nutrients.

It was concluded that;

1) no formal or specialized strategies have evolved within a number of the study sites,

2) unlike the woody component, neither divergence nor convergence was demonstrated within the grass layer,

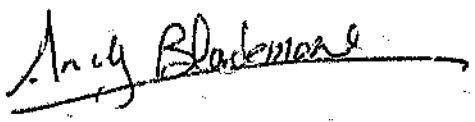
3) plant available nutrients did not appear to be a major determinant of either component. Although plant available moisture proved to be unimportant in the woody layer, it did play a role as a determinant of the grass layer, and

4) constancy of the plant traits was not demonstrated to occur over the growing season.

A successful classification would require the components to be separated, specific determinants be identified for each component, and an element of time be included into both edaphic and biotic measurements.

DECLARATION

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



ANDREW CRAIG BLACKMORE

1st Day of June, 1992

There seem always to have been two ways of looking at the world. One is the everyday way in which objects and events, although they may be unrelated causally and influence each other, are seen to be separate. And the other is rather a special way in which every thing is considered to be part of a much greater pattern.

Watson (1976)

ACKNOWLEDGMENTS

I would like to express my thanks to my supervisor, Mr ER Robinson for his advice and untiring support throughout the duration of the project. Miss NL Smithers, now Mrs NL Blackmore, requires a standing ovation for her assistance in both the field and the laboratory and for her encouragement, enthusiasm and support throughout the course of the project.

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CONVERSIONS AND ABBREVIATIONS

Net carbon exchange (Photosynthesis & respiration)

$\mu mol \cdot m^{-2} \cdot s^{-1} = mg \cdot m^{-2} \cdot s^{-1} \times 22.727$

Light intensity

$W \cdot m^{-2} = \mu mol \text{ quanta} \cdot m^{-2} \cdot s^{-1} = \mu E \cdot m^{-2} \cdot s^{-1}$

Leaf consistence

$g \cdot m^{2} = g \cdot dm^{-2} \times 100$

Lamina breaking strength

$N \cdot m^{-1} = dyne \cdot cm^{-1} \times 10$

Plant attributes*

PMAX = maximum photosynthetic rate (mg CO_2 $\cdot m^{-2} \cdot s^{-1}$)
QE = quantum efficiency ($\mu E \cdot mg\ CO_2^{-1}$)
DR = dark respiration (mg CO_2 $\cdot m^{-2} \cdot s^{-1}$)
CP = light compensation point ($\mu E \cdot m^{-2} \cdot s^{-1}$)
LTCT = leaf : chamber temperature ratio
SCL = leaf sclerophylly ($g \cdot dm^{-2}$)
SUC = leaf succulence ($g \cdot dm^{-2}$)
RAT = leaf turgid : dry weight ratio
BARK = woody bark thickness (mm)
BREAK = herbaceous lamina breaking strength ($dyne \cdot cm^{-1}$)

* Units were determined by either the experimental equipment, or by contemporary literature. SI conversions are given above.

Species lists[3]

Woody and forb

Aerio	Acacia erioloba
Alued	Acacia luederitzii
Ameli	Acacia mellifera
Anigr	Acacia nigrescens
Anilo	Acacia nilotica
Atort	Acacia tortilis
Axant	Acacia xanthophloea
Acara	Acaranthus sp
Aharv	Albizia harveyi
Atetr	Azima tetracantha
Bafri	Burkea africana
Chald	Cienfugiosa hildebrandii
Capic	Combretum apiculatum
Ccoll	Combretum collinum
Cmoll	Combretum molle
Czeyh	Combretum zeyheri
Dmela	Dalbergia melanoxylon
Dcine	Dichrostachys cinerea
Dcaff	Dovyalis caffra
Eundu	Euclea undulata
Gflav	Grewia flava
Gmont	Grewia monticola
Herma	Hermannia sp
Indig	Indigofera sp
Ldisc	Lannea discolor
Lcapa	Lonchocarpus capassa
Msene	Maytenus senegalensis
Opulc	Ochna pulchra
Oobov	Ozoroa obovata
Pafri	Peltophorum africanum
Rundu	Rhus undulata
Sbirr	Sclerocarya birrea
Sveno	Senecio venosa
Spanu	Solanum panuraformi
Tcamp	Tarchonanthus camphoratus
Tbrac	Terminalia brachystemma
Tseri	Terminalia sericea
Vrehm	Vitex rehmannii
Windi	Watheria indica

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3 Nomenclature follows Gibbs - Russell et al (1990)
Gibbs - Russell et al (1984)

Grasses

Acong	Aristida congesta
Binsc	Bothriochloa insculpta
Ccili	Cenchrus ciliaris
Cplur	Cymbopogon plurinodis
Deria	Digitaria eriantha
Dampl	Diheteropogon amplectens
Emuti	Elionurus muticus
Elehm	Eragrostis lehmanniana
Epall	Eragrostis pallens
Erigi	Eragrostis rigidior
Espe	Eragrostis superba
Hcont	Heteropogon contortus
Hfili	Hyparrhenia filipendula
Lsimp	Loudetia simplex
Mnerv	Melinis nerviglumis
Pmaxi	Panicum maximum
Psqua	Pogonarthria squarrosa
Ssang	Schizachyrium sanguineum
Spapp	Schmidtia pappophoroides
Snigr	Setaria nigrirostris
Sspha	Setaria sphacelata
Snite	Sporobolus nitens
Ttria	Themeda triandra
Uagro	Urelytrum agropyroides
Umosa	Urochloa mosambicensis

Study sites

K1 Kruger - Albizia harveyi / Dichrostachys cinerea savanna
K2 Kruger - Terminalia sericea savanna
K3 Kruger - Combretum apiculatum / Combretum collinum savanna

M1 Mkuze - Mixed Acacia savanna
M2 Mkuze - Acacia xanthophloea savanna
M3 Mkuze - Acacia tortilis / Acacia luederitzii savanna
M4 Mkuze - Combretum apiculatum savanna

N1 Nylsvley - Burkea africana savanna
N2 Nylsvley - Combretum apiculatum savanna
N3 Nylsvley - Acacia tortilis savanna

R1 Rooipoort - Tarchonanthus camphoratus savanna
R2 Rooipoort - Acacia mellifera / Acacia tortilis savanna
R3 Rooipoort - Acacia erioloba / Acacia mellifera savanna

T1 Timbavati - Acacia nigrescens savanna
T2 Timbavati - Terminalia sericea / Dichrostachys cinerea savanna

SOIL VARIABLES

ACID	-	Extractable acid
AmN2	-	Ammonium nitrogen
Ca	-	Calcium
CLAY	-	Percentage clay content
GDAYS	-	Number of days available for plant growth, in terms of water availability
K	-	Potassium
Mg	-	Magnesium
N2	-	Nitrogen
OC	-	Organic carbon
PO4	-	Resin extractable phosphorus
SAND	-	Percentage sand content
SILT	-	Percentage silt content

TABLE OF CONTENTS

LIST OF TABLES

TABLE OF ILLUSTRATIONS

1.0 INTRODUCTION

Current research in savannas includes the RSSD (Responses of Savannas to Stress and Disturbance) programme. The objective of this programme is to develop a predictive understanding of the ways in which savannas respond to both man-made and natural disturbances (Frost et al. 1986, Walker and Menaut 1988). Within this programme, a project was proposed to investigate the possibility of a functional classification of the South African savannas. This project was divided into two complementary studies, collecting data from identical regions within the South African savanna. The first was directed at the community level, concentrating on the structural aspects of the plants and their organization within the community[1]. The second, the present study, was directed solely at the species level.

The aims of this study were twofold. The first was to investigate a hypothesized relationship between various plant ecophysiological traits and suggested determinants of savanna structure and function. A significant relationship between the two would provide valuable insight into a possible link between savanna structure and function and long term environmental constraints. The second was to investigate the prospect of a functional classification of savanna plants at an ecophysiological level. A meaningful correlation between plant structure and function, and climatic and edaphic variables, is believed to provide the tools needed to predict the responses of different vegetation types to long term environmental change. The modifying effects of global climatic change have been identified as the single most important driving variable in vegetation change (Anon 1990).

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1 From Picket (in prep)

The present study draws heavily on the observation of Cody and Mooney (1978) that;

> "The forms and functions of unrelated organisms that occupy similar but distinct habitats often show parallels and similarities. Such comparability has been used as evidence of the strong role the environment plays in the evolutionary process and of the limited number of optimal adaptive solutions to a given environmental complex".

From this we are able to surmise that the selection against certain attributes, enables plants to develop strategies in order to cope with environmental constraints. Different plants under similar environmental conditions are likely to evolve similar strategies, as a consequence of the long term imposition of environmental limitations.

Identifying the key or principal determinants of savanna structure and function is believed to be fundamental in improving the understanding of savannas and their dynamics and ultimately improving savanna management. The determinants of savanna structure and function have been proposed by Frost et al (1986) to be (1) plant available moisture, (2) available nutrients, (3) herbivory and (4) fire. The first two are the primary determinants and the latter represent modifications. A fifth influence, Frost et al (1986) recognized, is the effect of human activity which may modify the four determinants.

The development and use of a structural-functional classification is not new. Humboldt (1807) considered the subject when studying broad geographic vegetation zones, using a biomass arrangement index for his classification. Since Humboldt's contribution, various structural-functional approaches have been followed. These range from selected species, to biomes and geographical areas. The majority of this literature is centred around Raunkiaer's (1934) life form concept. His classification was based on the position of

the perennating organ during the unfavourable season (see Adamson 1939 and Cain 1950 for extensive reviews). Raunkiaer's system has been widely accepted and applied, mostly to compare the vegetation of different climates, but has also been applied in studies of a localized nature (Adamson 1939, Butler 1954, Cooper 1961, Randall 1952, Whittaker 1960).

Plant features other than the perennating organ have been considered in structural and functional studies. These include leaf size (Adamson 1927, Raunkiaer 1934, Webb 1959, Parkhurst and Loucks 1972, Werger et al 1987, Camerick and Werger 1981, Knight and Loucks 1968, Givinish and Vermeij 1976, Werger and Ellenbroek 1978), vegetation reproduction (Butler 1954, Gimingham 1951, Randall 1952), method of dispersa[illegible]umata 1958, Randall 1952), leaf temperature (Gates 1968), leaf consistence (Cowling and Campbell 1983, Loveless 1962, Morrow and Mooney 1974, Werger and Ellenbroek 1978), photosynthesis (Baldocchi et al 1987, Black 1971, Friend and Woodward 1990, Pearcy et al 1987), to name but a few. This list could be expanded to include almost any autecological feature of the plant. The variation of these attributes has, in many cases, been related to local environmental gradients (eg Webb 1959, Beard 1946, Collins and Jones 1985, Cowling and Campbell 1983, Givinish and Vermeij 1976). The predominance of tropical and, to a lesser extent, Mediterranean vegetation types is evident in these studies. Similar studies in savanna vegetation are, however, conspicuous by their absence.

In what is probably the most effective statement on the floristic composition of South African vegetation, Acocks (1953) concentrated on the proportional species composition of plant communities. This classification has, however, its shortcomings, as its development was based on comparing areas of similar farming potential. Ignoring the agricultural importance of vegetation, Rutherford and Westfall (1986) classified the southern African vegetation on the dominance

and co-dominance of plant life forms on the basis of climatic indices.

Proportional species composition provides a classification at local levels where interrelationships between vegetation and other patterns are examined (see for example Frost 1987, Whittaker et al 1984). The identity of the species within a floristic classification rests heavily on the Linnaean system which assumes that each species is unique in its functional behaviour. These species may display variable functional responses over their geographical range (Gauch 1986).

Should the savannas consist of functionally unique Linnaean species, functionally based classifications would, in this instance, have little practical use. It is suspected, however, that the savannas do consist of both a few unique species and a large number of functionally similar species which can be condensed into a significantly smaller number of guilds. Classification based on functional characteristics rather than solely floristics would circumvent the impracticability of researching every savanna community. This would allow extrapolations of ecological predictions to other like-responding or functionally similar savannas to be made.

Global climatic change over the next half century has been widely forecast (Walker and Dickson 1988), and it is likely that the savannas will respond with a combination of functional, structural and floristic changes. In order to predict the direction and magnitude of these changes, a platform or model (Figure 1.1) linking savanna plants or communities, or both, to environmental gradients is required. Data for such a model may only be drawn from studies that record spatial or temporal changes in savanna plants or communities.

A spatial study, as with the present study, relates changes in vegetation components or sub-components to primarily edaphic, climatic or other gradients. Temporal studies take one of two approaches. The first requires the studying of long term photographic or management records, or both (eg

Randall 1988, Shantz and Turner 1958). The second approach is the application of field scale experiments to measure the effects of extreme events (see Walker and Turner 1990).

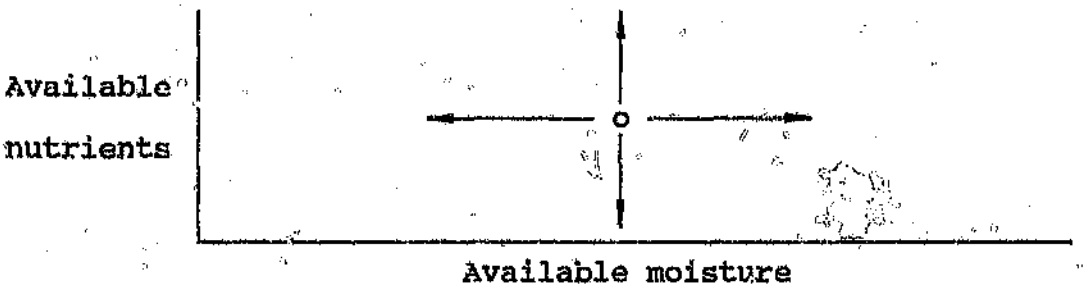

Figure 1.1. An example of a simple model describing possible direction of adaptation of an attribute 'o' in response to a change in either plant available moisture and nutrients, or both.

1.1 DEFINITION OF TERMS

Savanna is used in a biome sense unless qualified by a specific locality or type (eg Nylsvley savanna or Burkea savanna). A savanna is described, in this study, as a neotropical ecosystem occurring in a strongly seasonal moisture regime (Scholes 1987). It has a continuous herbaceous layer of predominantly C4 grasses and a discontinuous woody layer. Rutherford and Westfall (1986), and Huntley (1982) argue for further descriptive subdivisions which lie beyond the scope of this study.

Woody plants include trees (> 2 m tall, few stems) and shrubs (< 3 m tall, multi-stemmed). Forbs are the non-graminoid component of the herbaceous layer, which are periodically conspicuous following drought or good rains and often occur in areas of heavy herbivory.

Structure refers to the distribution of plant biomass in space (both horizontally and vertically) within a given plant community (Knight and Loucks 1968), while function refers to the products and processes of the plants' physiological system which are apparent adjustments to the environment (Fosberg 1961, Knight and Loucks 1968).

Leaf consistence is defined as the firmness and thickness of a leaf (see Cowling and Campbell 1983, Werger and Ellenbroek 1978). Succulence refers to the maximal water content per leaf area, and sclerophylly refers to the dry weight per leaf area.

1.2 OBJECTIVES

The present study is not intended to represent a pro-forma or definitive system, but rather to serve as a stimulus or platform for future research into the merits and demerits of a functional approach to vegetation classification.

In addressing a possible relationship between ecophysiological traits of plants and climatic and edaphic constraints, the following topics will be addressed.

(I) PLANT ATTRIBUTE RANGE

The aim of this section is to compare the variation of plant traits that occur at individual sites within the South African savanna to that of the total variation of the biome.

It is assumed that plants have, through a process of natural selection, derived attributes which enable them to persist under the constraints imposed by the environment. It would then follow that the attribute range at any one location within the savanna would be less than the total range of that attribute (see Figure 1.2a).

If, however, the attributes are randomly distributed throughout savanna, as would be the case in the absence of determinants of both structure and function, the attribute range at one location (study site) would equal the total variation of the entire biome (see Figure 1.2b).

Implications

If the variation at a single location within the savanna is noticeably less than the total variation, the assumption of Cody and Mooney (1978) may hold true, ie

that plants under similar environmental conditions have evolved similar strategies.

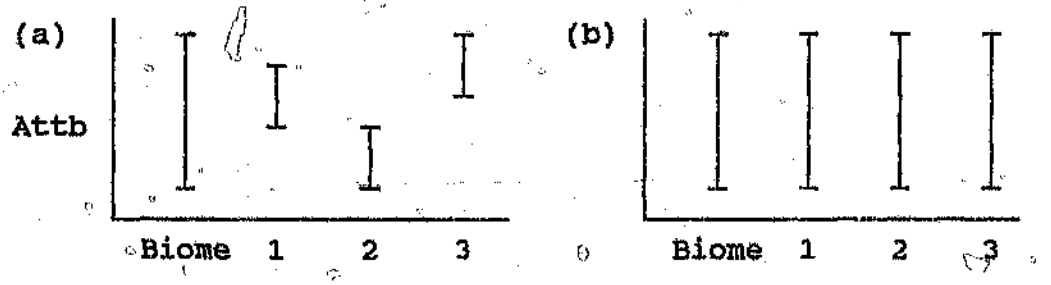

Figure 1.2. A simple comparison between a savanna that has been moulded by its determinants (a) and a savanna that has no determinants (b). Vertical bars symbolize the variation of an attribute (Attb) for the biome and selected study sites (1, 2 & 3).

Alternatively, should the attribute variation at individual sites equal that of the total variation of the savanna, then it may suggest that the savanna may consist of a large variety of functionally unique species. This in turn would make a functional classification ineffectual.

Spin-offs

Investigating each plant trait studied in this manner creates the opportunity to compare the three structural classes, namely; trees, grasses and forbs.

(II) SEASONAL CHANGE

The aim of this section is to determine the constancy of ecophysiological traits, as functional characters, over the span of a single growing season.

The absence of possible statements on seasonal variation of plant traits within structural / functional studies is cause for concern. It is obvious, but well worth mentioning that the repeatability, and hence the strength, of any experiment relies heavily on the constancy within the data.

Implications

The repeatability of the present study and others depends heavily on the variation of traits over a growing season being markedly less than the variation within a species at any point in time.

Spin-offs

Plant attributes may be divided into two categories, ie those that vary over a growing season and those that do not. The distinction between these two types of attributes will not only provide additional information concerning their autecology, but will enable plant traits to be selected with greater insight if a subsequent functional study is undertaken.

(III) DIRECT GRADIENT ANALYSIS

The aim is to determine whether ecophysiological traits vary predictably with a change in either available moisture or nutrients, or both.

Implications

If plant traits show a distinct pattern or trend along either nutrient or moisture gradient, then a simple approach may be opted for (see Figure 1.1). Similarly, confidence intervals may then be attached to predictions of possible attributes that occur in a known nutrient / moisture regime and vice versa.

Alternatively, if no pattern is detected, along either gradient, two options remain. The pattern has been masked by either noise or gradient(s) other than moisture or nutrients, or secondly, no extractable pattern exists within the data collected.

Spin-offs

Due to the limited autecological knowledge about many of the savanna plants, information gained in the present study is an important spin-off in itself.

(IV) INTER-SPECIES ANALYSIS

The aim of inter-species analysis is to determine functional similarities (or differences) between plants / species occurring at different points on the moisture / nutrient plain.

Implications

A functional classification assumes that different taxonomic species have strong functional similarities. Functional similarities between different floristic species underscores the role of ecological equivalence within savannas. A predictable relationship between functionally equivalent species, and climatic and edaphic gradients would facilitate extrapolations from one savanna to the next.

If, however, the savannas consist of a large variety of functionally unique species, the savannas (world wide) may be functionally unique. This would naturally negate the possibility of a functional classification both within and between the biomes. Emphasis could then be shifted away from the community (and the system) to the biome as a whole. This would divert current attention from vegetation change within a particular savanna type

to the biome as a whole. This shift in emphasis would, in turn, enhance current trends in global conservation.

Spin-offs

Functional equivalence of species is playing a greater role in the selection of plants in rehabilitation ecology. Increased knowledge of these species may lead to a dramatic reduction in the import of alien plants into an area that requires revegetation and rehabilitation. Indigenous plant species that are found to be functionally similar to those plants commonly used in rehabilitation projects, could be capitalized upon.

(V) INTER-SITE ORDINATIONS

The aim of inter-site analyses is to evaluate functional differences between plant communities which occur under different available moisture and nutrient regimes.

Implications

If plants growing under similar environmental constraints do encounter similar evolutionary pressures, then savanna communities, as separate units, would consist of an unique set of strategies which would enable them to cope and exploit the unique edaphic and climatic constraints they encounter. Strategies could thus be used to describe each community. By examining the soil and moisture regimes, conclusions on the functional 'content' of the community could then be drawn.

If, however, no relationship exist between savanna communities and determinants of both structure and function, three possible scenarios may exist.

(A) No correlation exists between the plant traits (at a community level) and the intensity of the environmental gradients.

(B) More than one strategy may be successful under a single set of environmental constraints.

(C) Plant strategies are derived from a different set (ancient) environmental constraints.

Spin - offs

If a strong correlation exists between plant traits (at a community level) and the intensity of environmental gradients, it would be necessary to sample only a limited number of savanna communities. From this, both functional and structural understandings could be projected to other similar savanna communities without the need for additional studies.

2.0 METHODS

2.1 Study Areas

Five study areas were selected within the South African savannas (Figure 2.1). Selection was based primarily on annual rainfall and geology. Mean annual rainfall within the South African savannas ranges between 200 mm and 800 mm per annum (Rutherford and Westfall 1986). The requirement of turgid plant material for many of the procedures used in the present study limited selection of possible study areas to a rainfall gradient of approximately 400 mm to 750 mm per annum. Each study area was represented by two to four sites selected on the following basis: (1) local mean annual rainfall, (2) parent material, (3) vegetation type and (4) local ecologist's and manager's recommendations. The ecologist or manager was requested to recommend areas that were (a) lightly grazed, (b) burnt at a fire frequency of approximately five years and (c) soils of either a 'fertile'(eutrophic) or 'infertile' (dystrophic) status.

2.1.1 Mkuze Game Reserve

The Mkuze Game Reserve is managed and administered by the Natal Parks Board. The Reserve (27° 30' to 27° 45' S and 32° 05' to 32° 25' E) is located on an ancient coastal plain to the east of the Lebombo mountains in north eastern Natal. The climate, summarized by Goodman (1991), is warm to hot (18.8° C to 27.1° C) and humid, and generally considered to be semi-arid with an annual potential evapotranspiration greatly exceeding annual rainfall. Annual rainfall is highly seasonal with the mean ranging between 600 mm and 800 mm per annum (Goodman 1991).

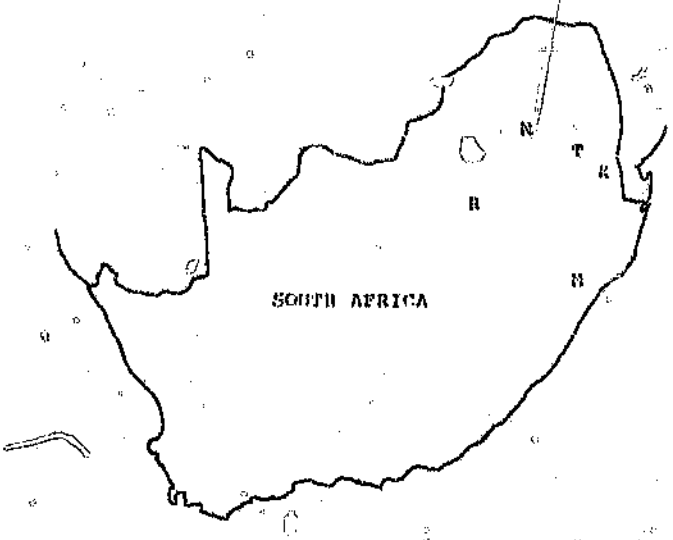

Figure 2.1 The location of the study [illegible] Kruger National Park, M = Mkuze Game Res[illegible]isvley, R = Rooipoort Private Game Reserv[illegible] T = [illegible]imbavati Private Nature Reserve)

A total of four study sites were selected within the reserve.

2.1.1.1 Mixed *Acacia* savanna (M1)

An open woodland to grassland dominated by *Acacia nilotica*, *Acacia tortilis* and the occasional *Acacia nigrescens* tree. The grass layer consists of *Themeda triandra*, *Panicum coloratum*, *Panicum maximum* and *Eragrostis superba*. The community is located on vertic clays (Goodman 1991) on basalt parent material.

2.1.1.2 *Acacia xanthophloea* savanna (M2)

Riverine forest and woodland typically occurs on alluvium (Goodman 1991). The dominant trees are *Acacia xanthophloea*, *Acacia tortilis*, *Rauvolfia caffra* and *Trichilia emetica*, and *Azima tetracantha* as the dominant shrub. *Cenchrus ciliaris*

and Panicum maximum were found to be common in the grass layer.

2.1.1.3 Acacia tortilis / Acacia luederitzii savanna (M3)

Described as dense thicket, in places impenetrable (Goodman 1991), occurring on flat, poorly drained vertic clays and hydromorphic gley soils. Dominant woody species are Acacia luederitzii, Acacia tortilis and Euclea undulata. Important grasses are Sporobolus nitens, Panicum maximum, Dactyloctenium australe, Enteropogon monostachyous, and Panicum deustum.

2.1.1.4 Combretum apiculatum savanna (M4)

Open woodland dominated by Combretum apiculatum, Acacia nigrescens, Themeda triandra, Heteropogon and Cymbopogon excavatus. The Combretum apiculatum savanna is limited to the crest slopes, occurring on lithosols consisting of a high concentration of Jozini Rhyolite Formation (Goodman 1991).

At the end of the growing season (May/June 1989) the A. nilotica (M1), A. xanthophloea (M2) and C. apiculatum (M4) sites were resampled so that a possible change in attributes studied over a season could be detected.

2.1.2 Nylsvley Provincial Nature Reserve

The savanna biome study site at Nylsvley (24° 40′ S : 28° 40′ E), is located on sandy soils about one meter deep, derived from sandstones of the Waterberg series (South African Geological Survey 1978). The Nylsvley area is of low relief, undulating between 1080 m (Nyl River floodplain) and 1140 m (low hill) altitude. The climate has been summarized by Anon (1975), and Huntley and Morris (1978, 1982). Approximately 90% of the mean annual rainfall of 620 mm occurs during the period October through March. The mean daily maximum summer

temperature is 28.4° C and the mean daily maximum winter temperature is 22.3° C. Relative humidity is low leading to an annual potential evapotranspiration greatly exceeding annual rainfall. A total of three study sites were located within the reserve.

2.1.2.1 *Burkea africana* savanna (N1)

The vegetation type is broad-leafed, dominated by *Burkea africana* in the tree layer and *Eragrostis pallens* in the grass layer. Soils are dystrophic, well drained and shallow with a low clay content (Blackmore *et al* 1990, Frost 1987).

2.1.2.2 *Combretum apiculatum* savanna (N2)

This savanna is dominated by *Combretum apiculatum*, *Combretum molle* and *Vitex rehmannnii* in the woody component, and *Diheteropogon amplectens*, *Loudetia simplex* and *Themeda triandra* as the dominant species in the herbaceous layer. The community is located uphill and away from the Nyl flood plain. The soils are shallow lithosols of a poorly developed structure and are underlain by felsite (see Frost 1987).

2.1.2.3 *Acacia tortilis* savanna (N3)

About 15% of the *Burkea* savanna is occupied by a fine-leaved savanna community, dominated by *Acacia tortilis* with *Cenchrus ciliaris* and *Aristida congesta* in the grass layer. *Acacia nilotica*, *Dichrostachys cinerea* and *Sclerocarya birrea* are common trees. These communities occur typically in discrete patches 50 to 500 m in diameter, and are associated with soils with markedly higher nutrient status (see Blackmore *et al* 1990) despite having a similar origin as the surrounding *Burkea* soils.

2.1.3 Rooipoort Private Game Reserve

The Rooipoort Private Game Reserve is owned and managed by De Beers Consolidated Mines Limited. The reserve occurs on Kalahari sands, and is situated approximately 50 km West of Kimberly in the Northern Cape (28° 39'S : 25° 17'E). No formal climatic data are collected within the bounds of the Reserve or neighbouring farms. Rainfall is said to be low averaging less than 400 mm pa (Acocks 1953). Summer temperatures frequently exceed 40° C and freezing temperatures are common during the winter months.

2.1.3.1 Tarchonanthus camphoratus savanna (R1)

The Tarchonanthus camphoratus savanna generally occurs on deep sands with the presence of a prominent calcrete layer (0 to 150 mm below soil surface). T. camphoratus and Grewia flava and, to a lesser extent, Rhus ciliata are the important woody plants, with Cenchrus ciliaris, Cymbopogon plurinodis and Schmidtia pappophoroides as common grasses.

2.1.3.2 Acacia mellifera / Acacia tortilis savanna (R2)

This community is typically an open shrubland dominated by Acacia mellifera and Acacia tortilis with a grass layer dominated by Eragrostis lehmanniana and Cymbopogon plurinodis, whilst Heteropogon contortus and Aristida sp (cf A. mollissima) occur in low densities.

2.1.3.3 Acacia erioloba / Acacia mellifera savanna (R3)

An Acacia erioloba and Acacia mellifera combination is common on the Kalahari sands forming an open thicket. Schmidtia pappophoroides, Aristida congesta and Eragrostis lehmanniana are dominants in the grass layer. Hermannia sp (cf H. tomentosa) is a common forb, occupying vast areas of the soil surface.

2.1.4 Kruger National Park

The Kruger National Park (22° 31' to 25° 30'S ; 30° 45' to 32° 02'E) is situated in the Eastern Transvaal Lowveld. The park encompasses a variety of vegetation types (see Greyling and Huntley 1984, Gertenbach 1983) of which three were selected.

2.1.4.1 Albizia harveyi / Dichrostachys cinerea savanna (K1)

This study site is situated to the south east of the Lower Sabie camp (25° 16'S : 31° 55'E). The study site is located on well drained Karoo sediments underlain by Sabie River Basalts with an occasional intrusion of dolerite (Gertenbach 1983). Rainfall ranges between 548 mm and 600 mm pa. Average daily temperatures range between 33.6° C (February) and 8.9° C (June) (Gertenbach 1983). The vegetation is dominated by a number of widely spaced trees of Sclerocarya birrea, Albizia harveyi, Dichrostachys cinerea and Maytenus senegalensis. The herbaceous layer is dominated by Themeda triandra and, to a lesser extent, Digitaria eriantha.

2.1.4.2 Terminalia sericea savanna (K2)

The site is located to the south east of Pretoriuskop (25° 11'S : 31° 18'E) on well drained sands of granite and gneiss parent material (Gertenbach 1983). This vegetation type is dominated by Terminalia sericea and Dichrostachys cinerea in the woody layer, with Hyparrhenia filipendula, Schizachyrium sanguineum and Diheteropogon amplectens as the dominant grasses. The annual rainfall varies between 600 and 1000 mm with an average of 744 mm pa (Gertenbach 1983). Average daily temperatures range between 32.1° C (March) and 8.8° C (June).

2.1.4.3 Combretum apiculatum / Combretum collinum savanna (K3)

Known as the Malelane Mountain Bushveld (Gertenbach 1983), this community occurs on shallow soils underlain by archain granite rock formation of the Swaziland System. The study site occurs to the east of Pretoriuskop (25° 12'S : 31° 23'E). Annual rainfall varies from 600 to 700 mm (Gertenbach 1983). The vegetation is dominated by Combretum apiculatum, C. collinum and C. zeyheri and, to a lesser extent, Terminalia sericea in the woody layer. Dominant grasses are Heteropogon contortus, Cymbopogon plurinodis and Diheteropogon amplectens.

2.1.5 Timbavati Private Nature Reserve

Two study sites were selected within the Timbavati Reserve (24°28'S : 31°30'E) which is situated adjacent to the Orpen Gate of the Kruger National Park. The climate is dryer than the study sites within Kruger National Park, with rainfall averaging between 550 and 600 mm pa (Gertenbach 1983). Mean monthly temperatures range between 8.9° C (June) and 33.6° C (February) (Gertenbach 1983).

2.1.5.1 Acacia nigrescens savanna (T1)

This site is located on a Gabbro parent material with deep clayey soil of mainly the Mayo soil form (Gertenbach 1983). The vegetation is dominated by Acacia nigrescens and the occasional Grewia flava and G. monticola. The grass layer is dense, dominated by Themeda triandra and Heteropogon contortus. The grasses Urochloa mosambicensis and Digitaria eriantha are common.

2.1.5.2 Terminalia sericea / Dichrostachys cinerea savanna (T2)

Located on granite and gneiss uplands with many dolerite intrusions (Gertenbach 1983). The soils are sandy, dominated by Hutton and Clovelly, and Cartref and Fernwood soil forms. The vegetation consists mainly of Sclerocarya birrea, Terminalia sericea and Dichrostachys cinerea. The herbaceous layer is dominated by Panicum maximum, Eragrostis rigidior and Digitaria eriantha.

2.2 DATA COLLECTION

2.2.1 Plant Data

Plants were selected using a plotless sampling method within each study site. Selection was on an a priori basis as a function of their (1) ecological dominance, (2) distribution and (3) autecology. Ecological dominance was defined as those individuals that constitute a significant proportion of the plants that occur within the study site, in both density and biomass. Plant distribution is defined as those plants that occur at lower densities but at an equivalent frequency to the 'ecologically dominant' plants. Highly clustered or locally grouped plants that do not occur throughout the community were avoided. Finally, plant species that were viewed as autecologically important, eg indicator species, were included in the study. Within each study site approximately ten individual plants were selected to represent each species. Criteria adhered to whilst selecting potential plants were as follows:

(a) The selected individual plants were evenly distributed throughout the study site (within the bounds of the soil sampling strategy see section 2.2.2 below),

(b) the plants were disease free, and

(c) animal disturbance was absent or negligible.

Selection of the plant traits were according to two pre-requisites, namely those that; (1) reflect the species evolutionary adaptation rather than its immediate environment or history and (2) are easily measured in the field.

There is almost no limit to the number of plant features that could be used in a structural-functional analysis. Any autecological attribute is potentially suitable, whether it be moisture requirement, nutrient requirement or light dependence. Some, however, are more easily observed than others. Various attributes of plant structural and functional aspects were selected within broad areas of net carbon (CO_2) exchange and morphology. These attributes, it is believed, will index the species rather than the individual.

2.2.1.1 Photosynthesis

A portable infrared gas analyzer (IRGA - Licor 1600) was used in situ, and in conjunction with neutral density filters, to establish four parameters which were derived from the relationship between irradiance and photosynthesis (Figure 2.2).

For each individual plant studied, the leaves were ranked along each branch or within each tuft according to age (undeveloped to mature). Only young, first [illegible]cond fully expanded leaves that occurred naturally in [illegible] sunlight were selected for photosynthetic studies. The leaves were placed into the chamber so as to cover approximately 25% of the chamber surface area.

To minimize stomatal heat loading and closure, dark respiration and low light intensity photosynthetic measurements were recorded until the light intensity approached 2500 $\mu E \cdot m^{-2} \cdot s^{-1}$. Thereafter full sunlight readings were recorded until ambient temperatures reached 28°C. Dark

respiration rates were achieved by placing the chamber in a light-tight container, and the lower light intensities by shading the leaves for 10 to 15 minutes prior to, and during, photosynthetic sampling.

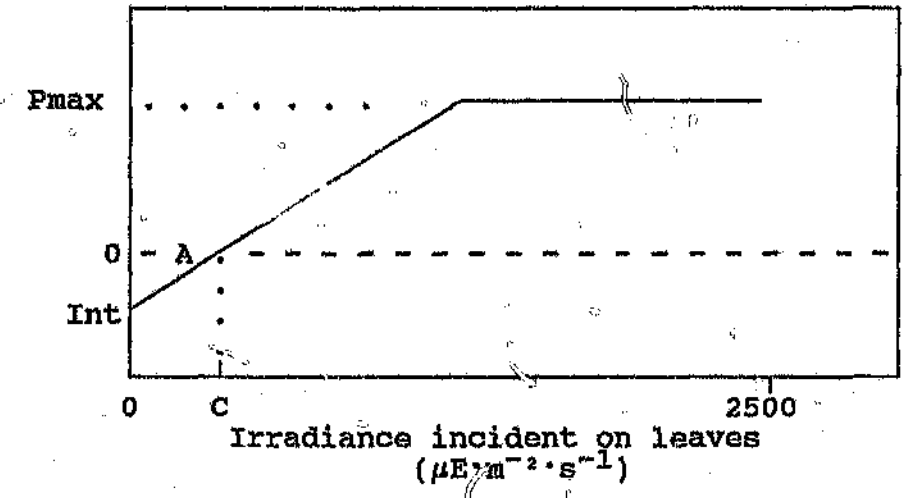

Figure 2.2. An example of a photosynthetic irradiance response curve. Pmax = maximum photosynthetic rate at 2500 ($\mu E \cdot m^{-2} \cdot s^{-1}$), A = quantum efficiency, Int = gross dark respiration rate and C = light compensation point.

The Licor 1600 chamber was sealed and the fan and pump activated to allow for equilibration. Photosynthetic readings were recorded once the CO_2 concentrations within the chamber began to drop. Fresh unused leaf material was used for each reading. Chamber sampling times were adjusted according to the rates of CO_2 uptake or release (full sunlight ± 2 seconds and low light intensities and dark respiration up to 10 seconds). Photosynthetic data were discarded if the initial chamber CO_2 concentration was greater than, or less than, 4 to 5% of the ambient concentration.

The photosynthetic data were corrected for slight temperature differences between readings by the following equation (Campbell 1977).

$$P(T) = P \cdot \frac{2(T_L + A)^2(T_M + A)^2 - (T_L + A)^4}{(T_M + A)^4} \quad (1)$$

where $P(T)$ = photosynthetic rate corrected for temperature,
P = observed photosynthetic rate,
T_L = the leaf temperature,
T_M = the temperature for maximum photosynthesis, and
A = constant (C_3 = 8.4 and C_4 = 27.8).

The gross leaf photosynthesis was estimated by the non-linear model based on a rectangular hyperbola (see Johnson and Thornley 1984).

$$P = \frac{A \cdot I \cdot P_M}{A \cdot I + P_M} \quad [+ C] \quad (2)$$

where P = gross leaf photosynthesis,
A = initial slope of the curve (quantum efficiency),
I = irradiance of photosynthetically active radiation,
P_M = photosynthesis at which no net increase of photosynthesis occurs, and
C = intercept (Included so that dark respiration may be determined directly by the model).

From this model the following were derived (Figure 2.2),

- maximum photosynthetic rate at 2500 $\mu E\ m^{-2}s^{-1}$ (full sunlight),
- quantum efficiency (mg CO_2 per μE absorbed),
- light compensation point (light intensity at which CO_2 uptake equals CO_2 release) and
- dark gross respiration rate (mitochondrial respiration rate or CO_2 efflux at zero light intensity).

In addition to the photosynthetic data, the leaf : chamber temperature ratio was calculated to form the attribute LTCT.

2.2.1.2 Morphology

Sclerophylly and succulence

From 30 to 50 first and second fully expanded leaves (see photosynthesis above) were collected from ten individuals of each species. The leaves were moistened, detached and sealed with their petioles or sheaths submerged in water, cooled to approximately 10° C and stored overnight. The leaves were blotted dry and then weighed. The area was determined using a planimeter (average of five replications). The leaves were then dried at 75° C to a constant weight and then re-weighed.

From this data the following were determined (see Camerick and Werger 1981, Cowling and Campbell 1983).

(a) Sclerophylly - defined as the leaf dry mass per leaf bifacial area ($g \cdot dm^{-2}$)

(b) Succulence - defined as the maximal leaf water content per bifacial area ($g \cdot dm^{-2}$).

(c) Leaf turgid : dry weight ratio.

(d) Linear relationships between leaf dry mass and leaf turgid mass, and leaf dry mass and leaf area.

Bark morphology

Bark thickness (see Knight and Loucks 1968) was determined by chiselling a 2x2 cm hole through to sapwood 1.5 m from the ground. Measurement was limited to the cork layer of the trunk. Within each study site a total of 20 trees for each species were selected and a minimum of three readings measured on each.

Grass lamina breaking strength

Estimates of the tensile properties was recorded for first and second fully expanded laminae of each grass species studied using a tensilmeter described in Martens and Booysen

(1968). The breaking force of grass lamina are reported as breaking tension (dynes per centimetre) (see Martens and Booysen 1968, Theron and Booysen 1968). The test section of the leaf was limited to the middle 2.5 cm of each grass blade. The breaking tension was calculated as the breaking mass x gravitational acceleration (9.82 ms^{-2}) per width of the broken edge in cm. The breaking strength of 30 individuals was recorded for each species.

2.2.1.3 Plant water relations

Four attributes may be derived from the relationship between leaf water potential and relative leaf water content, and transpiration rate and relative leaf water content. The characters are as follows,

(a) Maximum transpiration rate,
(b) Leaf water potential at stomatal closure,
(c) Leaf water potential at wilting, and
(d) Leaf osmotic potential.

Leaf water potential was measured using a modified filter paper technique described in Al Khafaf and Hanks (1974), Hamblin (1981), and McQueen and Miller (1968). Branches were cut and grass tufts were excavated and the plant material placed in shade to dehydrate. First and second fully expanded leaves were collected, at intervals of 10 to 20 minutes depending on ambient conditions, and packed into plastic, 20 ml scintillation vials. A strip of Whatman No. 32 filter paper, (10 x 30 mm) of known weight, was curled into the neck of the vial avoiding contact with the leaf material. The vial was sealed and stored, on its side, for 30 days in a light tight container at approximately 12° C. By a process of successive removal and weighing, the wet weight of both the filter paper and leaf material and the dry weight of the leaf material (entire vial dried at 75° C until constant weight) were determined. A total of 10 to 15 vials were filled for each species. Each species consisted of a minimum of eight individual plants.

Calculations of leaf water potential followed the procedure given in Campbell and Gee (1986).

The relationship between leaf transpiration rate and leaf water potential was expressed in terms of three characteristic parameters (Figure 2.3) (Cline and Campbell 1976).

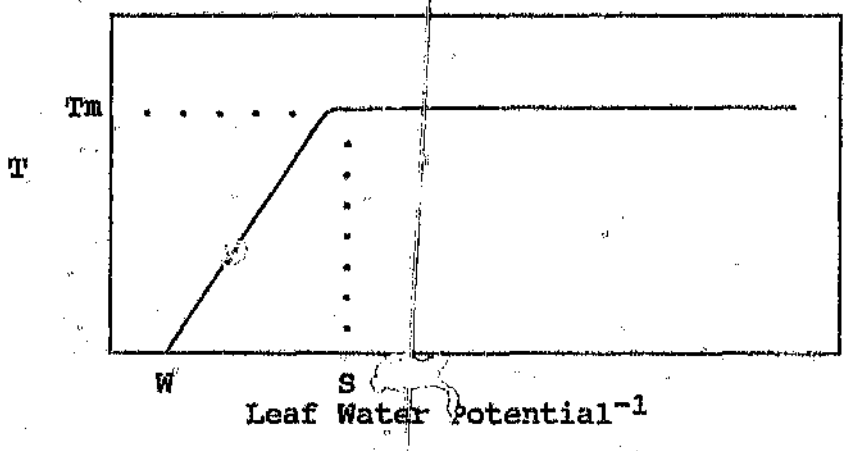

Figure 2.3. Diagrammatic representation of the relationship between transpiration rate (T) and the inverse of leaf water potential . Tm = maximum transpiration rate, S = stomatal closure and W = wilting point.

Relative leaf water content (RWC) is defined as

$$\frac{\text{wet weight - dry weight}}{\text{turgid weight - dry weight}} \qquad (3)$$

(see Slavik 1974). Three to five leaves were sampled from the branches or tufts and placed into vials of known weights and sealed. The vials were refrigerated at approximately 10° C until weighed (wet weight). The leaves were dried to a constant weight at 75° C and re-weighed (dry weight). Turgid

weights were calculated from the standard curves derived in section 2.2.1.2 above.

The relationship between leaf water potential and relative leaf water content (Slavik 1974, Tyree and Hammel 1972) describes the pressure volume curve (Figure 2.3), from which leaf osmotic potential may be determined.

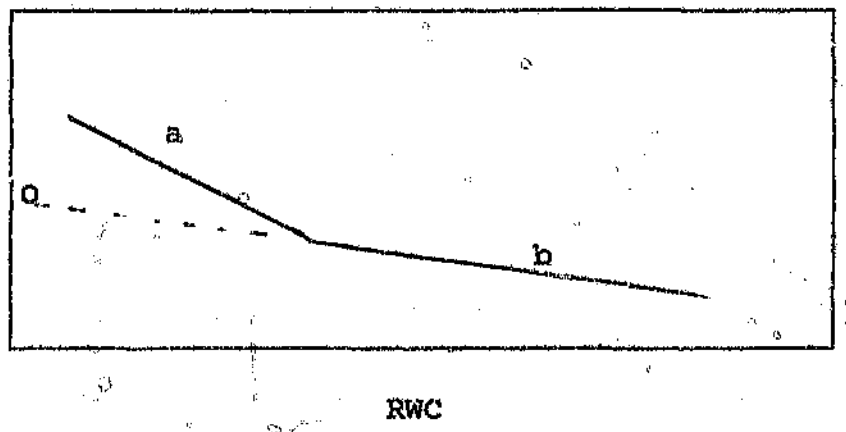

Figure 2.3. Diagrammatic representation of the relationship between leaf water potential (LWP) and relative water content (RWC). By solving for the intersection between the curves a and b, the osmotic potential (O) may be determined.

2.2.2 Soil Data

A single profile was excavated to bed rock or to a depth of 1.5 m. The profile was described (FSSA 1980) and classified (MacVicar et al 1977). A total of 17 (5 surface, 6 A and 6 B horizon) soil samples were collected in a 50 mm x 300 mm stainless steel tube.

Bulk density was calculated from the mass per volume of the surface cores. The cores were then sieved (2 mm mesh) and

dried to a constant temperature at 75° C. The stone fraction was determined as the mass (g stones/g soil) of the inorganic particles greater than 2 mm. For each site the soil samples were bulked to represent an average A (3 to 6 A horizon + 5 surface samples) and B (3 to 6 B horizon samples) horizon samples.

The samples were analyzed for,

- Total nitrogen[1] (A horizon only) using the digestion method (Dorich and Nelson 1983) and ammonium nitrogen methods (Keeny 1982),
- Organic carbon[1] (A horizon only) (Nelson and Sommers 1975),
- Resin extractable phosphorus[1] (Murphy and Riley 1962, Sibbesen 1977, 1978),
- Major cations (Adamson and Ingram 1987),
- pH and extractable acid (Adamson and Ingram 1987), and
- Texture using the particle size method (Black 1965).

Potential biomass production[2] was determined by seeding the soil samples with Panicum maximum and harvesting the biomass produced at regular intervals. Biomass assays derived from site M1 were water stressed throughout the experiment and thus were excluded from the analyses.

Saturated hydraulic conductivity[1] (Ksat) (Amoozegar and Warrick 1986) of the surface soil was determined in situ at each soil sampling point.

Soil data (excluding potential biomass production data) was sent to five experts in the field and a pedologist to rank the soils from least to most fertile.

Number of growth days available for plant growth (Growth days[1]) was determined using a water balance model (Scholes

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1 Pickett (In prep).
2 From Feuchtenbeiner - Walsh (1990).
1 Picket (In prep).

unpublished data) which estimates plant available moisture derived from rainfall sequences (simulated 100 year rainfall sequences - Zucchini and Adamson 1984) and potential evaporation on a daily basis (Lineacre 1977).

2.3 Data analysis

2.3.1 Season

An instantaneous measurement of the ecophysiological of a plant attributes (used in this study) assumes that the attributes do not vary with time. Data was collected from the Mkuze study sites (M1, M2 and M4) at the beginning and again at the end of the growing season. Direct gradient analysis was used to highlight the variation of the individual attributes over this period. Statistical analysis was limited to a comparison of means (SAS 1982).

2.3.2 Attribute range

The dominant growth forms in savannas are the woody plants and the grasses. The two components differ not only in the position of their perennating organ as in Raunkiaer's (1934) life form classification, but also in the entire complex of genetically-determined phenological, morphological and reproductive characteristics, suggesting a sound ecological distinction between the two groups. Physiological differences, for at least savanna plants in situ, between woody and grass elements remain uncompared. The present study provides the opportunity to compare both physiological and morphometric processes between the two components.

A comparison of means test (SAS 1982) was used to determine whether the woody and grass division is a valid functional

distinction at a physiological level. Forbs were excluded from the comparison due to their limited numbers.

2.3.3 Environmental data analysis

The environmental data may be divided into chemical and physical data, and supplementary data (potential biomass production index, number of growth days and ecologists' and pedologist's rankings). The aim of collection and analysis of environmental data was two fold.

a) Determine a fertility index for each site drawing on the soil chemical analyses, potential biomass production index and ecologist's rankings.

   Soil data (both physical and chemical) were ordinated using a principal component analysis (Fatti pers. com.[4]). A similar, but passive analysis (see Ter Braak 1988), of the supplementary data was overlaid onto the soil chemical and physical ordination. The overlay creates the opportunity to infer a fertility index from the potential biomass production data, ecologists' and managers' experience, and aspects of the soil physical and chemical data.

   The PCA ordination will indicate whether the remaining elements of the supplementary data set have compounding effects on inferences from either index.

b) Rank the sites along a plant available moisture and available nutrient index within a biplot of these two indices.

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2.3.4 Direct gradient analysis

The attributes were plotted against indices of plant available moisture and nutrients to determine whether the attributes vary predictably along these gradients.

2.3.5 Inter-species comparisons

Species attributes were ordinated using a principal component analysis (Ter Braak 1988) to determine inter-attribute correlations (Fatti pers. com.[4]) for woody, grass and forb elements. Information pertaining to both functional groups of species and their strategies may be obtained from the two ordinations.

2.3.6 Inter-site comparisons

The investment of carbon into plant biomass draws heavily on both available nutrient and water pools (Chapin et al 1987, Lambers et al 1983, Lauenroth et al 1978, McDermitt and Loomis 1981). The study sites were selected primarily on the basis of rainfall and soil fertility, and these gradients may be indirectly expressed within the plant or community biomass. To determine variation within the plant attributes on a study site basis, the attribute must be expressed as a function of the total biomass of each study site.

Total site biomass was divided into both the woody and grass components deriving inter-woody-site and inter-grass-site comparisons respectively. The forb component was excluded from this analysis as the forb densities were significantly lower than either the woody or grass components. Biomass estimates, for both woody and grass species, were defined as the product between the average basal area ($m^2 \cdot ha^{-1}$) and the

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4 Professor P Fatti, Department of Statistics, University of the Witwatersrand, Johannesburg.

average height[1]. For each study site, the biomass of each species was expressed as a fraction of the total woody or grass component biomass. The species with highest relative biomass estimate was assigned a rank of 1.00 and the remaining species ranks' calculated proportionally. Each attribute was then multiplied through by the proportional biomass rank estimate. The attribute data were ordinated using a detrended correspondence analysis (Fatti pers. com.[4]). By using this method it is believed that functional differences between sites that experience different moisture and nutrient constraints can be obtained.

1 Pickett (In prep).
4 Professor P Fatti, Department of Statistics, University of the Witwatersrand, Johannesburg.

3.0 RESULTS

3.1 EXCLUSIONS

It was necessary to exclude a number of measurements from the study prior to analysis. These were (a) the water relations section and (b) photosynthetic rates of the woody component at the first site at Timbavati Game Reserve, and (c) the leaf consistence of the grass component at the second study site at Timbavati Game Reserve. Justification for the exclusions is given below.

A pilot study on the filter paper technique for the estimation of leaf water potential suggested an equilibration period of four days for Rhus longifolia and five to seven days for Terminalia sericea. Fear of insufficient equilibration time arose and it was suggested that the equilibration period be extended between 25 and 30 days.

A 25 to 30 day equilibration period led to the leaf material degrading and, in many instances, large amounts of mould was present within the equilibration vials. Both cellular degradation and fungal growth would have released bound water, increasing the water potential estimate to a nonsensical level. Following this reasoning together with spurious results, the water relations section of this study was omitted from analyses. Information was, however, retained as the potential of the technique in determining plant water potential is yet to be realized.

Each sampling period, except that at Timbavati, was preceded by substantial rain allowing plants to reach complete or near complete turgidity. The Timbavati Nature Reserve, however, experienced an early winter drought, particularly in the A. nigrescens savanna (T1). To counter the lower soil water potentials, individual

plants of each species were selected and watered (100-300 l / day) for three days prior to sampling. Despite the watering, it was believed that the water status of the woody component was not equivalent to that of the other study sites and the photosynthetic studies were therefore sacrificed. On returning to the second site for the collection of herbaceous leaf material, it was discovered that the watered grass tufts had senesced beyond recovery.

3.2 PLANT ATTRIBUTE RANGES

This section compares the variation of individual sites within the South African savanna to variation of the biome (see OBJECTIVES I above).

For the woody layer, the attribute range of at least one site approaches or equals that of the total savanna attributes variation (Figure 3.1). Similarly with the grass layer (Figure 3.2), attribute ranges of a number of site's approach that of the total range. This is particularly prevalent for sites N2 (quantum efficiency and light compensation point), N3 (dark respiration) and M3 (leaf temperature : ambient temperature ratio and sclerophylly) for the woody component, and sites M1 (quantum efficiency), and N2 (succulence and leaf turgid:dry weight ratio) for the grass component.

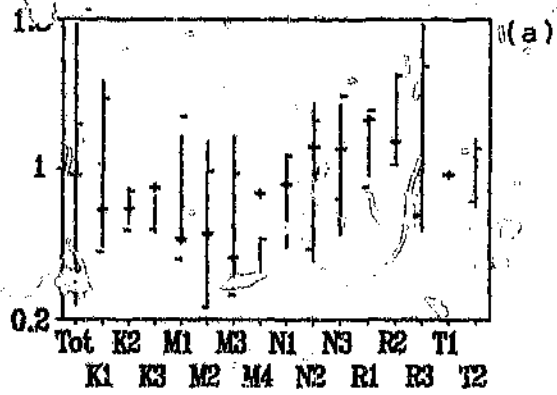
For both the woody and grass components, the data that constitutes a site is highly variable. This can be recognized by the standard deviations about the means, in many cases, lying beyond the minimum and maximum points. The most striking feature of the attribute ranges, is that the minimum, maximum and standard deviation are, in many cases, unique for each site (see also Direct Gradient Analysis below).

Comparisons between woody, grass and forb components are given in Figure 3.3. Despite the high degree of overlap

Figure 3.1 Comparison of the individual sites to the total variation of the entire savanna woody component. The axes are given as plant attributes (Y axis; see below) versus study sites (X axis).

The diagrams are given as; (a) Maximum photosynthetic rate (mg CO_2 m^{-2} s^{-1}), (b) Quantum efficiency x 10^3 ($\mu E \cdot mg\ CO_2^{-1}$), (c) Gross dark respiration (mg $CO_2 \cdot m^{-2} \cdot s^{-1}$), (d) Light compensation point x 10^{-2} ($\mu E \cdot m^2 \cdot s^{-1}$), (e) Sclerophylly ($g \cdot dm^{-2}$), (f) Succulence ($g \cdot dm^{-2}$), (g) Turgid : dry weight ratio, and (h) Bark thickness (mm).

Tot = Total variation for all sites, site addresses are given in ABBREVIATIONS, and points are given as maximum, minimum and standard deviations about the mean (x).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1.8
1
0.2
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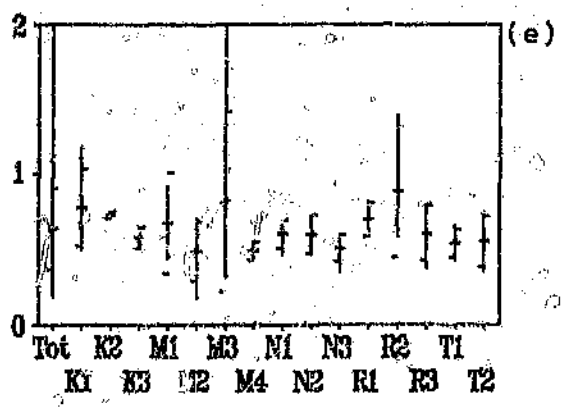
K1 K3 M2 M4 N2 R1 R3 T2


(e)
2
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0
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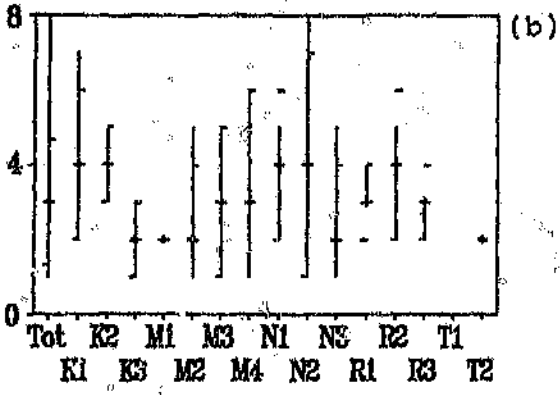
K1 K3 M2 M4 N2 R1 R3 T2


(b)
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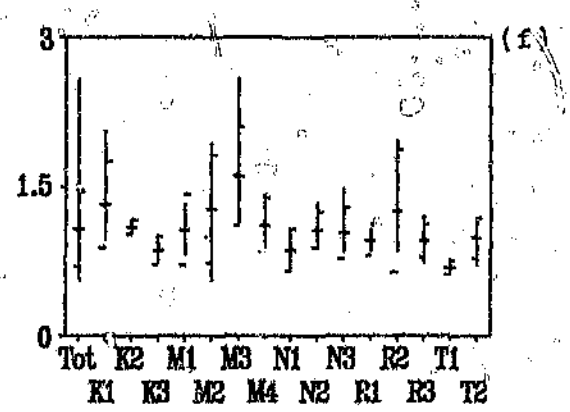
K1 K3 M2 M4 N2 R1 R3 T2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1.5
0
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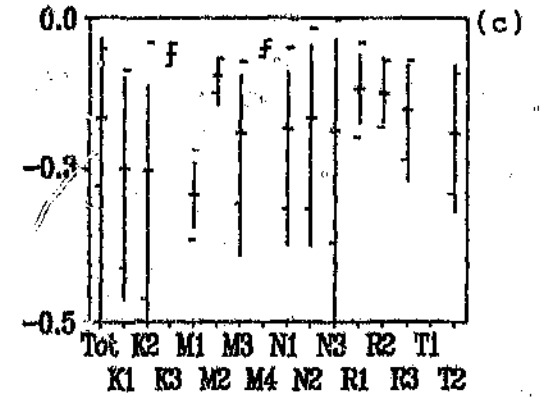
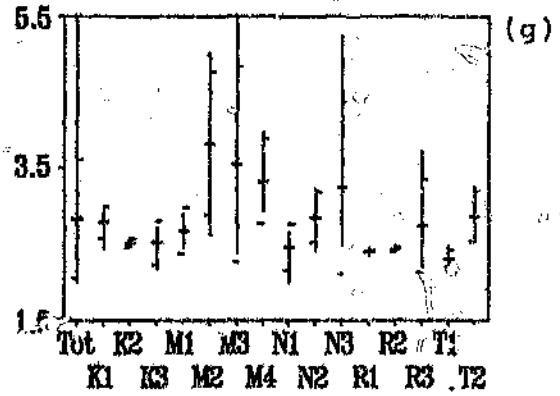
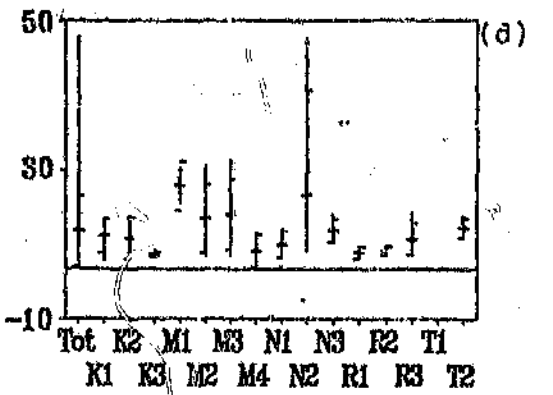
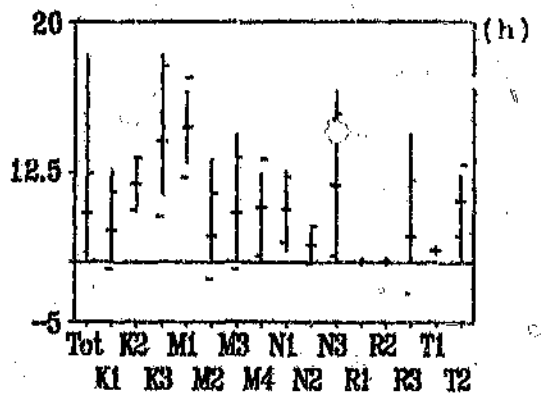
K1 K3 M2 M4 N2 R1 R3 T2


(c)
0.0
-0.3
-0.5
Tot K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2


(g)
5.5
3.5
1.5
Tot K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2


(d)
50
30
-10
Tot K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2


(h)
20
12.5
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Tot K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2

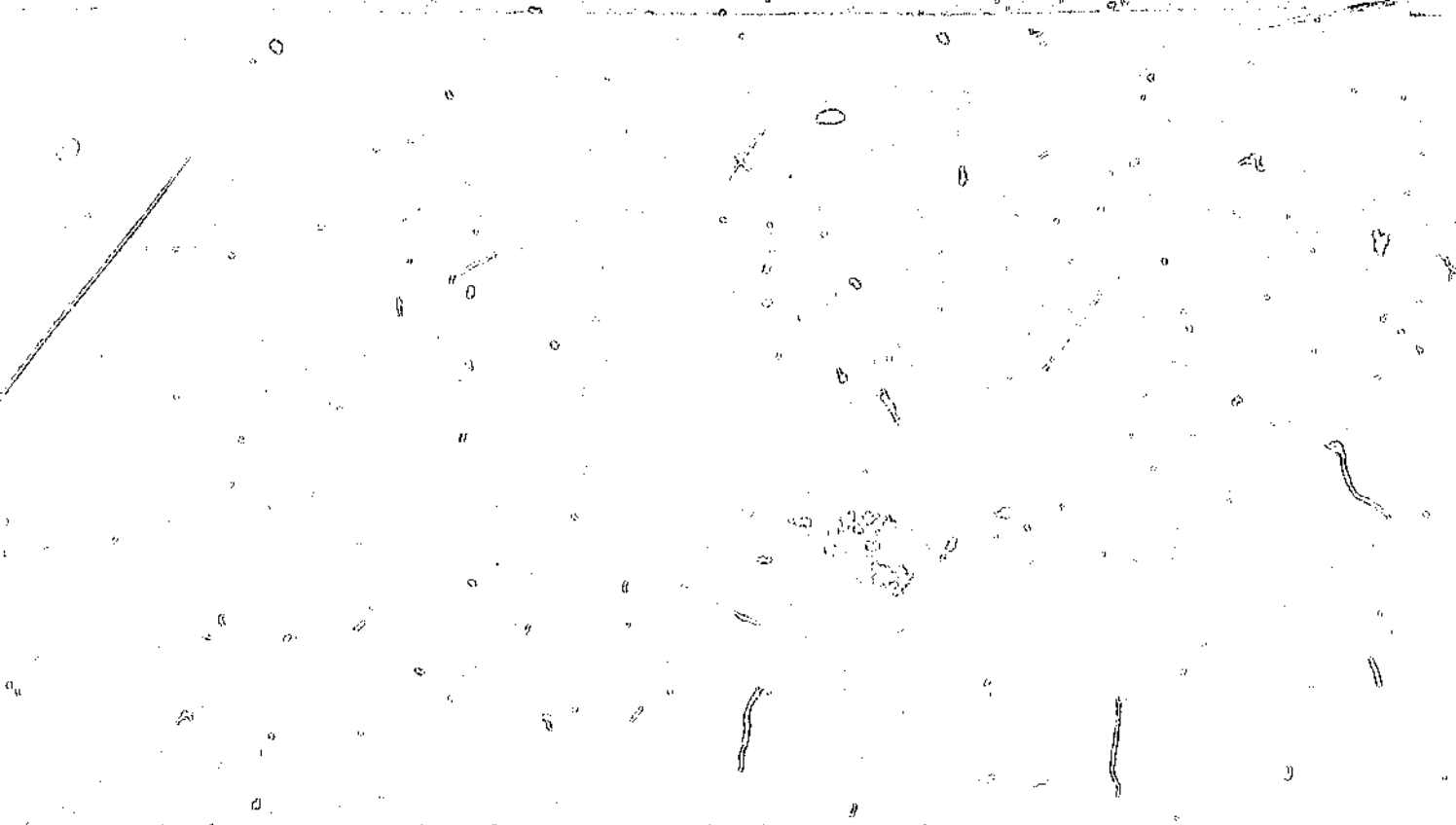


Figure 3.2 Comparison of the individual sites to the total variation of the entire savanna grass component. The axes are given as plant attributes (Y axis; see below) versus study sites (X axis).

The diagrams are given as; (a) Maximum photosynthetic rate (mg CO_2 m^{-2} s^{-1}), (b) Quantum efficiency x 10^3 ($\mu E \cdot$mg CO_2 $^{-1}$), (c) Gross dark respiration (mg $CO_2 \cdot m^{-2} \cdot s^{-1}$), (d) Light compensation point x 10^{-2} ($\mu E \cdot m^{-2} \cdot s^{-1}$), (e) Sclerophylly ($g \cdot dm^{-2}$), (f) Succulence ($g \cdot dm^{-2}$), (g) Turgid : dry weight ratio, and (h) Lamina breaking strength (dynes cm^{-1}).

Tot = Total variation for all sites, site addresses are given in ABBREVIATIONS, and points are given as maximum, minimum and standard deviations about the mean (x).

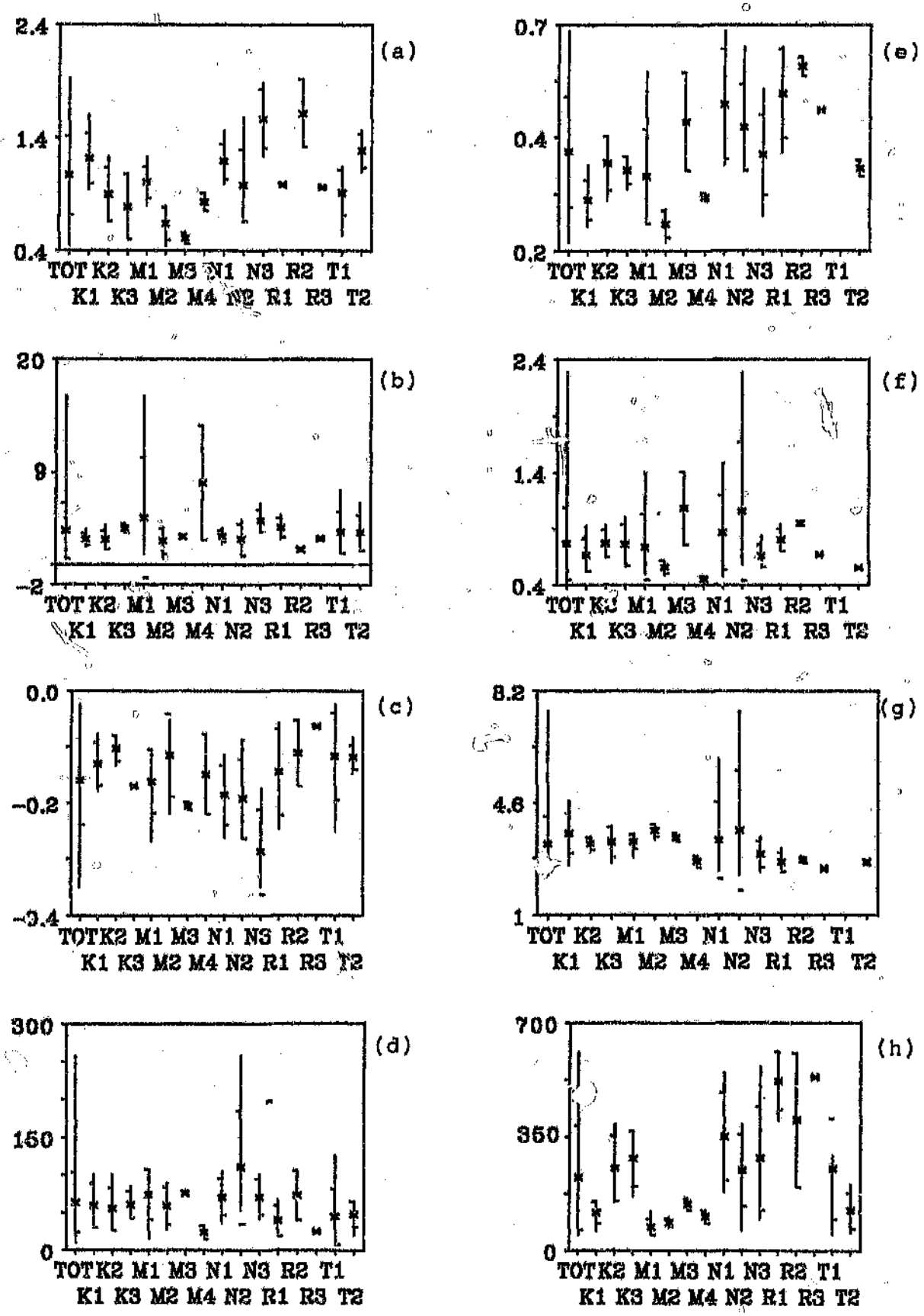
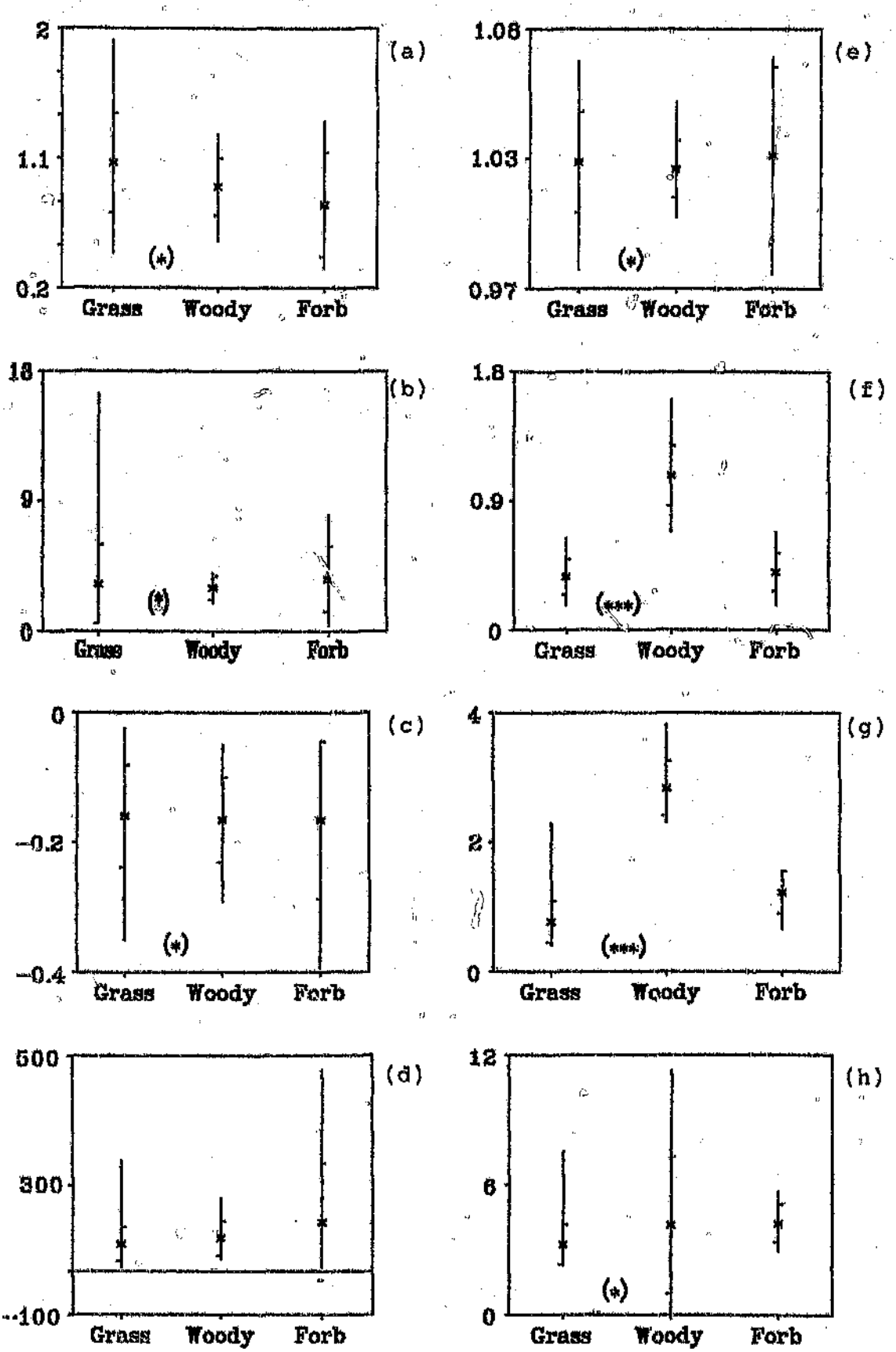

(a)
2.4
1.4
0.4
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(b)
20
9
−2
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(c)
0.0
−0.2
−0.4
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(d)
300
150
0
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(e)
0.7
0.4
0.2
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(f)
2.4
1.4
0.4
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(g)
8.2
4.6
1
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2
(h)
700
350
0
TOT K2 M1 M3 N1 N3 R2 T1
K1 K3 M2 M4 N2 R1 R3 T2

Figure 3.3. Ranges, means and standard deviations given for woody, grass and forb layers, $p<0.001$ suggests a highly significant difference between woody and grass layers. The axes are given as plant attributes (Y axis; see below) versus study sites (X axis).

The diagrams are given as (a) Maximum photosynthetic rate (mg CO_2 m^{-2} s^{-1}), (b) Quantum efficiency x 10^3 ($\mu E \cdot mg\ CO_2^{-1}$), (c) Gross dark respiration (mg CO_2 $\cdot m^{-2} \cdot s^{-1}$), (d) Light compensation point ($\mu E \cdot m^{-2} \cdot s^{-1}$), (e) Leaf temperature : chamber (ambient) temperature ratio, (f) Sclerophylly ($g \cdot dm^{-2}$), (g) Succulence ($g \cdot dm^{-2}$), and (h) Turgid : dry weight ratio.


(a)
2
1.1
0.2
(*)
Grass
Woody
Forb
(e)
1.08
1.03
0.97
(*)
Grass
Woody
Forb
(b)
18
9
0
(*)
Grass
Woody
Forb
(f)
1.8
0.9
0
(***)
Grass
Woody
Forb
(c)
0
−0.2
−0.4
(*)
Grass
Woody
Forb
(g)
4
2
0
(***)
Grass
Woody
Forb
(d)
500
300
−100
Grass
Woody
Forb
(h)
12
6
0
(*)
Grass
Woody
Forb

between the woody and grass maximum photosynthetic rates, the difference in mean values were marginally significant. No significant differences in quantum efficiency, dark respiration, light compensation point and leaf:chamber temperature ratio were detected between the two plant types.

An example of the derived and observed photosynthetic curves and equations for both a grass and a woody species, are given in Appendix A.

A significant difference exists between the attributes of leaf consistence for woody plants and grasses (Figure 3.3.).

3.3 SEASON

This section determines the constancy of ecophysiological traits, as functional characters, over the span of a single growing season (see OBJECTIVES II above).

Bark thickness was the only plant attribute to remain unchanged over the season for all the woody plants studied. Large differences do occur between the beginning and end of a growing season in many of the remaining plant traits studied. Serving merely as examples, the differences in lamina breaking strength of selected grass species are presented in Figure 3.4. The remaining breaking strengths are presented, together with the other traits, in Appendix B. It must be noted that seasonal differences in leaf photosynthesis cannot be measured with any statistical significance, given the limitations of the non-linear algorithm used. Large differences between the two sampling periods have, however, been highlighted.

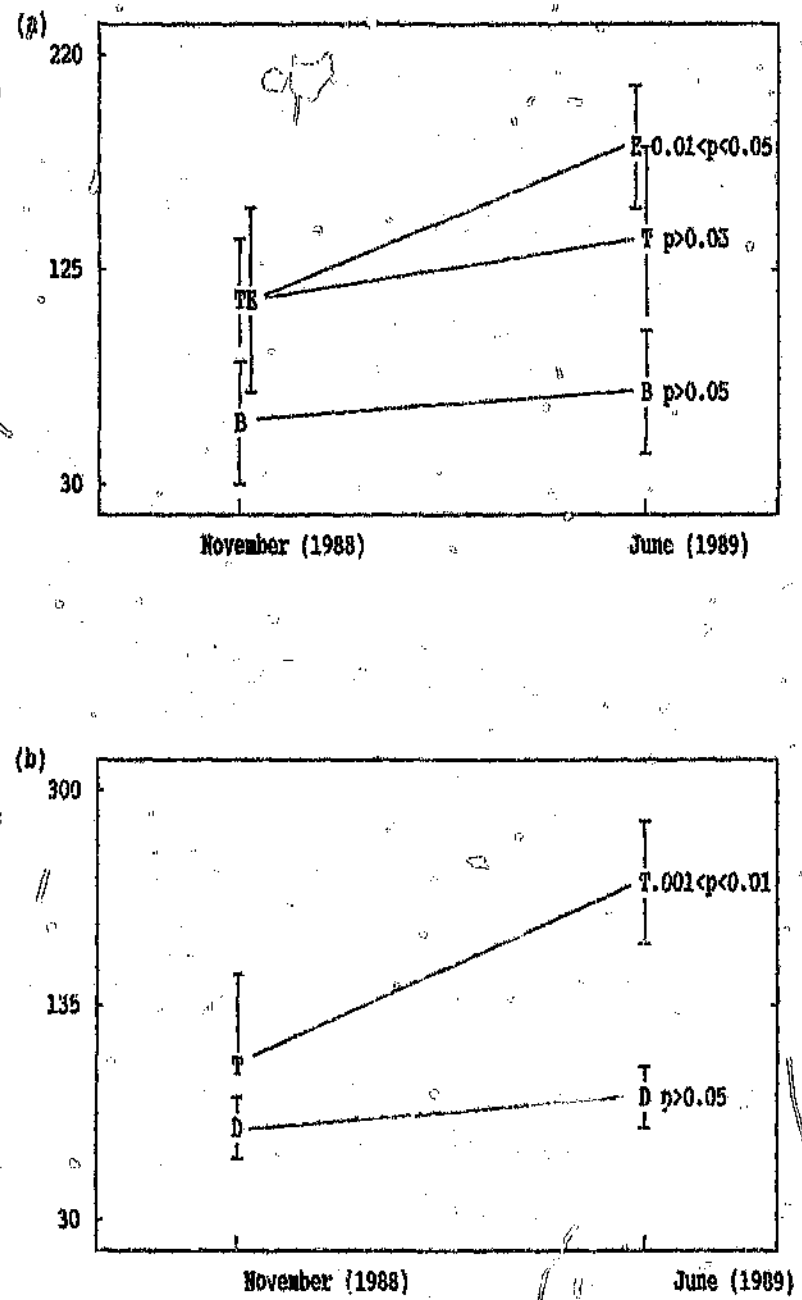


Figure 3.4. The change in lamina breaking strength of grass species, Bothriochloa insculpta (B), Diheteropogon amplectens (D), Eragrostis superba (E) and Themeda triandra (T), between the beginning and end of a growing season for sites M1 (a) and M4 (b). Statistical differences are given as p values.

These differences in the plant attributes (other than bark thickness) were not consistent with either species or attribute. This observation effectively groups the attributes used in this study into a category which requires a seasonal component for them to have an application in a functional classification (see OBJECTIVES II above). The significance of this observation is discussed in greater detail in sections 4.1.8 and 4.4 below.

3.4 SOIL ANALYSIS

A principal component analysis was used to enable correlations between the soil variables to be detected. An abridged interpretation of the PCA ordination biplot is as follows (consult Jongman et al 1987, Ter Braak 1988 for detailed explanations):

The intersection of the axes (.:.) represents the sample mean or nodal point. The arrows represent the approximate direction of the maximum variation of the variable, whereas the length of the arrow equals the rate of change in that direction. The angle between respective arrows provides an estimate of correlation. Arrows that point in the same direction indicate positively correlated variables, perpendicular arrows indicate a lack of correlation and arrows pointing in opposite directions indicate negatively correlated variables. The principal components (axes) may be quantified by dropping a perpendicular from each variable to the respective axes. The proportional contribution of the variables to each principal component is the length of the segment from the nodal point to the intersection of the perpendicular with the axis.

The first principal component of the soil analysis (Figure 3.5) comprised entirely of physical and chemical

variables. The position of the chemical variables in the ordination space suggests that a plant available nutrient

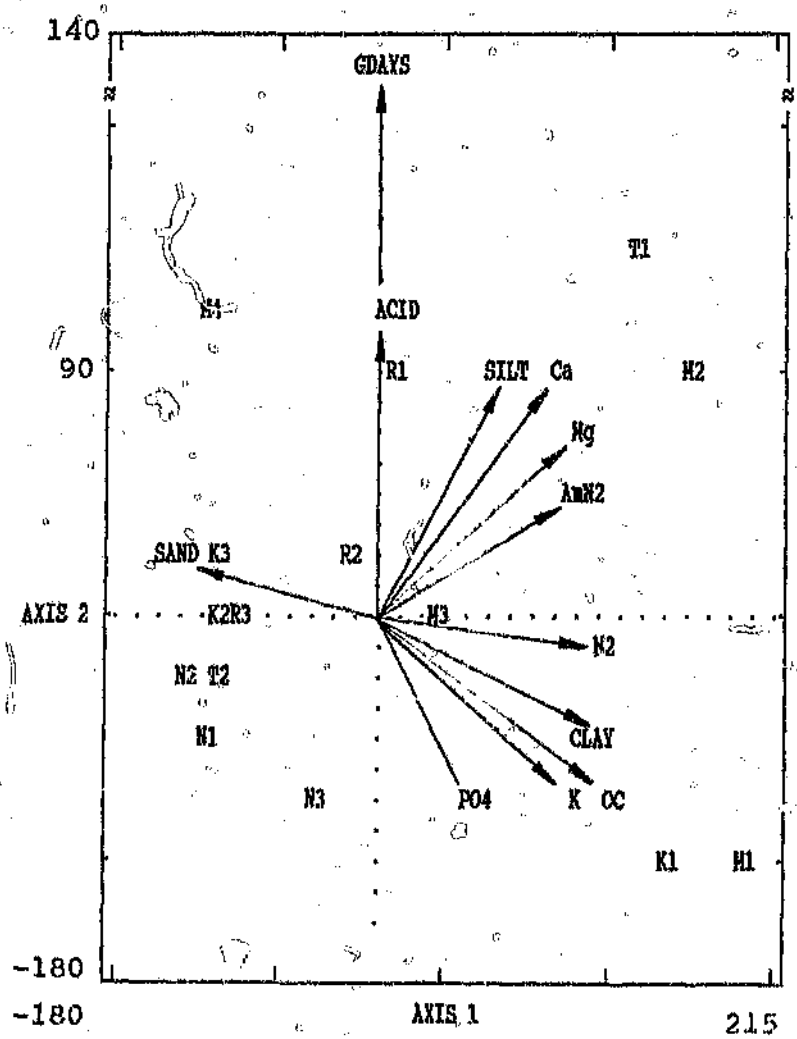


Figure 3.5. Biplot based on a principal component analysis of soil (A horizon) variables corrected for stone fraction. Eigenvalues are 0.763, 0.411, 0.127 and 0.059 for the first four axes. Abbreviations are presented in ABBREVIATIONS above.

index would possibly lie to the right of the origin. The position of this index may lie on, or to either side of the first axis. This in turn suggest that study sites M1, M2, K1 and T1 should be considered as nutrient rich sites and N1, N2 and M4 as nutrient poor.

A passive ordination of the soil fertility rankings of the ecologists and potential biomass production estimate for each site (Figure 3.6), supports the hypothetical positioning of a nutrient index within the ordination space discussed above.

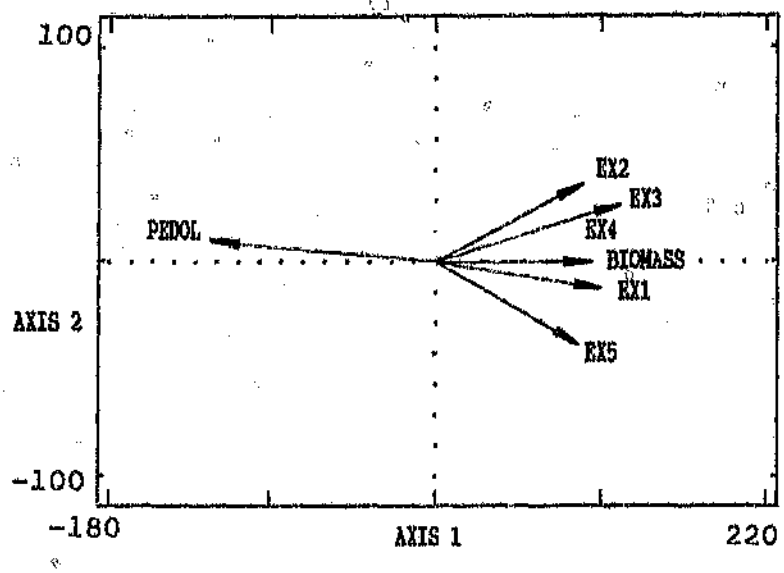


Figure 3.6. Passive principal components analysis (based on Figure 3.5) of intuitive 'fertility' ratings by five ecologists (EX) and a pedologist (PEDOL), and a potential biomass (BIOMASS) production assay for the 15 study sites. Eigenvalues are 0.651, 0.423, 0.125 and 0.023 for the first four axes.

Soil nitrogen concentration was favoured by the ecologists when scoring the study sites for fertility. Two of the five ecologists favoured an ammonium nitrogen / magnesium / calcium combination, whereas the remaining three ecologists consider total nitrogen, potassium and

phosphorus as important indicators of soil fertility. The pedologist, however, indicated a greater importance of sandy soils in the facilitation of plant growth, and hence ignored the role of fine fractions in the nutrient status of the soil. This fertility estimate was thus excluded from further investigations.

The potential biomass production assay within the passive ordination (Figure 3.6) indicated that the relative fertility of the study sites is synonymous with the first principal component (cf Figure 3.5). Despite the limitations of the biomass production assay (see section 4.1.6.3 below), the agreement between this parameter and the ecologists' ranks and chemical and physical data resulted in the potential production assay being used as an indicator of plant available nutrients.

The second principal component of the environmental variable ordination (Figure 3.5) was composed, to a large degree, of soil moisture (GDAYS). The soil physical and chemical variables, however, do play an important role in the derivation of this axis. This suggests that plant available moisture and available nutrient indices are not independent. This assumption was made at the onset of this project (see Figure 1.1). The lack of independence may be attributed to:

a. the number of growth days being calculated as a function of both average annual rainfall and soil texture. The latter, particularly the fine fractions, had a strong positive correlation (see Figure 3.5) with the mineral nutrients, and

b. possible nutrient availability and leaching. An increased rainfall, particularly on sandy soils, would increase the availability of soil nutrients. An increased rainfall, however, increases leaching as can be seen from the high correlation between GDAYS and extractable acid (ACID) (Figure 3.5).

The manipulation of the environmental data enabled the study sites to be divided into three categories (Table

3.1), low, intermediate and high, for both indices of plant available moisture (GDAYS) and nutrients (BIOMASS).

An extended table of soil variables and number of growth days for each site is presented in Appendix C.

3.5 DIRECT GRADIENT ANALYSIS

This section determines whether ecophysiological traits do vary predictably with a change in either available moisture or nutrients, or both (see OBJECTIVES III above).

Table 3.1. The division of the study sites into three (high, medium and low) categories (see Cate and Nelson 1971) for both available growth days (≈ Moisture gradient) and biomass production estimate (≈ Nutrient gradient).

Nutrient	Moisture	
M1	K2	
M2	K3	
K1	M4	HIGH
T1	M3	
M3	N2	
R1	T1	
R2	T2	
N3	N1	
R3	M2	INTERMEDIATE
K2	N3	
T2	K1	
K3	M1	
M4	R3	
N1	R1	LOW
N2	R2	

No marked trends were noted in plots between either the traits of the woody or the grass plants, and the climatic and edaphic variables. Plots of attribute versus available growth days (moisture gradient), and attribute

versus potential biomass production index (nutrient gradient) were retained in Appendix D for reference purposes.

3.6 INTER-SPECIES ANALYSIS

The aim of this section is to determining functional similarities or differences between plants or species occurring at different points on the moisture or nutrient plain (See OBJECTIVES IV above).

3.6.1 Woody

A strong positive correlation (Figure 3.7) exists between maximum photosynthetic rate (PMAX) and gross dark respiration (DR). Positive correlations also exist between sclerophylly (SCL), succulence (SUC), light compensation point (CP) and bark thickness (BARK); and quantum efficiency (QE) and leaf:ambient temperature ratio (LTCT). Leaf turgid:dry weight ratio (RAT) was negatively correlated with QE, LTCT, DR and PMAX.

The majority of the woody species are distinguished by the second principal co-ordinate. This axis is essentially composed of DR, PMAX and LTCT and to a lesser extent the remaining attributes. The distribution of Acacia nilotica (see Figure 3.8) within the ordination, however, follows the first principal co-ordinate. This axis is defined by mainly SUC, SCL, CP, QE and BARK (Figure 3.7 a). The spatial variation of these attributes within the species' ordination space cannot be linked to either soil moisture or nutrient gradients.

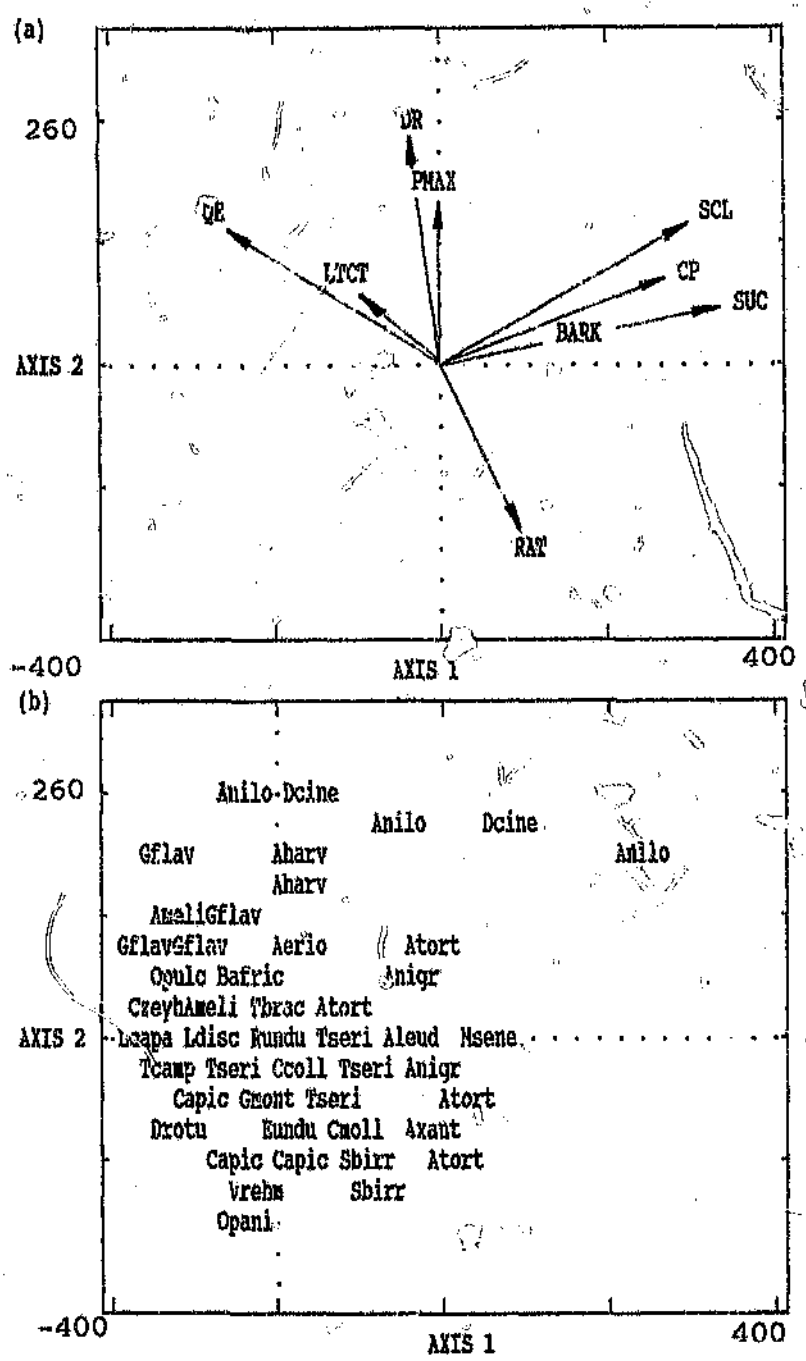


Figure 3.7. Principal component analysis of attributes for the woody layer (a) and the species (b). Multiple occurrences species of the same generic and specific names represent different study sites. Eigenvalues are 0.593, 0.423, 0.196 and 0.033 for the first four axes. Abbreviations are presented in ABBREVIATIONS above.

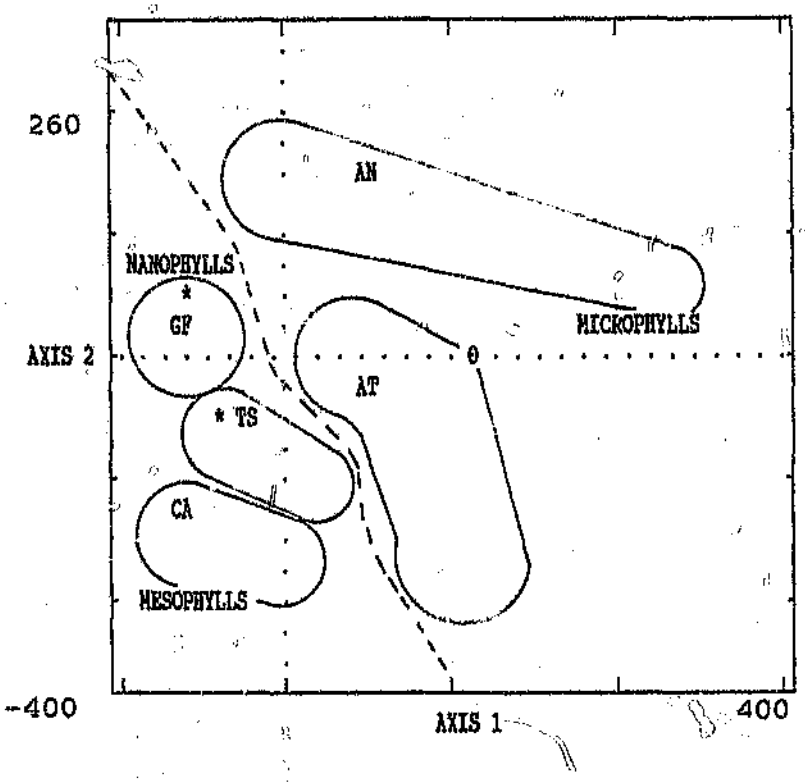


Figure 3.8. Distribution outlines (from Figure 3.7) of common species (Acacia nilotica AN, Acacia tortilis AT, Combretum apiculatum CA, Grewia flava GF and Terminalia sericea TS) are indicated. The positions of Acacia mellifera (*) and Meytenus senegalensis (θ), either side of an inferred division (¦) between microphylls, and nanophylls and mesophylls, are given.

The distribution of the woody species within an attribute ordination, however, indicates the presence of groups of species despite a prominent nodal tendency towards the origin of the ordination. An outline of the distribution of the common species (Figure 3.8, cf Figure 3.7) indicates a possible presence of functional ranges in which these species occur. The functional ranges may overlap, although this is not shown.

A division exists (see Figure 3.8) between the microphyllous species (Acacia, Albizia and Dichrostachys), and the nanophyllous and mesophyllous species. This suggests that this division may have a functional significance. The occurrence of A. mellifera

(a microphyllous species) well within the mesophyllous leafed division, and M. senegalensis (a nanophyllous species) within the microphyllous leafed division, are interesting exceptions. The low number of individuals of these two species studied, however, prevents further investigation of the functional significance of this deviation.

3.6.2 Grass

Strong positive correlations exist between grass SCL and CP, and PMAX, DR and lamina breaking strength (BREAK) (Figure 3.9). A weaker correlation exists between RAT and SUC.

Despite the central tendency of the grass component, suggesting a high degree of similarity between the species, the majority of the grass species occur along the first principal co-ordinate. This axis comprises mainly SCL, BREAK, CP and PMAX and LTCT and QE (Figure 3.9 a). Variation of Diheteropogon amplectens (Dampl), particularly individuals of this species sampled at Nylsvley (N3), is along the second axis which is defined by SUC and RAT. This species at Nylsvley was noted for fleshy leaves (personal observation). The remaining attributes were not, however, markedly different from a same species sampled at other study sites, namely; K2, K3 and M4 (see Figure 3.9a).

3.6.3 Forb

Strong positive correlations exist between PMAX, QE, DR and SCL (Figure 3.10). Unlike the woody and grass components, forb leaf:chamber temperature ratio (LTCT) was negatively correlated with quantum efficiency (QE). The present study sampled relatively fewer forbs than either woody or grass species. The forbs, by definition,

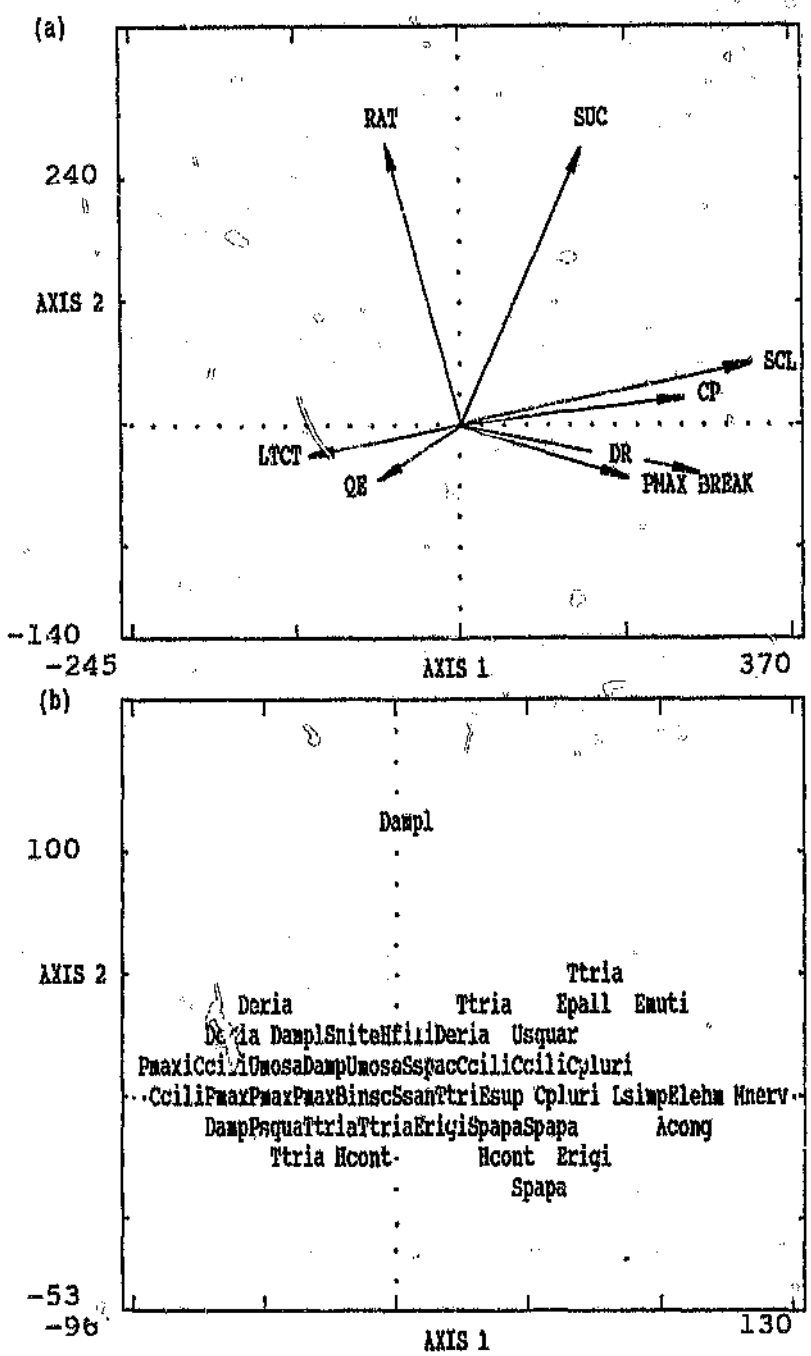


Figure 3.9. Principal component analysis of attributes (a) and the grass species (b). The origin of the axes have been expanded so that each species studied may be examined. Multiple occurrences of species of the same generic and specific names represent those species at different study sites. Eigenvalues are 0.678, 0.398, 0.105 and 0.021 for the first four axes. Abbreviations are presented in ABBREVIATIONS above.

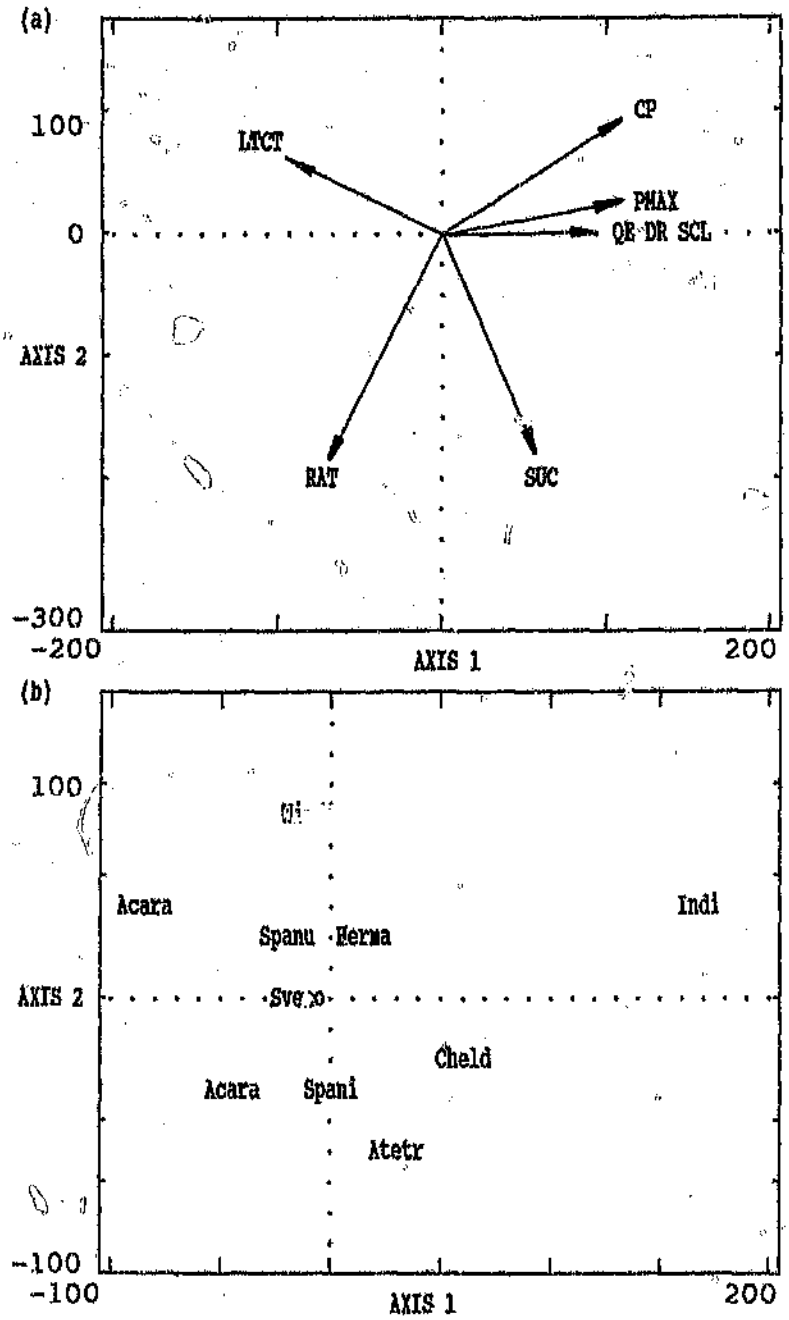


Figure 3.10. Principal component analysis of attributes (a) and the forb species (b). Multiple occurrences of species of the same generic and specific names represent those species at different study sites. Eigenvalues are 0.422, 0.388, 0.204 and 0.111 for the first four axes. Abbreviations are presented in ABBREVIATIONS above.

are a diverse combination of woody, succulent and weedy plant types. The categorization of these species into a single group may, therefore, be misleading. The data was, however, retained for both interest and reference purposes and will not be discussed or referenced in the discussion section below.

3.7 INTER-SITE ORDINATIONS

This section evaluates functional differences between plant communities which occur under different plant available moisture and nutrient constraints (see OBJECTIVES V above).

3.7.1 Maximum photosynthetic rates

A prevalent outlier, in the form of a Combretum apiculatum dominated vegetation type (K3, N2 and M4), is evident within an ordination of the maximum photosynthetic rates of the woody component, when expressed as a function of a ranked biomass index (Figure 3.11). These study sites are considered to be moist and of low nutrient status (see Table 3.1). A grouping of Acacia dominated sites (M1, M2, M3 and T1) occurs within the top left quadrant of the ordination. Terminalia (K2 and N1) dominated communities occur within the bottom left quadrant, which are closely associated with the dry sites (R1, R2 and R3).

The distribution of the sites does not indicate the presence of either a nutrient or moisture gradient (cf Table 3.1), even with the exclusion Combretum dominated sites from the ordination procedure.

The first ordination axis for the maximum photosynthetic rates of the grass layer (Figure 3.12), may be viewed as a moisture gradient between the dry sites (R1, R2 and R3) and the moist sites (K2, K3, M4 and M3) with the

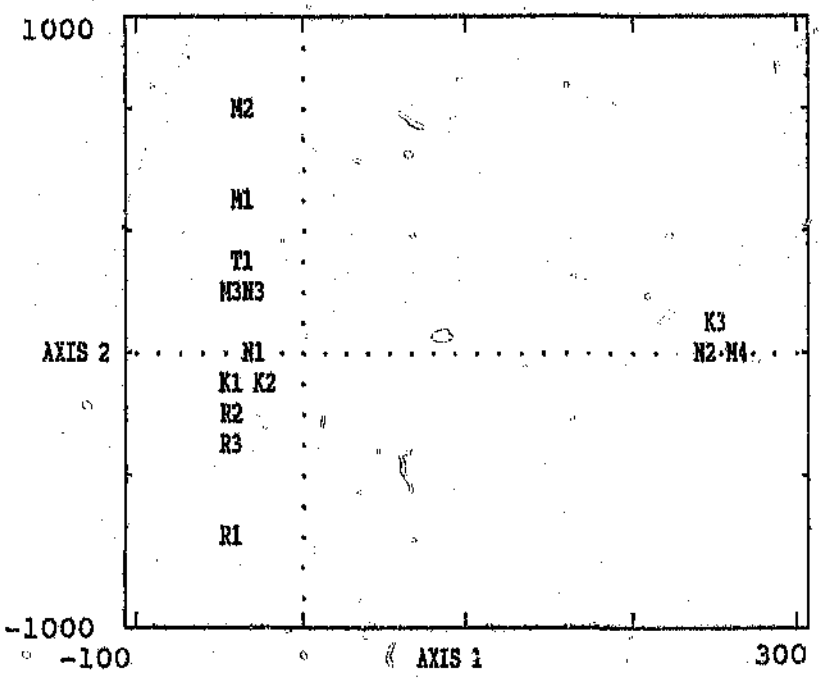


Figure 3.11. A detrended correspondence analysis of the maximum photosynthetic rate for the woody layer expressed as a function of the study sites' total plant biomass. Eigenvalues for the four axis are 0.559, 0.321, 0.185 and 0.011. Abbreviations are presented in ABBREVIATIONS above.

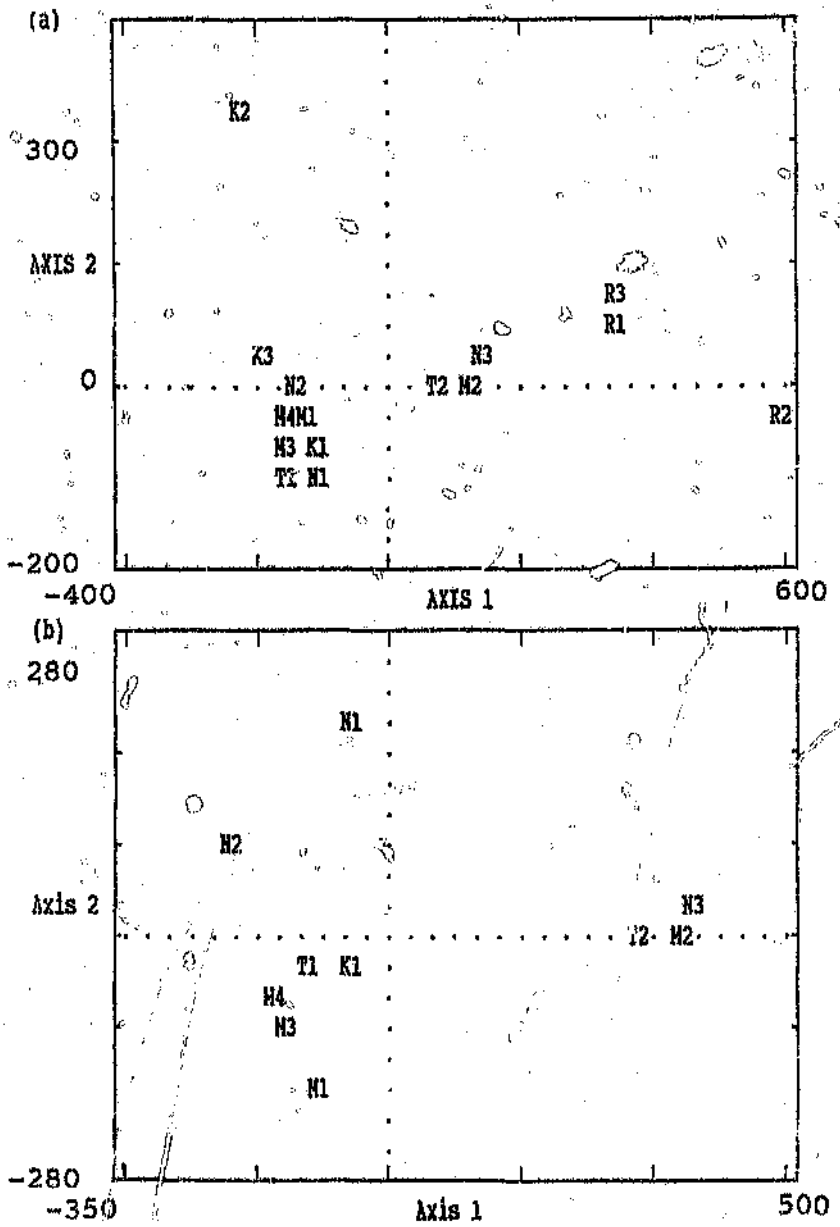


Figure 3.12. Detrended correspondence ordination of grass maximum photosynthetic rates expressed as a function of the total biomass of each study site. All sites are represented in (a) and the outliers (K2, K3, R1, R2 and R3) excluded in (b). Eigenvalues for the four axes are given as 0.531, 0.214, 0.102 and 0.015, and 0.554, 0.398, 0.132 and 0.020 for (a) and (b) respectively. Abbreviations are presented in ABBREVIATIONS above.

intermediate moisture sites (M2, N3 and T2) between the two (cf Table 3.1).

The exclusion of the outliers (K2, K3, R1, R2 and R3) reveals a possible nutrient gradient, with the exception of M4, along the second axis (Figure 3.12b) between nutrient poor sites (N1 and N2) and nutrient rich sites (K1, M1, M3, and T1).

3.7.2 Quantum efficiency

The second axis of the quantum efficiency of the woody component (Figure 3.13) may represent a moisture gradient consisting of moist sites (K3, M4 and N2) and the dry sites (R1, R2 and R3) (cf Table 3.1). Although the Combretum dominated site (K2) was estimated to be the wettest site, it is believed that factors other than plant available moisture or nutrients (eg soil depth), play a important role in grouping this site together with the Burkea / Terminalia (N1) and Albizia (K1) dominated sites.

Ordination of quantum efficiency of the grass layer (Figure 3.14) indicates the presence of a moisture gradient as the first axis between the dry sites (R1 and R3, and R2) and the moist sites (K2, K3, N2 and M4). A weak (justified by a few of the sites) nutrient axis was detected in the second ordination axis when sites K2, K3 and R2 were excluded.

3.7.3 Gross dark respiration

As with quantum efficiency of the woody layer, four main clusters arise from the ordination of dark respiration (Figure 3.15). The first consists of the dry sites (R1, R2, and R3). The second, the moist sites (K3, M4 and N2). The third, the intermediate moisture sites (K1, N1 and

T1) excluding K2 which is considered to be a moist site, and the fourth, the Acacia communities (M1, M2, M3 and N3). Despite the clear association of sites according to moisture, moisture (or nutrient) gradients were not extracted as principal axes.

An ordination of the grass dark respiration indicates a possible moisture gradient along the first ordination axis (Figure 3.16) extending from the dry sites (R1, R2 and R3) to the moist sites (K1, K3, M4, M3 and N2) (cf Table 3.1). The presence of a nutrient gradient was not evident within the ordination space.

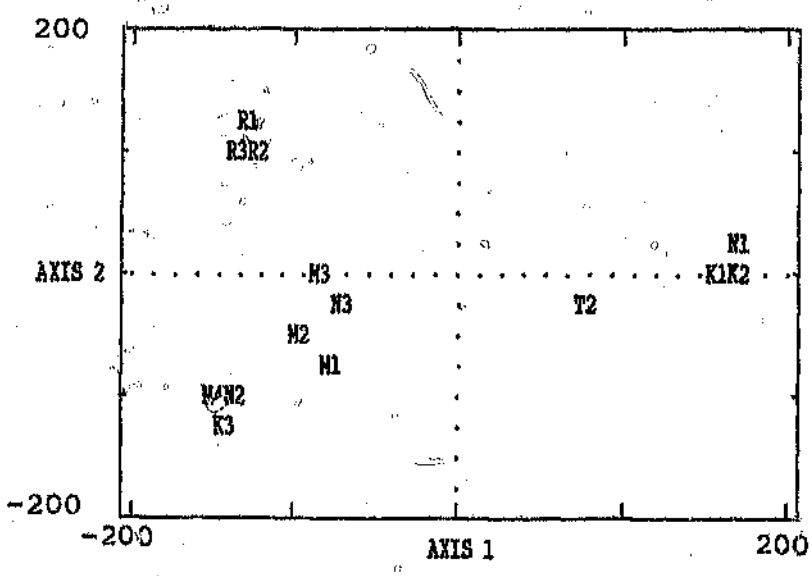


Figure 3.13. Detrended correspondence ordination of quantum efficiency for the woody component expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.564, 0.258, 0.159 and 0.014. Abbreviations are presented in ABBREVIATIONS above.

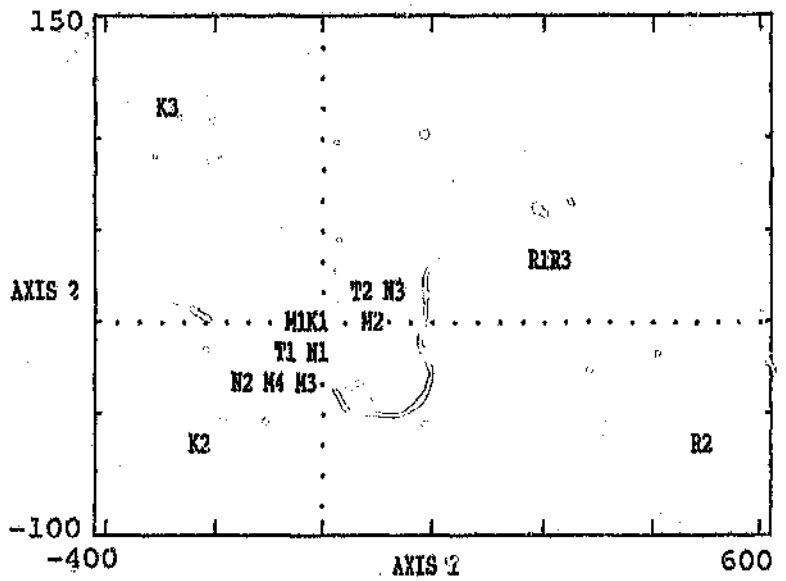


Figure 3.14. Detrended correspondence ordination of grass quantum efficiency expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.568 0.325, 0.112 and 0.101. Abbreviations are presented in ABBREVIATIONS above.

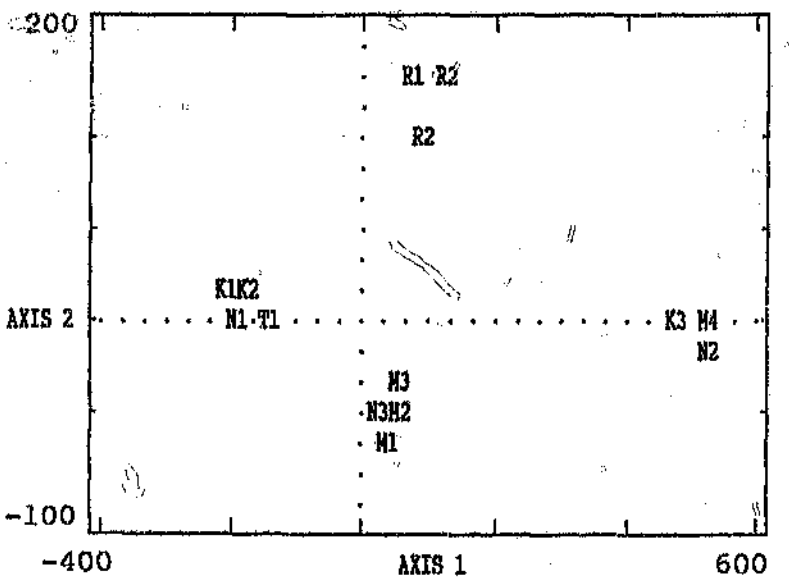


Figure 3.15. Detrended correspondence ordination of dark respiration for the woody component, expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.553, 0.267, 0.125 and 0.011. Abbreviations are presented in ABBREVIATIONS above.

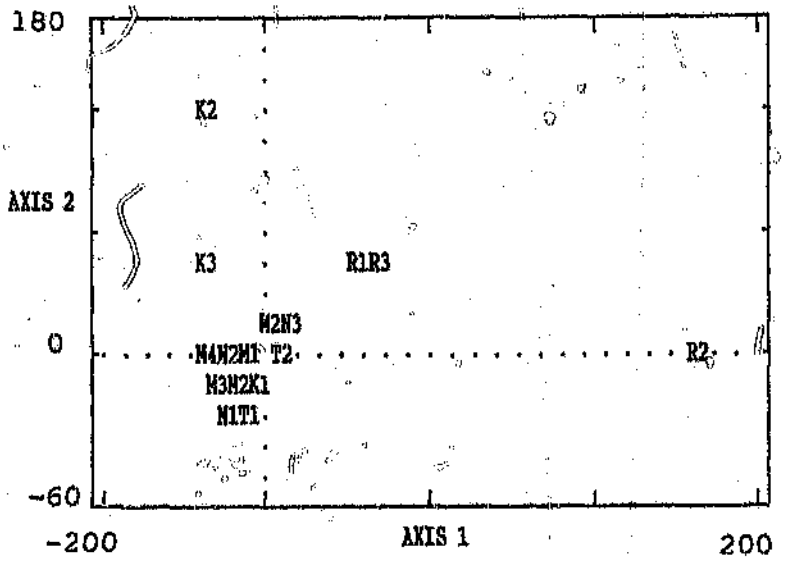


Figure 3.16. Detrended correspondence ordination of gross dark respiration of the grass layer expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.547, 0.387, 0.209 and 0.158. Abbreviations are presented in ABBREVIATIONS above.

3.7.4 Light compensation point

Neither moisture nor nutrient gradients were detected in an ordination of the light compensation point for the woody component (Figure 3.17a). The clusters of specific sites, mentioned above, were evident.

The exclusion of the Combretum dominated sites (K3, M4 and N2) (Figure 3.17 b) reveals a microphyll : nanophyll split along the first axis, with the exception of R1. The position of R1 in the ordination diagram leads to speculation on the presence of other compounding environmental factors, (eg the calcrete layer) and their influence on plant function.

Ordination of the light compensation points of the grass layer (Figure 3.18) indicates the presence of a moisture gradient along the first axis. This forms a continuum

from the dry sites (R1, R2 and R3) to the moist sites (K2, K3, M3, M4 and N2) (cf Table 3.1) with the intermediate sites (M2, N3 and T2) between the two. The presence of a nutrient gradient was not evident within the ordination space.

3.7.5 Leaf:chamber temperature ratio

Ordination of the leaf:chamber temperature ratio for the woody component indicates a distinct grouping of the dry sites (R1, R2 and R3) (cf Table 3.1) on the first axis (Figure 3.19) away from the moist sites. This may suggest a moisture gradient along the first axis. A moisture gradient is not revealed once the dry sites have been excluded from the ordination procedure. In spite of the absence of a nutrient or moisture gradient, the grouping of sites of similar species, ie the Combretum sites (K3, M4 and N2), the Terminalia sites (K2, N1 and T2) to which the Albizia : Dichrostachys dominated site (K1) is closest, and the Acacia dominated sites (K3, M4 and N2), may suggest an inherent functional basis to the present floristic classifications.

The first axis of the ordination of leaf:chamber temperature ratio for the grass component (Figure 3.20) indicates a possible moisture gradient between the dry sites (R1, R2 and R3) and the moist sites (K2, K3, M4, M3 and N2). The presence of a nutrient gradient was not evident within the ordination space.

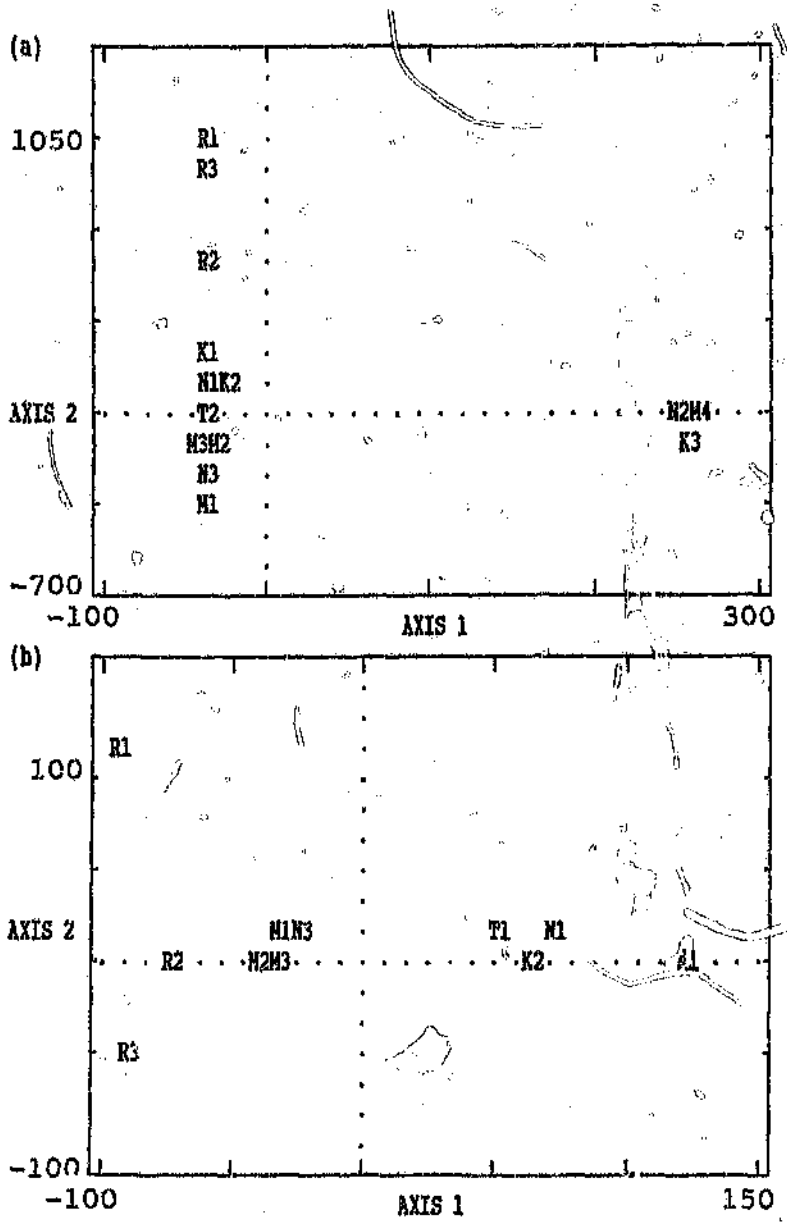


Figure 3.17. Detrended correspondence ordination of light compensation point for the woody layer, expressed as a function of the total biomass of each study site. Ordination (a) includes all sites, whereas, ordination (b) excludes the Combretum sites (K3, M4 and N2). Eigenvalues for the four axes are 0.557, 0.224, 0.152 and 0.092, and 0.624, 0.498, 0.153 and 0.063 for (a) and (b) respectively. Abbreviations are presented in ABBREVIATIONS above.

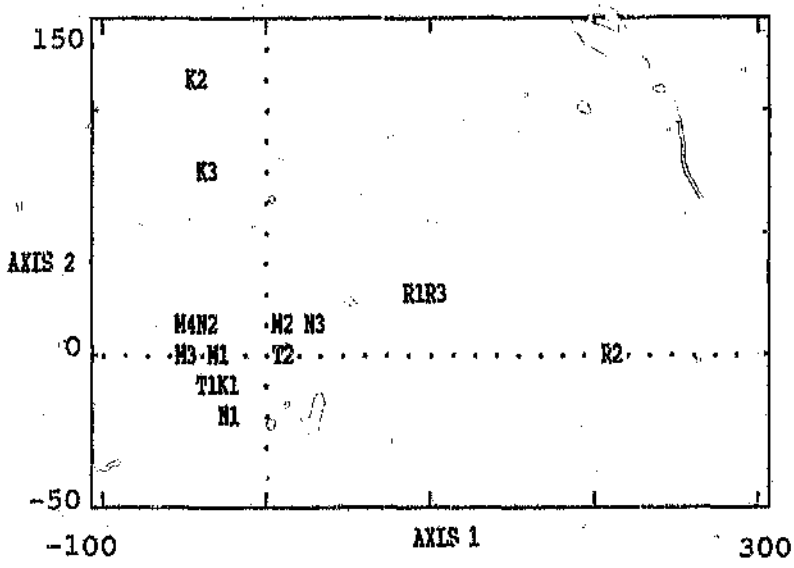


Figure 3.18. Detrended correspondence ordination of light compensation point of the grass layer expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.655, 0.486, 0.198 and 0.048. Abbreviations are presented in ABBREVIATIONS above.

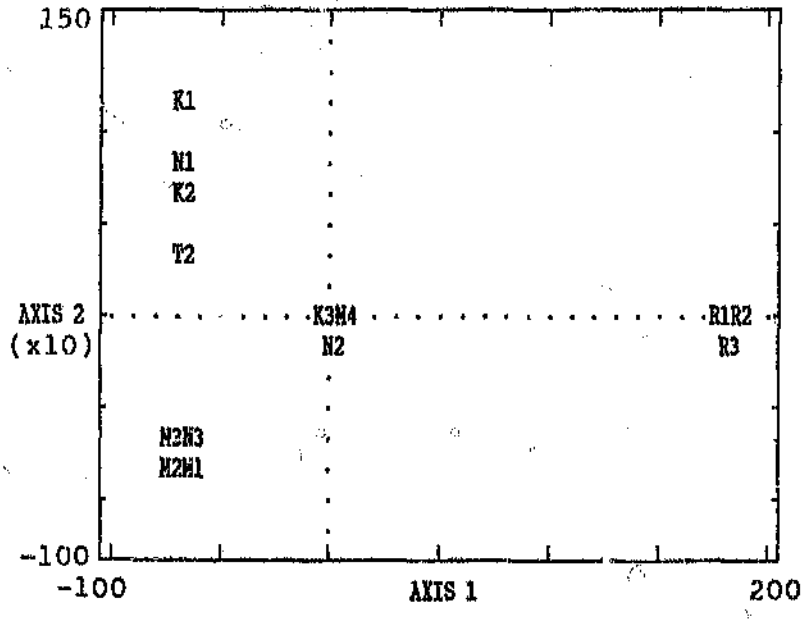


Figure 3.19. Detrended correspondence ordination of leaf:chamber temperature ratio for the woody component expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.598, 0.354, 0.129 and 0.023. Abbreviations are presented in ABBREVIATIONS above.

3.7.6 Sclerophylly

The ordination of sclerophylly for the woody component (Figure 3.21a) indicates that K1 is very different from the other study sites. With or without the exclusion of the Albizia : Dichrostachys dominated site (K1), neither a nutrient nor a moisture gradient was detected. The Acacia dominated dry sites (R2 and R3) were grouped with the other Acacia dominated sites (M1, M2, M3, N3 and T1). This observation is considered unique when comparing this ordination to ordinations of woody traits discussed above.

The exclusion of K1 (Figure 3.21b) from the ordination procedure, emphasizes groups of sites of similar leaf morphologies within the woody layer. The lower left hand sector of the ordination (Figure 3.21b) reveals a group of sites dominated by microphyllous plants, whereas the top left hand sector reflects sites dominated by nanophyllous woody plants. The right hand side of the ordination diagram reveals a cluster of sites dominated by mesophyllous plants. The presence of a nutrient gradient was not evident within the ordination space.

The first axis of the ordination of sclerophylly for the grass layer (Figure 3.22) represents a strong moisture gradient between the dry sites (R1, R2 and R3) and the moist sites (K2, K3 M3, M4 and N2). The presence of a soil nutrient gradient was not evident.

3.7.7 Succulence

The ordination of succulence for both the woody and grass components was distinctly similar to that of sclerophylly (Figure 3.21, Figure 3.22) in both pattern and magnitude of Eigenvalues for the four ordination axes. Interpretation of succulence will thus be similar to that of sclerophylly.

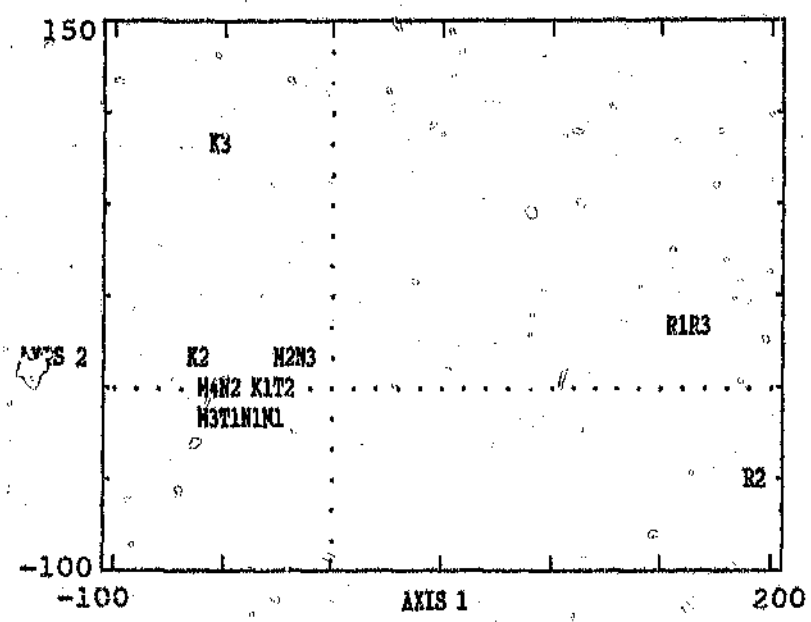


Figure 3.20. Detrended correspondence ordination of leaf:chamber temperature ratio for the grass layer expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.652, 0.378, 0.184 and 0.043. Abbreviations are presented in ABBREVIATIONS above.

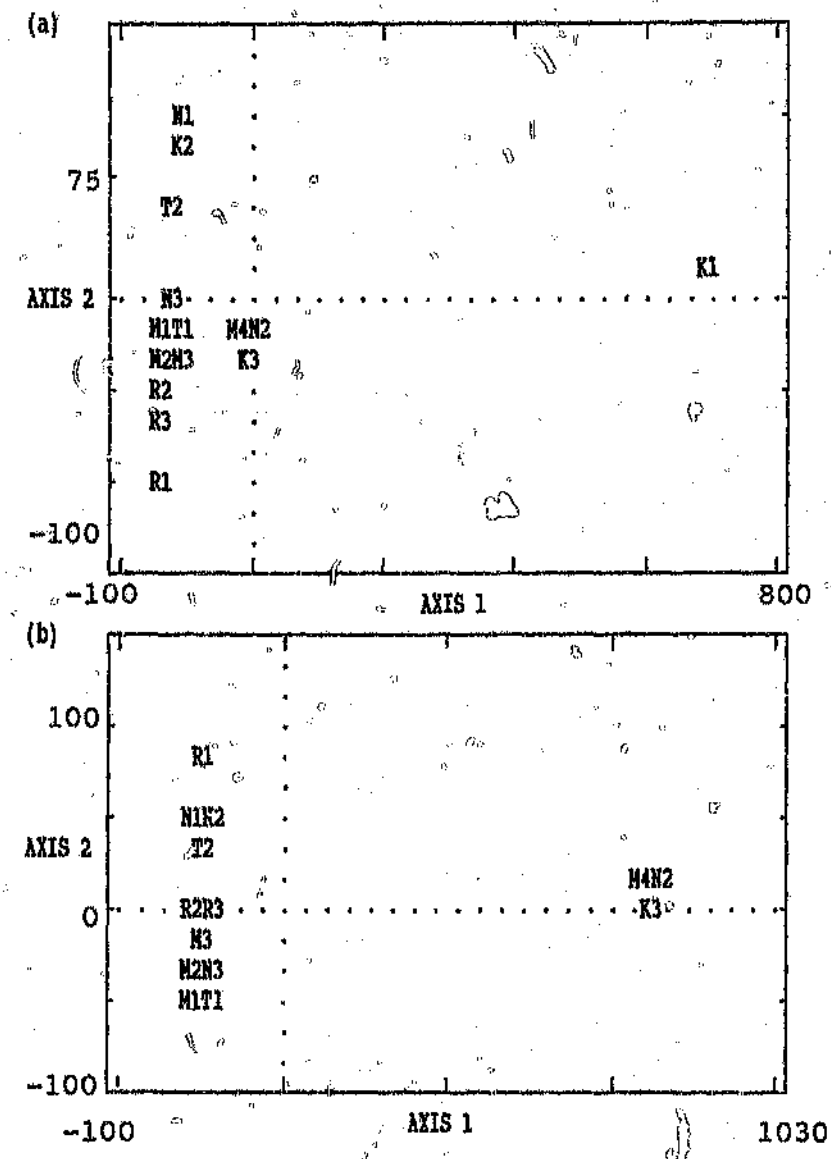


Figure 3.21. Detrended correspondence ordination of sclerophylly for the woody layer, expressed as a function of the total biomass of each study site. Ordination (a) includes all sites, whereas, ordination (b) excludes site K1. Eigenvalues for the four axes are 0.586, 0.384, 0.131 and 0.015, and 0.523, 0.218, 0.109 and 0.015. Abbreviations are presented in ABBREVIATIONS above.

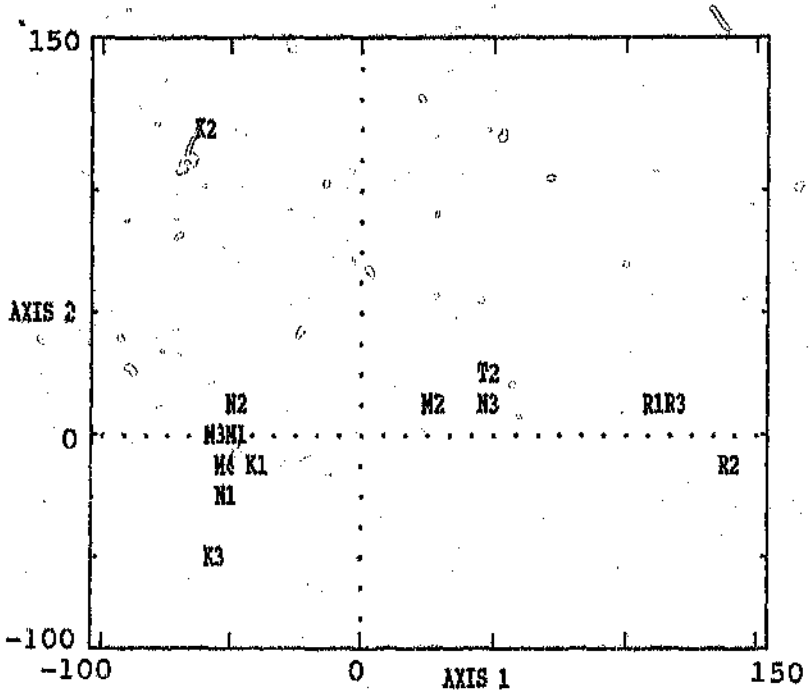


Figure 3.22. Detrended correspondence ordination of sclerophylly for the grass component, expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.587, 0.388, 0.134 and 0.015. Abbreviations are presented in ABBREVIATIONS above.

3.7.8 Turgid : dry weight ratio

The interpretation of the leaf turgid : dry weight ratio ordination (Figure 3.23) for the woody component is similar to that of sclerophylly and succulence. An interesting difference is the separation of the Acacia nigrescens dominated sites (T1 and M1) from the other Acacia dominated sites (Figure 3.23b).

Ordination of leaf turgid : dry weight ratio for the grass component (Figure 3.24) indicates a strong moisture gradient along the first axis. A nutrient gradient was not detected within the ordination.

3.7.9 Woo[illegible] bark thickness

The ordination of bark thickness (Figure 3.25) did not indicate the presence of either a nutrient or a moisture gradient (cf Table 3.1).

3.7.10 Grass lamina breaking strength

The first axis of an ordination on the lamina breaking strength (Figure 3.26) indicates a presence of a strong moisture gradient ranging from the dry sites (R1, R2 and R3) to the moist sites (K2, K3, M3 and M4), with the intermediate moisture sites between the two (cf Table 3.1). The presence of a nutrient gradient was not evident within the ordination space.

A summary of the inter-site ordinations is given in table 3.2.

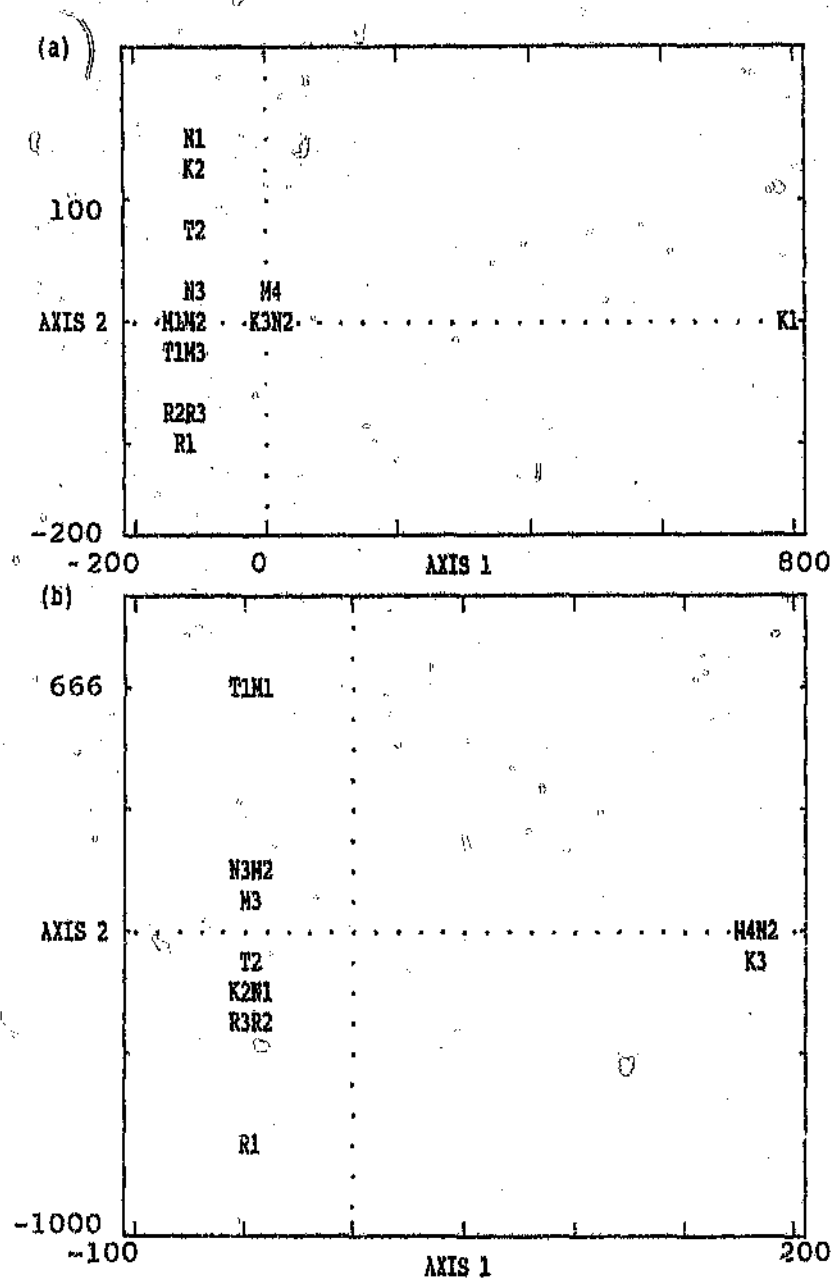


Figure 3.23. Detrended correspondence ordination of leaf turgid : dry weight ratio for the woody layer expressed as a function of the total biomass of each study site. Ordination (a) includes all sites, whereas, ordination (b) excludes outlier site K1. Eigenvalues for the four axes are 0.567, 0.334, 0.162 and 0.081, and 0.624, 0.398, 0.153 and 0.063 for (a) and (b) respectively. Abbreviations are presented in ABBREVIATIONS above.

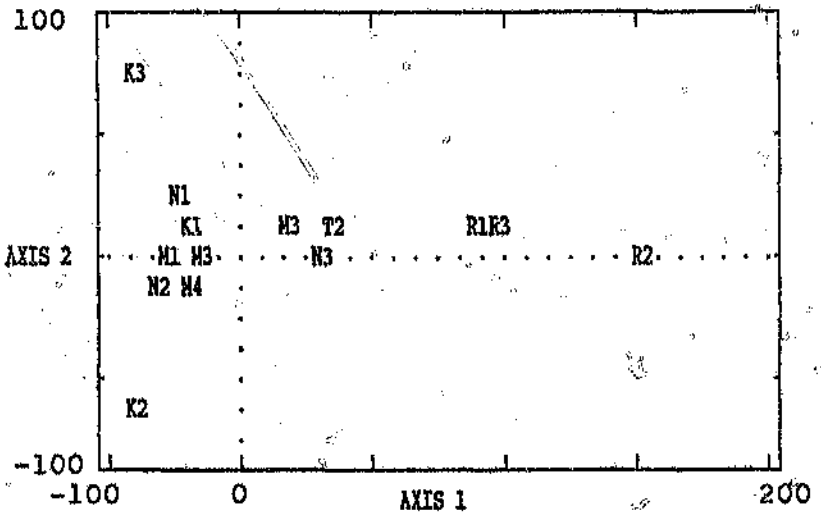


Figure 3.24. Detrended correspondence ordination of leaf turgid : dry weight ratio for the grass component expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.595, 0.216, 0.123 and 0.017. Abbreviations are presented in ABBREVIATIONS above.

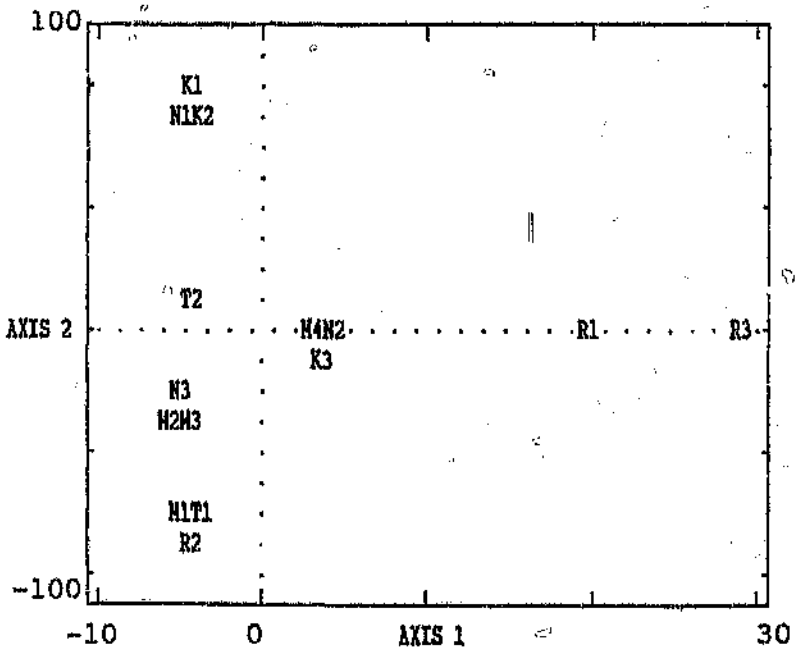


Figure 3.25. Detrended correspondence ordination of bark thickness expressed as a function of the total biomass of each study site. Eigenvalues for the four axes are 0.652, 0.429, 0.171 and 0.021. Abbreviations are presented in ABBREVIATIONS above.

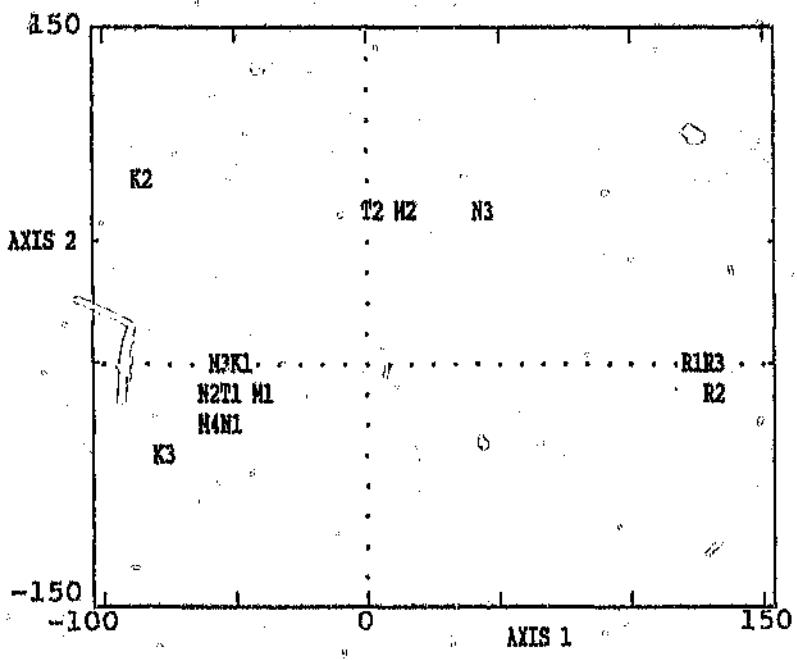


Figure 3.26. Detrended correspondence ordination of tensile strength for grass lamina, expressed as a function of the total biomass of each study site. Ordination (a) includes all sites, whereas, ordination (b) excludes outlier sites R1-3. Abbreviations are presented in ABBREVIATIONS above.

Table 3.2. Presence (✓) or absence of plant available moisture and nutrient gradients within the inter-site ordinations for both the woody and grass components. Plant attributes are given in ABBREVIATIONS above (X = no evidence of the particular gradient, ✓ = evidence of the particular gradient and ± = particular gradient is weakly evident within the ordination space)

	Woody		Grass	
	Moisture	Nutrient	Moisture	Nutrient
Pmax	X	X	✓	X
QE	✓	X	✓	±
DR	X	X	✓	X
CP	X	X	✓	X
LTCT	±	X	✓	X
SCL	X	X	✓	X
SUC	X	X	✓	X
RAT	X	X	✓	X
BARK	X	X	±	-
BREAK	-	-	✓	X

4.0 DISCUSSION

4.1 COMMENTS ON LIMITATIONS

4.1.1 Pseudoreplication

Hurlbert (1984) criticizes ecological studies that use inferential statistical tests in which replication is absent, or where the replicates are not statistically independent. This criticism is well founded, but does not apply, in principle, to the present study. A trade off exists between concentrating on a small number of study sites with a high degree of replication, and a larger number of sites with little or no replication. The replication of the sampling strategy within a limited number of study areas sacrifices generality for robust statistical inference.

Criteria laid down by Hurlbert (1984) to avoid pseudoreplication cannot be met in this study, as both rainfall and soil nutrient gradients cannot be replicated in the field. Inferential statistical techniques were, however, excluded from the analysis according to Hurlbert's recommendations. The comparison of means test used to detect 'seasonal' variation of the attributes should be interpreted in the light of the sampling strategy.

4.1.2 Altitudinal differences

Altitude differences (Friend and Woodward 1990, Friend et al. 1989, Ledig and Korabobc 1983) which are measured in indices of barometric pressure (Gale 1973), temperature (Billings 1974a 1974b, Bunce 1983, Eagles 1967, Slatyer 1977) or CO_2 concentrations (Cooper 1986, Gale 1986), have a marked influence on a variety of plant ecophysiological traits.

These studies, and others, concentrate on extreme altitudinal differences, for example the Himalayas and Alps (see Müller 1982). The elevation of these mountains span approximately 300 to 2000 m and 300 to 3000 m in height, respectively. Changes in plant traits over 800 m altitude, as has occurred with the present study, remains uninvestigated in the savannas at large. Those studies that investigated the effects of a change in barometric pressure with altitude offer little guidance on what may exist under the South African conditions. Projections from data presented in the above mentioned studies over an 800 m altitude change may be minimal.

4.1.3 Carbon dioxide concentrations

Billings et al. (1961), Edwards and Walker (1983), Körner and Diemer (1987), and others, have noted changes in photosynthetic rates with extensive fluxes in ambient CO_2 concentrations. Many of these studies have concentrated on describing the photosynthetic rates of various plant species along a CO_2 gradient. The models developed from these studies describe photosynthesis as a CO_2 gradient across a complex of leaf diffusion resistances. These models were interpreted, however, to be insensitive to 4 - 5% variation about ambient CO_2 concentrations as applied in the present study (see section 2.2.1.1). Thus, correction of the CO_2 flux was omitted from the study to avoid unnecessary manipulation of the photosynthetic data.

4.1.4 Secondary determinants

The influence of fire and grazing on different life-forms (or communities) varies greatly with different climatic and edaphic situations (see Friedel et al. 1988, Friedel and Blackmore 1988, Westoby 1981). The criteria, lightly grazed and a fire frequency of five years, as adhered to in the

present study, may not be equivalent for all the study sites. The magnitude of the inequivalence between the study sites cannot be ascertained without both intensive and extensive investigations of these variables. An additional study of this scale falls beyond reasonable limits of the present study.

4.1.5 Water availability and scale differences

A time scale difference exists between the Lineacre (1977), and the Zucchini and Adamson (1984) models. Scholes (unpublished) combines the two models, together with soil texture, to produce the bucket type water index model. Both Lineacre (1977) and Zucchini and Adamson (1984) discuss the limitations of their respective models. The combination of different temporal and spatial scales, and the limitations of the two models, however, were not addressed in the Scholes model (Scholes pers. com.[6]). There are various studies that use rainfall gradients (Cowling and Campbell 1980, Cowling and Campbell 1983, Friedel et al 1988, Morrow and Mooney 1974, Werger et al 1987, Werger and Ellenbroek 1978) to determine water availability. These studies, however, use mean average rainfall exclusively as measured at selected meteorological stations. The incorporation of both soil texture and the historical aspect of rainfall, despite the limitations discussed, is superior to a single rainfall figure from which to infer plant available moisture.

For the purposes of this study, it was assumed that a reliable correlation exists between the number of days available for plant growth (as calculated by the Scholes model) and plant available moisture. Confidence in the Scholes model was augmented due to the fact the local ecologists and managers agreed that this model ranked the study sites that occurred in their respective areas accurately, in terms of perceived water availability. Any

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discrepancies that might exist between the actual water availability and its index, as used in this study, may be not critical in pursuing the objectives.

4.1.6 Available nutrient indices

No universal plant available nutrient index exists. Nobel (1989) tackled the subject by deriving a nutrient index for agaves and cacti. He linked productivity of Agave derserti and A. tequilana to soil concentrations of N, P, K, B, and Na and found marked differences in nutrient exploitation between the two species. This observation suggests that each plant species may require a dedicated fertility index . Due to the high species diversity encountered within a savanna environment, this approach to determine an accurate index of fertility remains impractical.

Three 'generalist' approaches (see sections 2.2.2 and 3.4 above) to a nutrient index were considered. Each of these have marked limitations.

4.1.6.1 Soil elemental levels

Chemical analysis can only be viewed as a function of the techniques used (ie acid digestible nitrogen or resin extractable phosphorus). It can, however, be assumed that a positive relationship exists between the concentration of the element extracted in the analysis and plant availability (see Figure 3.5). The elements as single 'independent' units do not provide sufficient detail to derive a suitable nutrient index.

4.1.6.2 Ecologists' ranks

Many factors other than a table of chemical data and a brief description of the vegetation influence the fertile / infertile perception of the local ecologists and managers.

Both the ecologists and managers were, however, consistent in ranking their areas locally and the ranking of their areas (unknowingly) using the data supplied. As with the soil elemental levels, the value of the ecologists' ranks was to contribute to the confidence in selecting a parameter which may be interpreted as a reliable index of plant available nutrients.

4.1.6.3 Potential production estimate

The potential biomass production index study is subject to a number of criticisms. The three fundamental limit tions of the study are given below.

The biomass production of Panicum maximum may not be representative of either the herbaceous or the woody components. The present study assumes that plants (or groups thereof) are functionally dissimilar. Thus, the exploitation of soil nutrients between two plants or plant groups, may also be dissimilar.

Within the study of potential production, the Mixed Acacia Savanna (M1) soils received significantly less water than the soils from the other study sites (see Feuchtenbeiner-Walsh 1990). Potential production estimates for this site were estimated using soil nitrogen concentrations (Nobel pers. com.[5]). This weakens the predictive power of this technique in determining a plant available nutrient index.

The presence of mycorrhizal fungi and nitrogenase activity, or both, may dramatically alter the perceived fertility of soils at a particular study site (see Rehder and Schäfer 1978, Zietsman et al 1988). The dominant trees in both the Burkea and Acacia communities, at Nylsvley (N1 and N3), are legumes. Neither community has been demonstrated to support nitrogen fixing bacteria, despite extensive investigation

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(Zietsman et al. 1988). Mycorrhizal fungi have, however, been found to occur in both communities (Dames pers. com.[7]). The presence of either mycorrhizal fungi or nitrogen fixing bacterial associations, in the remaining study sites, were not determined to occur in the communities sampled. The presence or absence of microbial activity, which enhance nutrient absorption, may alter the assumed fertility of a study site to an undetermined extent. In mitigation, however, the presence of the microbial activity of this nature, would not markedly alter the dystrophic : eutrophic poles of the assumed nutrient gradient (see Table 3.1).

The absence of a meaningful or comprehensive plant available nutrient index is not seen to impede the identification of 'nutrient based' gradients within the present study. The objectives of the present study solicits a mere detection of potential nutrient gradients, rather than a site-for-site inventory.

4.1.7 Time scale conflicts

By definition, the plant traits used in this study were derived over ecological and evolutionary time scales, ie plants are products of a historical set of environmental constraints. These constraints may not now be present in equivalent intensities. Hence, an obvious scale conflict may manifest when inferring causal mechanisms or even simple correlations between a particular plant trait and measured environmental variables (see Larcher 1983, Wiegert and Kozlowski 1984). The present study is not immune from criticism that originates from bridging evolutionary time scales. Nonetheless, the constraints perceived today are products of their ancestral constraints. If correlations can be perceived between the present day constraints, then a functional classification is possible. If not, a derivation of a functional classification would be unachievable.

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4.1.8 Season

The possible variation of plant traits in response to seasonal variation of climatic conditions (rainfall, temperature, day length, etc), or to a change in the internal environment of the plant (seed set, aging, senescence, etc), or both, presents an additional time scale conflict. The concept of variation of ecophysiological traits throughout a season or life span of the plant has not been investigated in the savanna environment. Grass lamina breaking strength has, however, been recorded to increase towards the end of autumn and winter (see Theron and Booysen 1968). This was observed despite an adherence to the selection of first fully expanded leaf material. The variation of lamina strength and the other traits investigated effectively negates the present study's ability to pursue the objectives.

The change in attributes from the beginning to the end of the growing season indicates that instantaneous or point measurements of functional attributes can no longer be relied upon. The measurement of these attributes has to be modified to incorporate an element of time, eg the range of the plant trait over the entire season. The aspect of seasonal variation of ecophysiological traits is discussed in greater detail in section 4.5 below.

4.2 CONCLUSION TO LIMITATIONS

A considerable number of limitations have been identified in the present study. These limitations vary in significance, and those which may have profound repercussions on the conclusions drawn, are discussed. The limitations discussed above (other than the effect of season) do not conflict detrimentally with the methods used to fulfil the objectives. The benefits of the exercise in pursuing the objectives, despite the large number of limitations, in particular the

seasonal variation of the plant traits, far exceed the cessation of the present study (see Loehle 1987).

4.3 NUTRIENT GRADIENTS

A wide variety of techniques are available to determine an index of nutrient availability. Amongst these techniques are four which have been used in this study. These include; studies that consider soil type and parent material, experience of local ecologists, chemical analyses and calculations of potential biomass production.

The inference of soil fertility from bot[illegible] material and soil type has been demonstrated to be u[illegible] geographical scale (Bell 1982, East 198[illegible] Riedel et al 1988) but is, however, inadequate for the finer scales required for functional studies. Soil nutrient distribution is markedly patchy within the landscape despite a homogeneous parent material. Even at a fine scale of sample sites less than 50 m in diameter, nutrient discrepancies may vary ten fold (see Blackmore et al 1990). Reasons for the lack of soil nutrient homogeneity are numerous. These range from aspect differences (Goodman 1988), to the deposition of soil fine fractions (Tinley 1981), to the impacts of Iron Age Man (Blackmore et al 1990) on the landscape.

The initial selection of study sites, in the present study, was based on the experience (gut feeling) of the ecologists in the field. The lack of formal documentation of this knowledge base, in terms of soil fertility, should not deter its use. The subjective ranking of the soil samples, provided by local ecologists, was used indirectly in the selection of a potential nutrient availability index (see below).

The inference of soil fertility from soil elemental concentrations has been widely used (Blackmore et al 1990, Cowling and Campbell 1983, Mooney and Harrison 1972, Tolsma et al 1987, Walker and Knoop 1977). Determining the elemental

pool within a soil sample or profile down-weights the importance of one or more limiting elements, and emphasizes the value of, for example, nitrogen, phosphorus and potassium. The elemental form in which a nutrient may occur and the various combinations in which they are found, are considered important in determining soil fertility (cf ecologists' biases : Figure 3.5). Nobel (1989) addressed the role of selected soil elements in the derivation of a nutrient index for agaves and cacti. He integrated iterative biomass estimates for various concentrations of soil N, P, K, B and Na elements. A nutrient availability model of this intensity is needed, but remains impractical for the savanna environment given the large numbers of species.

A potential biomass production estimate is probably the simplest subjective technique available. It may circumvent the complexity and intensity of the Nobel (1989) approach, but it does, however, suffer two major drawbacks. The first is the limited number of plants used. A comprehensive study would include a minimum of 30 to 50 species, depending on the size of the study, and the plant diversity experienced. The second is that woody vegetation is precluded from the estimate. Woody plants, are in many respects, structurally dissimilar (ie rooting distribution - Rutherford 1982, nutrient demand - Frost 1985, etc) to grasses, and therefore inferences from an index derived from grasses to the woody layer is difficult and uncertain. The potential production estimate, within the boundaries of the present study, concurs with the 'gut feeling' of the local ecologists, and positively weights the value of both nitrogen and phosphorus (Nobel pers com[5]). It also incorporates the presence of limiting elements into the estimate.

It is tempting to go to great lengths to measure a nutrient index within a micro gram of each nutrient (see Nobel et al 1988, Nobel 1989) to determine, with great accuracy, the

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5 Dr PS Nobel. Department of Biology and Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles

fertility difference between samples. There can be no extrapolation of soil chemical data from a soil sample, after its removal, drying, sieving and sub-sampling, to a plant community scale. This method cannot be rewarded with a worthier use other than determining the relative nutrient concentrations between soil samples. Both plant nutrient demands (see below) and soil nutrient concentrations are bound to vary with time (see Tolsma et al 1987). This may have repercussions in determining a plant based index under the constraints of a single sampling technique. An accurate determination of a nutrient index for a plant community would thus entail the determination of the nutrient index in situ, using both undisturbed plants and soil over a significant proportion of the plant community, for at least an entire season.

The degree of refinement of either the nutrient (or moisture) availability index need not supersede the precision needed to meet the objectives. The objectives do not require fine graduations within either index. No progress is made if the relevance of the functional study is limited to excessive expenditure of time and finances. The financial investment in increasing the detail of both nutrient and moisture indices would be prohibitive for both the present study and future studies.

4.4 PLANT ATTRIBUTE RANGE

Objective (i) : To compare the variation of plant traits that occur at individual sites to that of the biome.

Until recently, a significant proportion of ecological research in South African savannas, has been directed under a model savanna (eg Nylsvley; Huntely pers com[9]). These areas were selected so as to represent, at least structurally, a vast majority of the elements that occur within the savanna

9 Mr B Huntely. National Botanical Institute. Cape Town.

biome. Evidence presented in section 3.2 above suggests that the variation of both structural and functional plant traits in one or two study sites equals that of the entire biome. This in turn implies that for these sites no formal or specialized strategies have evolved. This observation is not, however, ubiquitous, as the sites, that equalled the variation of the biome were not consistent for each trait studied. It could therefore, be conceived that, for an intensive study of a single plant trait, one or two sites could be selected which would represent the entire biome. The cost, in terms of finances and man hours, would preclude the option of sampling a wide variety of savanna communities for the few which would represent the entire biome, being exercised. Literature supporting these observations have not been procured. Information available on the variance of plant traits is dominated by monospecific studies, in which each species is represented by a number of individuals either at a fixed point or along a defined gradient. These studies address, in broad terms, hybridization (see Stace 1975, 1980), phenotypic plasticity (see Baldocchi et al. 1987, Black 1971, Camerick and Werger 1981, Chapman 1973, Cody and Mooney 1978, Friend and Woodward 1990, Givinish and Vermeij 1976, Knight and Loucks 1968, Pearcy et al. 1987, Stace 1980, Werger and Ellenbroek 1978) and taxonomy (see Bradshaw 1962, Chapman 1973, Stace 1980). Studies that include a number of diverse species fail to capitalize on 'study site' variance and as a result, interpret their data using mean points (see Gillison 1981, Friend and Woodward 1990). Thus the total variation of plant traits, independent of species, and the relation of the variation to environmental gradients remains uninvestigated. This observation has important consequences in terms of deriving a functional classification of savanna plants. The variation of a plant trait would, therefore, need to be determined in toto before its inclusion into a classification could be considered.

Plant ecophysiological traits that are directly related to plant structure (eg sclerophylly, succulence and leaf turgid : dry weight ratio) indicate a functional difference between

woody plants and grasses. Traits that relate to plant physiology, however, do not follow a woody : grass split. Thus the ratio of structural to functional related traits in a classification, such as that proposed in the present study, becomes vitally important. A bias in the selection of plant traits will have profound effects on the outcome of the classification.

A highly popularized difference between C3 plants and C4 grasses is the elevated photosynthetic rates of the latter (Black 1971, Edwards and Walker 1983, Noggel and Fritz 1983, Siegelman and Hind 1978). The present study encompassed woody C3 plants and grasses having C4 photosynthetic pathways (Ellis et al 1980, Vogel et al 1980). The initial discovery of the C4 pathway raised a variety of questions; Why did this pathway evolve? What kinds of plants have evolved a C4 photosynthetic pathway? What are the physiological and anatomical differences between C4 and C3 plants? In which plant communities do these plants occur? What is the proportion of C4 to C3 plants in these communities? What is the agricultural significance of a C4 photosynthetic pathway? The questions that had been ignored within the savanna environment are as follows; Are these differences measurable in situ? Are traits that are related to photosynthesis, other than the maximum potential rate, different between C4 and C3 plants? The present study has demonstrated that, for savanna plants in situ, (1) the maximum potential photosynthetic rates of C4 grasses may be only marginally higher than the woody (C3) plants measured, and (2) the remaining physiological and structural traits (see Figure 2.2) do not follow a C3 : C4 division.

Although the physiological traits used in the present study (eg photosynthesis) have been extensively studied by other researchers, the structural aspects (eg lamina strength and bark thickness) have not been as well documented. The studies that have pioneered the use of leaf consistence in ecological studies (Bond 1981, Cowling and Campbell 1983, Loveless 1962 Werger and Ellenbroek 1978) have concentrated on either

defining leaf consistency or relating changes in leaf consistency to an environmental gradient, or both. Studies of grass lamina strength (O'Reagen pers com[10], Martens and Booysen 1968) have concentrated on the pastoral significance of the tensile strength of grass leaf blades. No literature, other than purely anatomical studies, involving bark thickness is available.

These observations lead to speculation that the functional approach to vegetation classification has not evolved sufficiently to attract innovative research. Two criteria support this speculation. The first considers the omission of a statement on functional significance within conclusions drawn in these studies, while the second highlights the absence of a wide variety of ecophysiological traits in the current literature.

4.4.1 Conclusion to Plant Attribute Range (Objective I)

The solution to the dilemma presented in Objective (i) (section 1.1) is complex. The results from a limited number of the sites studied indicate that plant traits may be randomly distributed, whereas, the majority sites indicate to the contrary, ie that similar strategies may exist. The difference in two categories of sites may be attributed to the differences in the intensity of the selectional pressures that played a role in trait expression. If this conclusion holds true, then the mean may no longer be meaningful in functional studies, however, the variance itself may prove to be paramount in understanding functional variation within plant communities.

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4.5 SEASONAL CHANGE

Objective (ii) : To determine the consistency of ecophysiological traits, as functional characters, over the span of a single growing season.

Terrestrial studies that investigate plant traits in terms of their occurrence or magnitude, as those cited in the present study (other than Theron and Booysen (1968)), fail to address the significance of seasonal fluctuations within their data. The methods described in the majority of cases (eg Baldocchi et al. 1987, Butler 1954, Friend and Woodward 1990, Körner and Diemer 1987, Loveless 1962, Pearcy et al. 1987), reflect that data collection spanned at least an entire growing season. If the data presented within these studies have been collected over an extended period, then one of two assumptions may be drawn. Two conclusions would then naturally follow, namely;

(1) Sample variance in these studies exceeds seasonal variation of that trait.

Evidence presented in both Figure 3.4 and Appendix B, indicates that sample variation does not consistently exceed seasonal variation and that significant fluctuations may occur in the plant traits between the beginning and end of a growing season.

The assumption that sample variation exceeding seasonal variation of a particular plant trait cannot, therefore, be relied upon.

(2) Variance presented in the literature in terms of standard deviations, for each plant attribute, includes seasonal variation (ie plants were sampled continuously throughout the season, although not indicated in the methods).

The standard deviations, noting the absence of a species overlap between the present and referenced studies, are

of an equivalent order of magnitude without the inclusion of seasonal variation. This suggests that seasonal variation has not been included within the data presented within these studies.

By deduction, two sampling strategies may be assumed in the above referenced studies. The first, data collection was by means of sampling successive study sites, as with the present study. The second, entire plants or parts thereof were collected and transported to a laboratory and measurements made (eg Cowling and Campbell 1983). Both approaches to data collection fail to address the importance, or significance, of a seasonal variation of plant traits studied.

The principle aim of the study by Theron and Booysen (1968) was to quantify changes in tensile properties of a number of indigenous grasses. They indicated that the tensile strength of grass laminae showed little change over a growing season but increased significantly towards the end of the season. The present study supported this observation despite the adherence to the selection of first and second fully expanded grass laminae (not followed in Theron and Booysen) as well as the notable delay of the dry season. The failure of the remaining references cited in the present study (eg Friend and Woodward 1990) to realize the significant influence of a change in season on the expression of both structural and functional attributes is misleading. The demonstration of the importance of seasonal change in the expression of plant traits in the present study highlights the need for a thorough investigation of each aspect of data collection.

4.5.1 Conclusion to Seasonal Change (Objective II)

The conclusions, drawn from the marked influence that season appears to have on the expression of the majority of plant traits, are twofold.

The first concerns the ability of the present study to achieve the goals discussed in section 1.2. The marked influence of the lapse of time between sampling periods indicates that objectives iii to v of the present study cannot be adequately addressed. Grounds for the potential exclusion are based on the inherent assumption that plant traits would remain constant during the sampling period. The continuance of the study, however, has been motivated for in terms of an academic exercise, see section 4.3 and 4.1.11 above.

The second indicates that the success of functional studies relies heavily on the inclusion of an element of time in the delimitation of functional traits.

4.6 DIRECT GRADIENT ANALYSIS

Objective (iii) : To determine whether ecophysiological traits vary predictably with a change in either available moisture or nutrients, or both.

Changes in environmental constraints (both temporally and spatially) are important in causing genetic and phenotypic differences within plant populations (eg Baldocchi et al. 1987, Billings 1974a 1974b, Bunce 1983, Chapin et al. 1987, Cody and Mooney 1978, Cooper 1986, Cowling and Campbell 1983, Eagles 1967, Friend and Woodward 1990, Friend et al. 1989, Gale 1986, Ledig and Korobobo 1983, Slatyer 1977). It has been debated that differences in plant attributes along environmental gradients appear to be of selective advantage. This argument, however, assumes that for each set of environmental constraints a single set, or a select few, of genetic and phenotypic solutions (strategies) would prevail. Evidence provided in the present study (see section 3.5 above) indicates that no distinct pattern exists between the two dominant determinants, viz. soil moisture and nutrients (see section 1.0 above), and the magnitude of the expression

of plant traits. These results are in accordance with the strong warnings of both Larcher (1983), and Wiegert and Kozlowski (1984) that both morphological and physiological responses of plant traits may reflect historical information about environmental influences which may not pertain to the site(s) as they are at present, reducing correlations between the magnitude of the plant trait and the intensity of an environmental trait to irrelevalence (see section 4.1.8 above).

The misidentification of the determinants or the underestimation of either (1) synergism between determinants or (2) their mode of action on both structure and function, inhibits the derivation of a simple functional model. It is therefore clear that the simple statement of suspected determinants (see Frost et al. 1986) provides little information to functional studies.

4.6.1 Conclusion to Direct Gradient Analysis (Objective III)

The solution of a functional approach to vegetation classification cannot be resolved into a simple model such as that presented in Figure 1.1. The pattern that would contribute to this model has not been shown to occur using a direct gradient analysis technique. The pattern, should it exist, may be masked by (a) an inherent adaptation of the plant traits to an ancient set of environmental constraints, (b) by the insensitivity of the methods exercised in the present study to additional unknown gradients, or (c) a lack of an adequate understanding of the hypothesized determinants themselves.

4.7 INTER-SPECIES COMPARISON

Objective (iv) : To determine functional similarities (or differences) between plants / species occurring at different points on the moisture / nutrient plain.

A large number of studies (eg Cody and Mooney 1978, Cowling and Campbell 1983, Parsons and Moldenke 1975) have demonstrated, to varying degrees, convergence of seemingly floristically diverse species along marked climatic and edaphic gradients or in analogous but spatially separated ecosystems. These illustrations provide support for the concept that plant communities, ecosystems and biomes consist of a range of functionally similar species.

The basic assumption that plants which share similar attributes may be grouped into guilds or functional groups is not, however, clearly evident from the present study. The first and foremost feature of the clustering of species with respect to their attributes, particularly the herbaceous layer, is the tendency of the species to occur at a nodal or mean point within a PCA ordination space. This limits the possible occurrence of meaningful variation, and hence functionally dissimilar guilds remain unidentified. This in turn suggests that the species studied, in the present study, are inherently similar and have not diverged sufficiently for functionally independent groups of plants to have evolved. This observation is in direct contrast to the findings of the studies in the literature as discussed above.

Despite the similarity of woody plants in the present study, an aspect of a simple structurally based classification, in terms of leaf size, was evident. It has long been realized that shapes and sizes of angiosperm leaves reflect adaptations to environmental conditions (Bailey and Sinnott 1916, Raunkiaer 1916). This relationship, in recent literature, has been expressed more quantitatively using multivariate analyses (Box 1981, Cowling and Campbell 1980 : 1983, Gale 1973, Gates 1968, Gillison 1981, Givinish and

Vermeij 1976, Knight and Loucks 1968). Predictions in leaf size and shape along environmental gradients have been based on water economy (Cowling and Campbell 1983, Knight and Loucks 1968, Parkhurst and Loucks 1972, Pickett and Bazzaz 1976, Werger and Ellenbroek 1978, Werger et al 1987), soil fertility (Cowling and Campbell 1980 : 1983, Loveless 1962, Morrow and Mooney 1974) and photosynthetic performance (Baldocchi et al 1987, Black 1971, Friend and Woodward 1990, Pearcy et al 1987). The observation of recognizable leaf size/shape classes within the woody component of the present study is particularly significant as the association was not a product of measured leaf size and shape, but the product of both morphometeric and functional traits. It may be obvious, but well worth mentioning, that similar evolutionary pressures may have acted independently on both structure (ie leaf shape) and function (eg photosynthesis) or that all plant attributes evolved simultaneously under a simple set of environmental constraints, or a combination of the two. Regardless of the nature and history of evolution of the plant and plant traits, a strong handshake, for the woody species, is perceived to exist between structurally and functionally based attributes.

The similarity between selected woody plants enables the concept of ecological equivalence to be addressed within the present study. The term 'ecological equivalence' was derived from the notion that two species may be ecologically substituted for one another (Cain 1939, Dirks-Edmunds 1947, Knight and Loucks 1968, Naveh 1967, Odum 1959). Woody species, in the present study, which were suspected of being functionally equivalent are Acacia nilotica and Dichrostachys cinerea, Meytenus senegalensis (see Figure 4.1) was seen to be equivalent to a number of microphyllus species, whereas Acacia mellifera was perceived to indicate functional tendencies towards both Grewia flava and Terminalia sericea. The occurrence of functional equivalence within the woody species that occur within the South African savanna highlights the importance of vegetation nomenclature and the

use of locally indigenous plants in reclamation, rehabilitation and restoration studies.

The classification of savanna communities using either dominant or indicator species (see Gauch 1986) that are functionally equivalent, provides little functional information. Classifications, therefore, unquestionably, should opt to include both indicator and dominant species within the description, so as to ensure comprehensive characterization of the community from a functional basis. The knowledge of functional equivalence for a wide range of savanna species would enable information derived from successful restoration studies to be capitalized upon. This process would then allow utilization of locally indigenous species in the restoration process, thus conserving the floristic integrity of the areas within and surrounding the restoration site (see Jordan et al 1987).

The lack of distinct guilds in the grass component indicates that, with respect to the traits covered in the present study, a large majority of savanna grasses are functionally interchangeable (ecologically equivalent). The inherent functional similarity of, and lack of divergence within the grasses suggests that a functional classification would be impractical. Should this observation prove consistent with all grass species that occur within the South African savannas, then no additional information is added to a description of a vegetation type (ie Burkea africana savanna), if the dominant grass species is included (ie Burkea africana, Eragrostis pallens savanna). Thus a vegetation type described as a Burkea africana, Eragrostis pallens savanna may perhaps be functionally similar to a Burkea africana, Heteropogon contortus savanna, and vice versa.

If the South African grasses are inherently similar, the question arises whether grasses that occur within other savanna biomes (eg Australian, Brazilian, East African savannas) are functionally similar to those that occur within

the South African savannas. Should the savannas of the world be functionally dissimilar, global conservation as well as movement of grass species between biomes become important issues requiring prompt attention. The loss of savanna communities (eg through the action of modern man), may then result in potentially functionally unique vegetation types being lost. This would require increased conservation status of savanna biomes (globally) in order for genetic, floristic and functional diversity to persist over time. Both the local and global conservation strategies as proposed by Anon (1990), and Walker and Dickson (1988) on global change would, hence, require significant modification. If, however, a large degree of functional overlap occurs between the different savanna biomes, current conservation strategies (eg Natal Parks Board Mission Statement 1991, National Parks Board Policy Statement 1991) would remain pertinent. Functionally under-represented communities, globally, would thus require identification and their conservation status increased to ensure their continuance over time. The development of a platform from which the similarities and differences between savanna biomes has been cited as an important objective of the IUBS/UNECO MAB programme on the Responses of Savannas to Stress and Disturbance (Walker and Menaut 1988).

The presence and absence of guilds in woody and grasses respectively, may indicate a need to split both vegetation management and conservation into two elements, so as to prevent a management action, in response to a change in one component, adversely affecting the functional integrity of the other. The presence of potential functional groups within the woody plants indicates promise in the derivation of a functional classification. The significance of changes in environmental determinants could then be addressed, as floristic changes may not necessarily indicate a functional change within a plant community. Functional information may provide the tools needed to assess the effectiveness and accuracy of exemplary savanna and grassland bench-marks provided by the Department of Agriculture.

4.7.1 CONCLUSIONS TO INTER-SPECIES COMPARISON (OBJECTIVES IV)

Comparative plant morphology has been utilized as one of the basic lines of evidence for the demonstration of convergent evolution. The argument indicates that morphology, which is said to be environmentally selected, reflects the functional adaptations of plants. Neith[illegible] divergence nor convergence of species into guilds have been demonstrated with the grass species. Evidence of convergent evolution is seen to occur within the woody component. The inherent similarity of the savanna plants denies, in the present study, the identification of meaningful strategies, which is in direct contrast to the conclusions of the literature cited.

4.8 INTER-SITE ORDINATIONS

Objective (v) : To evaluate functional differences between plant communities which occur within different plant available moisture and nutrient regimes.

Evidence supporting the phenomenon that plant communities growing under similar environmental constraints on a site basis have developed similar traits or strategies has been widely published (eg Baldocchi et al 1987, Black 1965, Cowling and Campbell 1980; 1983, Gillison 1981, Friend and Woodward 1990, Knight and Loucks 1968, Loveless 1962, Morrow and Mooney 1974, Parkhurst and Loucks 1972, Pearcy et al 1987, Pickett and Bazzaz 1976, Werger and Ellenbroek 1978, Werger et al 1987).

It is assumed within the present study, as with the current literature, that the majority of plants occurring at a particular site within a vegetation type, experience(d) similar environmental constraints. It would, therefore, naturally follow that a suite of plants occurring at one particular site would be functionally dissimilar to a suite of plants occurring at a different (in terms of past and

present environmental constraints) site. The major two determinants responsible for the dissimilarities, it is argued, are plant available moisture and available nutrients (Frost et al. 1986).

The ordination of attributes, in the present study, measured from a number of plants that occur at different points on the moisture : nutrient plane, do not indicate an overriding presence of both plant available moisture and available nutrient gradients.

There is little doubt that soil moisture, alone, played a significant role in the derivation of the grass attributes. This observation is consistent with the findings of Cowling and Campbell (1983), who reported distinct patterns along a moisture gradient for leaf consistence within the non-fynbos communities. The synergistic role of soil fertility in the observed patterns could not, however, be excluded when compared to fynbos communities occurring on highly dystrophic soils. It may, therefore, be surmised, that a cut off point may exist above which the moulding capacity of soil fertility becomes insignificant, and the soil fertility of South African savannas occurs above the cut off point.

Two questions arise; (1) Why is there a difference between the grass and woody components? and (2) Why do soil nutrient levels fail to have an overriding importance in determining the plant traits examined in the present study, given the persuasive argument presented by Frost et al. (1986)?

The entire complement of woody plants selected in the present study were mature. They would, therefore, be expected to have an extensive root system, drawing both moisture and nutrients from a large area (Rutherford 1982). The root systems of Burkea africana have been recorded to extend 40 m (Rutherford 1982) into nutrient rich patches (see Blackmore et al. 1990 and Scholes 1990) and Ruschia sp. was recorded to have penetrated 20 m deep into slightly moister soil layers (personal observation) at Vaalputs, North western Cape. The relative distribution of rooting material and volume of soil

exploited by woody and grass plants may provide the solution to the two questions cited above.

The relative amount of soil nutrient volume a grass species exploits is potentially on a similar scale to that of woody species (Figure 4.2), adequately matching both the structural and functional demands imposed by plant growth.

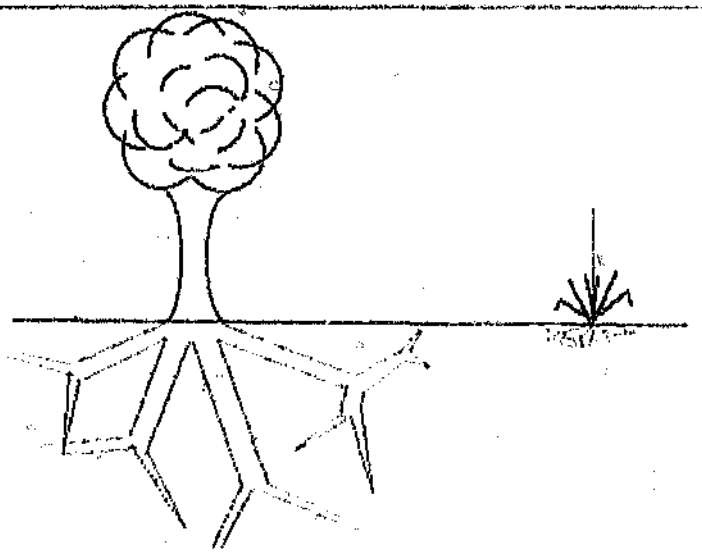


Figure 4.2 Distribution of woody and grass roots within the soil profile (see text for details).

Unlike the woody plants, grasses do not have equivalent access to moisture found in deeper soil horizons. It is, therefore, suspected that a far greater dependence is placed on rainfall by the herbaceous layer than woody plants. This conjecture is supported by the post-rain flush which savanna grasses frequently exhibit.

The repeated association of selected sites for all attributes measured, in the present study, despite the vast geographical separation of the sites suggests that one or more gradients are regulating the expression of the plant traits. The absence of these gradients, to which the attributes would have moulded, would have resulted in a random association for

each attribute measured. It is clear that one of these gradients operating on herbaceous layer may indeed be plant available moisture, but the determinants of the woody component remain unidentified. The inability to effectively identify the regulatory gradients in the expression of plant traits supports the idea that these gradients may not be linear and that thresholds may exist (see Cowling and Campbell 1983). Likewise, once the threshold is traversed, the moulding capacity becomes insignificant and is replaced by one or more different regulatory variables.

4.8.1 CONCLUSIONS TO INTER-SITE COMPARISON (OBJECTIVES V)

There exists little doubt that both structure and function of the grass layer are dependent on the availability of soil moisture. The level of correlation between the expression of the trails and the magnitude of available (inferred) soil moisture is not, however, sufficiently robust for a predictive model to be developed. The observation that soil nutrient concentrations do not appreciably regulate the expression of the grass trait measured in the present study was noted. The suggested regulatory role of this parameter is, therefore, challenged.

No correlation existed between the expression of traits of the woody component and intensities of either plant available moisture or nutrient gradients was observed. The role of these determinants in the expression of ecophysiological traits, within the woody component, has not met the expectations cited in the literature.

5.0 GENERAL CONCLUSION

The study was undertaken within the South African savannas to examine the prospect of a functional classification of savanna plants at an ecophysiological level.

A total of fifteen experimental sites were selected on the basis of rainfall, parent material, vegetation type and local ecologist's and manager's recommendations. Within each study site, plant species were selected on their ecological dominance, distribution and autecology. Various ecophysiological traits within broad areas of leaf photosynthesis, plant water potential and morphometric traits were selected. Plant water potential data were omitted from the study due to an inconsistency in the technique used. The water potential techniques use were, however, retained as the potential of this approach remains to be fully realized.

The primary objectives of this study were to (1) compare the variation at the plant community level to that of the savanna biome, (2) determine the constancy of the plant attributes investigated over the span of a single growing season, (3) determine whether the traits vary predictably with a change in either available moisture or nutrients, or both, (4) determine functional similarities between plants / species occurring at different points on the moisture / nutrient plane, and (5) evaluate functional differences between plant communities which occur under different moisture and nutrient regimes.

The present study highlights two broad categories (ie determinants and seasonal variation) that require both intensive and extensive investigation before meaningful criticism can be lodged at the relevance of a functional classification of South African savanna plants at an ecophysiological level. It is clear, however, that the savannas are, or have been, subjected to moulding environmental constraints. The assumption that the two

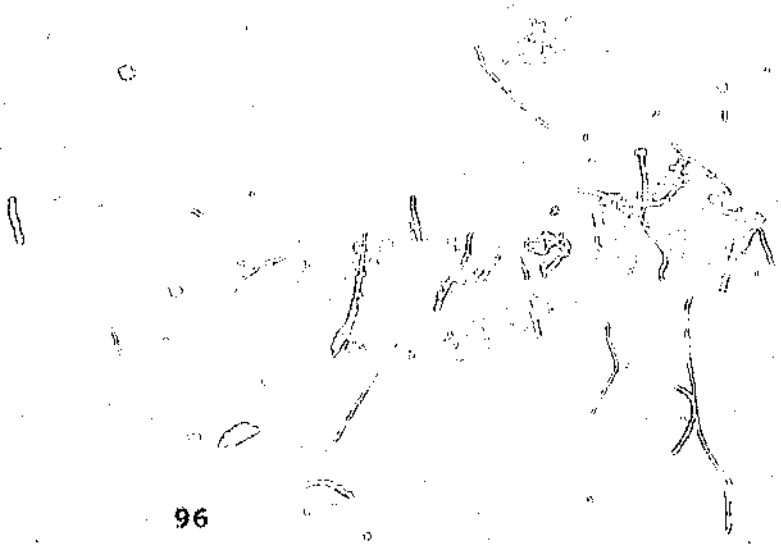
overriding constraints are most likely to be plant available moisture and available nutrients is not supported by the present study. Likewise the uniform intensity of the determinants throughout the savanna biome cannot be sanctioned. It is believed that cut off points operate and once these points are traversed a new set, or a new combination of determinants begin to govern. The likelihood of an ancient set(s) of determinants that no longer exist, that influence the relationship between plant trait expression and environmental gradients (diffusive causality), is cause for concern. The possible presence of diffusive causality continually inhibits an effective and meaningful examination of a functional approach to vegetation classification.

As with determinants, the influence of time or seasonal change on the expression of the plant traits requires close scrutiny. Attempts to standardize the sampling techniques used in the present study have not been effective in excluding the influence of seasonal change on the expression of plant traits. It is suspected that sampling methods will have to be extended from an instantaneous technique to one that encompasses the change in expression of the plant trait over the entire growing season. The derived functional classification would therefore embrace a plant attribute profile rather than the attribute being represented by a single observation. The influence of seasonal change on plant traits effectively prevented both inter-species and inter-site comparisons to be made. The reduction in the importance of a change in season on the expression of plant traits enables the present study to generate meaningful hypotheses and observations in the two categories.

Savanna plants, particularly the grasses, are inherently similar at an ecophysiological level although a recognizable pattern of leaf morphology (derived from characters other than leaf morphology) was evident within the woody component. The contrast between the inherent similarity of the grass and recognizable pattern in the woody layer may

suggest that future classifications of savanna plants should separate the components and derive a unique classification for each.

As a general conclusion, a functional classification of plants, at an ecophysiological level, remains in its infancy. Conclusions on the success of such an exercise would, therefore, be premature. Many conceptual and technical problems require solving prior to a functional classification being formally addressed. An alternative to the current floristic classifications remains, however, essential if understanding of the savannas is to be increased. The need of a classification which embraces information other than species composition far outweighs the research need to meet this mandate.



APPENDIX A

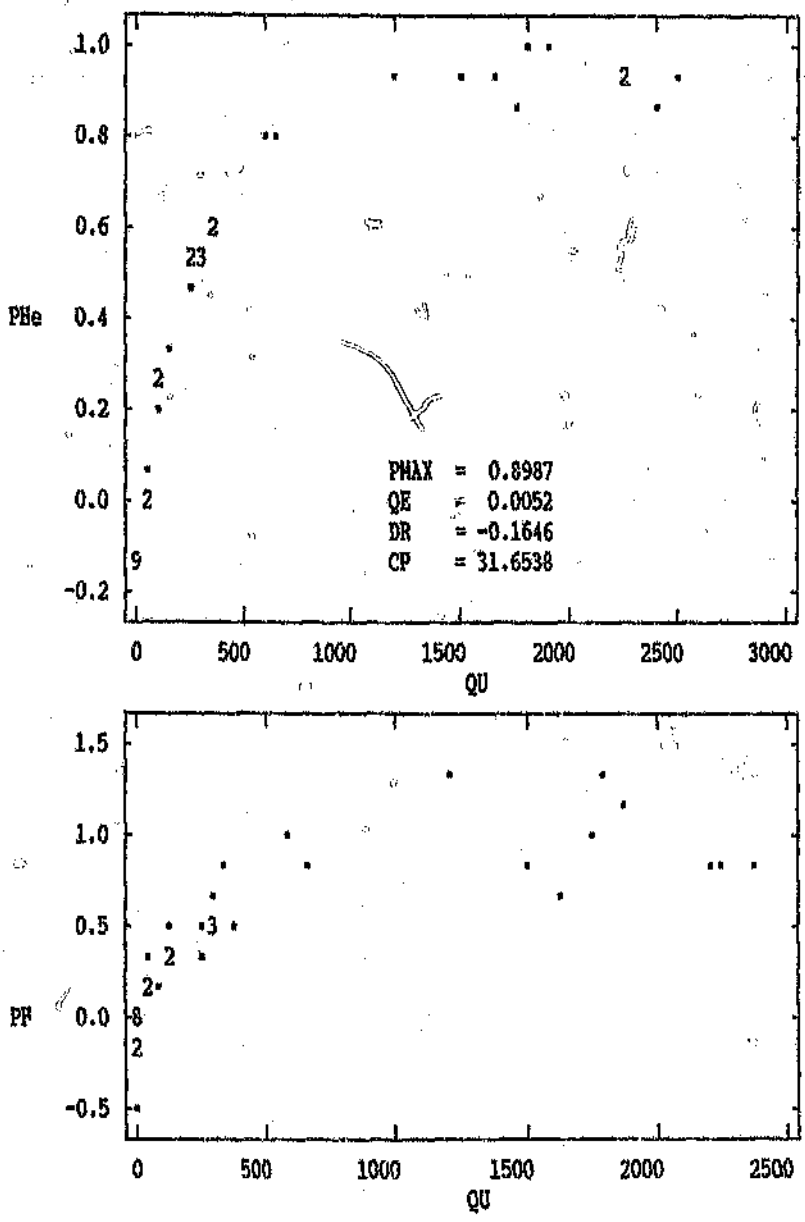


Figure A 1. A photosynthetic irradiance response curve (derived (a) and measured (b)) for Burkea africana at Nylsvley. PMAX = maximum photosynthetic rate at 2500 $\mu E \cdot m^{-2} \cdot s^{-1}$, QE = quantum efficiency ($mg \cdot \mu E^{-1}$), DR = gross dark respiration ($mg \cdot m^{-2} \cdot s^{-1}$), CP = light compensation point ($\mu E \cdot m^{-2} \cdot s^{-1}$), PH & PHe = photosynthetic rate ($mg \cdot m^{-2} \cdot s^{-1}$) and QU ($\mu E \cdot m^{-2} \cdot s^{-1}$) = irradiance. Integers represent overlapping data points.

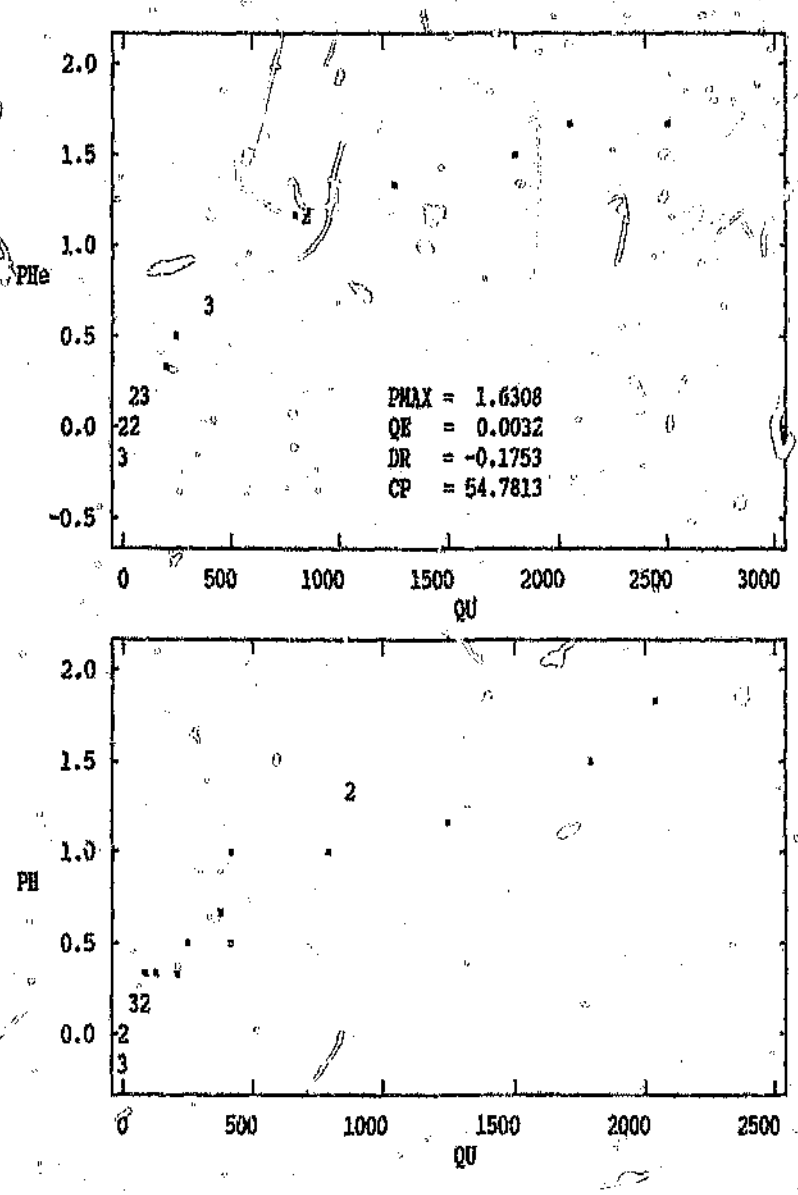


Figure A 2. A photosynthetic irradiance response curve (derived (a) and measured (b)) for the Cenchrus ciliaris at Nylsvley. PMAX = maximum photosynthetic rate at 2500 $\mu E \cdot m^{-2} \cdot s^{-1}$, QE = quantum efficiency ($mg \cdot \mu E^{-1}$), DR = gross dark respiration ($mg \cdot m^{-2} \cdot s^{-1}$), CP = light compensation point ($\mu E \cdot m^{-2} \cdot s^{-1}$), PH & PHe = photosynthetic rate ($mg \cdot m^{-2} \cdot s^{-1}$) and QU ($\mu E \cdot m^{-2} \cdot s^{-1}$) = irradiance. Integers represent overlapping data points.

APPENDIX B

Table E 1. A persentage differences are given for the comparison of attributes of plant production between the beginning (November) and the end (June) of the growing season (A = 0-20%, B = 21-40%, C = 40-80%, D = 80-150%, E = 150-500% and '-' indicates a decrease).

Species	Site	Pmax	QE	DR	CP
Grass					
Binsc	M1	C	B	-A	-B
Ccili	M1	C	-C	-B	E
Pdeus	M1	D	C	D	B
Pmaxi	M1	B	A	-B	-C
Ccili	M2	B	E	E	-B
Pmaxi	M2	C	D	B	-B
Dampl	M4	A	-B	-C	-C
Ttria	M4	B	-D	-B	E
Woody					
Anigr	M1	C	C	A	B
Anilo	M1	A	D	A	C
Axant	M2	-B	E	-B	C
Capic	M4	B	C	-A	C
Opani	M4	A	C	D	B
Forb					
Acara	M2	C	E	E	B
Atetr	M2	A	-A	-C	-B
Sveno	M4	A	-C	B	E

Table E 2. A comparison of sclerophylly, succulence and leaf turgid : dry weight ratio between the beginning (November) and end (June) of the growing season. 'A' designates a statistical difference of $0.001<p<0.01$, 'B' $0.01<p<0.5$ and 'C' $p>0.5$.

Species	Site	SCL	SUC	RAT
<u>Grass</u>				
Binsc	M1	A	A	C
Ccili	M1	B	A	A
Pdeus	M1	A	C	C
Pmaxi	M1	B	C	C
Dampl	M4	C	C	C
Ttria	M4	C	C	C
<u>Woody</u>				
Anigr	M1	B	A	C
Anilo	M1	B	B	C
Axant	M2	C	B	C
Capic	M4	C	C	C
Opani	M4	B	B	C
<u>Forb</u>				
Acara	M2	B	B	C
Atetr	M2	B	B	C
Sveno	M4	C	C	B

Table E 3. A comparison of grass lamina strength between the beginning (November) and end (June) of the growing season. 'A' designates a statistical difference of $0.001<p<0.01$, 'B' $0.01<p<0.5$ and 'C' $p>0.5$.

Species	Site	Strength
Binsc	M1	B
Ccili	M1	C
Esupe	M1	C
Pmaxi	M1	C
Ttria	M1	B
Dampl	M4	B
Ttria	M4	A

APPENDIX C

Table C 1. Soil physical and chemical properties (A horizon only) for the study corrected for stone fraction (Bnhm Bonheim, Cvly Clovelly, Dndee Dundee, Gnr Glenrosa, Htn Hutton, Mph Mispah, Tbklu Tanbankulu, Vrvr Vaalrivier : Alluv Alluvium, Bslt Basalt, Flte Felsite, Gnte Granite, Rlte Rhyolite, Sdstn Sandstone ; cly clay, lm loam).

Site	K1	K2	K3	M1	M2	M3	M4	N1	N2	N3	R1	R2	R3	T1	T2
Form	Bnhm	Cvly	Htn	Tbklu	Dndee	Vrvr	Mph	Htn	Mph	Htn	Gnr	Gnr	Htn	Mayo	Ctrf
Parent Material	Bslt	Gnte	Gnte	Bslt	Alluv	Sdstn	Rlte	Sdstn	Flte	Sdstn	Sdsin	Adte	Sdstn	Gbro	Gnte
Horizon Depth	24	26	30	20	44	26	31	17	0	25	64	37	20	39	14
% Clay	24	13	14	20	34	23	31	12	21	16	28	19	12	34	14
% Silt	22	10	10	21	38	25	28	5	16	6	22	8	9	12	11
% Sand	22	77	76	16	28	52	54	83	63	78	50	73	79	54	75
Stone (g/g)	0.01	0.05	0.5	0.11	0	0.01	0.9	0	0.69	0.01	0.03	0.07	0	0.01	0.1
Textural Class	Clay	Sandy loam	Sandy loam	Clay	Clay loam	Sandy cly lm	Sandy loam	Loamy sand	Sandy ..y lm	Sandy loam	Sandy cly lm	Sandy o loam	Sandy loam	Sandy cly lm	Sandy loam
Bulk density (g/)	0.93	1.53	1.46	0.99	1.25	1.54	-	1.49	1.65	1.45	1.45	1.4	1.54	1 24	1.5
pH (1M KCL)	4.85	4.55	5.2	4.9	5.9	5	5.85	4.1	4	4.9	5.3	4.9	5.2	6.1	4.9
Ca (cmol(+)/kg)	17.38	1.41	1.65	13.99	20.97	6.02	1.39	1.05	0.56	5.13	6.37	15.94	4.85	33.03	2.24
Mg (cmol(+)/kg)	3.49	0.68	0.46	3.97	4.65	2.56	0.18	0.72	0.25	0.9	1.78	3.8	1.28	4.05	0.82
Mg (cmol(+)/kg)	1.25	0.51	0.29	0.139	1.82	0.93	0.1	0.54	0.26	0.71	0.77	0.71	0.68	0.79	0.54
Extractable PO4 (mg/kg)	19.36	4.09	4.01	12.02	1.17	12	12.02	6.43	49.01	11.76	3.47	2.29	4.64	24.4	3.54
Total N2 (mg/kg)	934.05	201.96	148.55	1316.76	1875.26	536.96	125.4	247.08	157.07	526.8	483.33	248.77	125.19	794.3	184.45
Ammonium N2 (ug/g)	31.16	19.78	18.4	64.511	62.867	32.07	7.412	19.69	5.54	21.3	28.02	13.5	22.135	35.17	5.7
Organic C (mg/kg)	2.82	0.37	0.26	3.12	1.87	1.04	0.29	0.55	0.34	0.78	0.37	0.72	0.3	2.24	0.42
Growth Days	53.5	82.6	78.1	53.1	58.5	62.8	65.7	65.3	70	65.1	28.4	29.7	36	53.9	57.1
Biomass production (g)	2.59	1.749	1.406	-	2.798	1.793	0.41	0.744	1.055	2.191	1.084	3.17	1.169	2.056	1.482

APPENDIX D

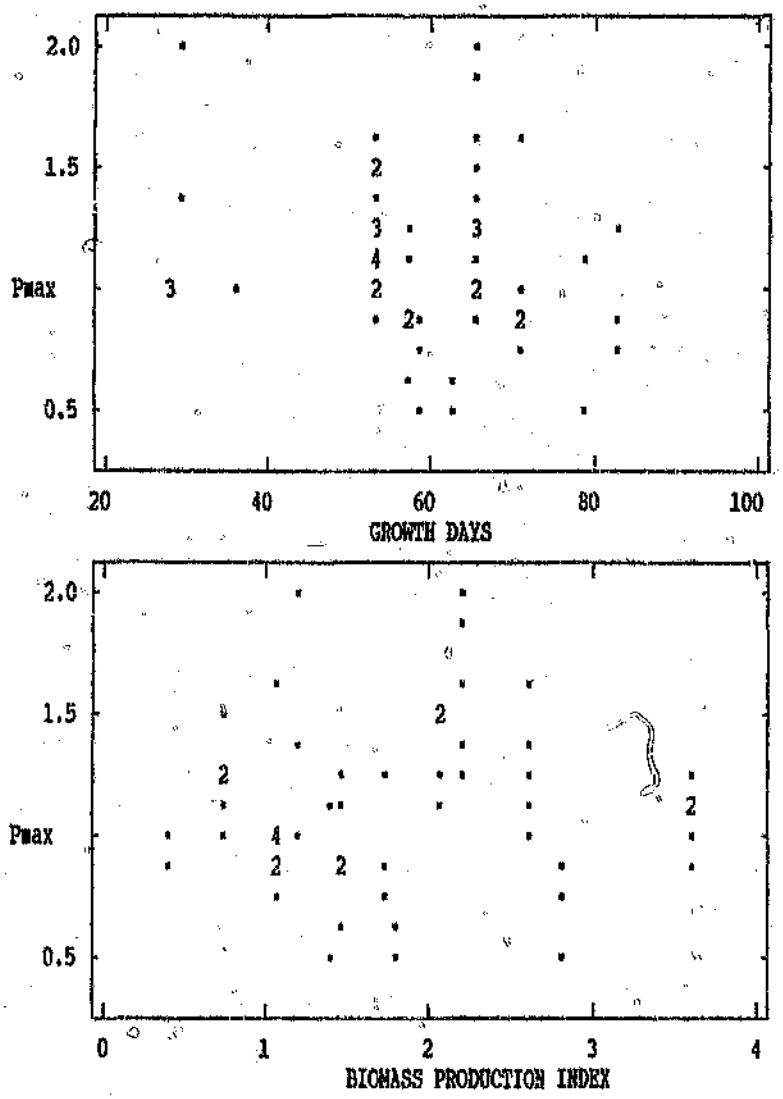


Figure D 1 Direct gradient analyses for maximum photosynthetic rates (Pmax : mg $CO_2 \cdot m^{-2} \cdot s^{-1}$) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

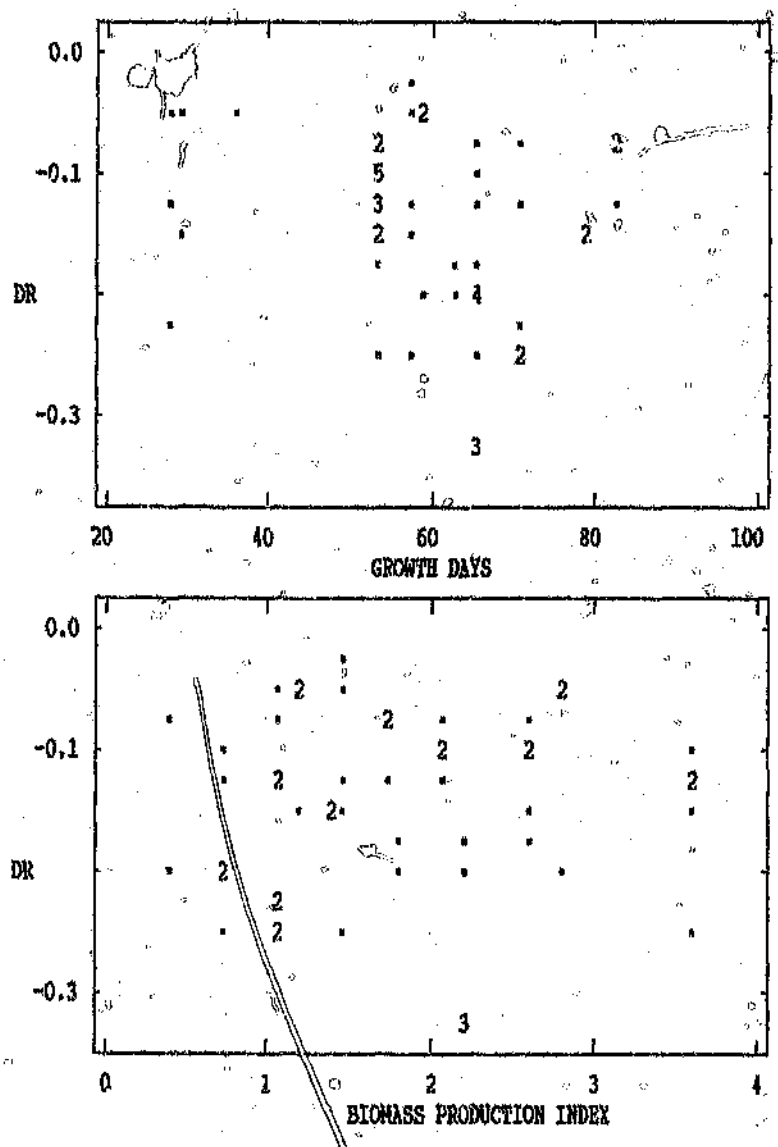


Figure D 2 Direct gradient analyses for gross dark respiration (DR: mg $CO_2 \cdot m^{-2} \cdot s^{-1}$) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

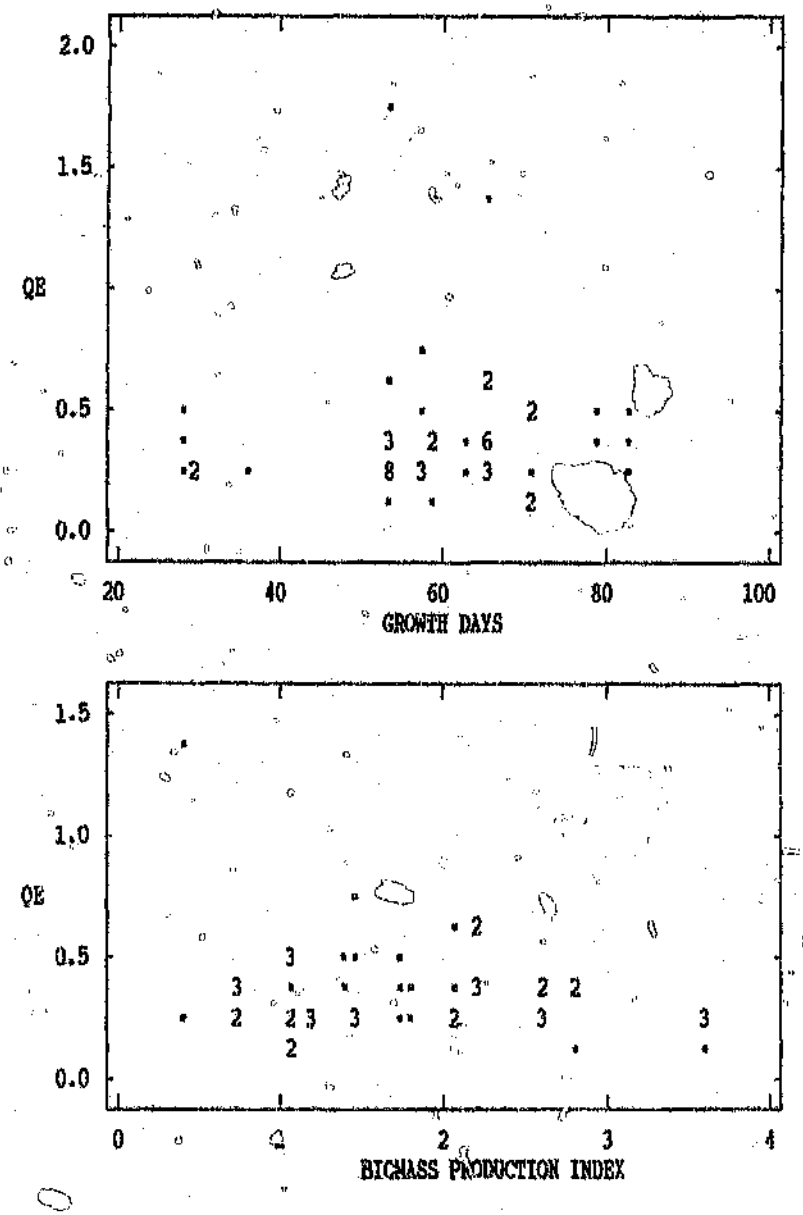


Figure D 3 Direct gradient analyses for quantum efficiency (QE : $\mu E \cdot mg\ CO_2\ ^{-1}$) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

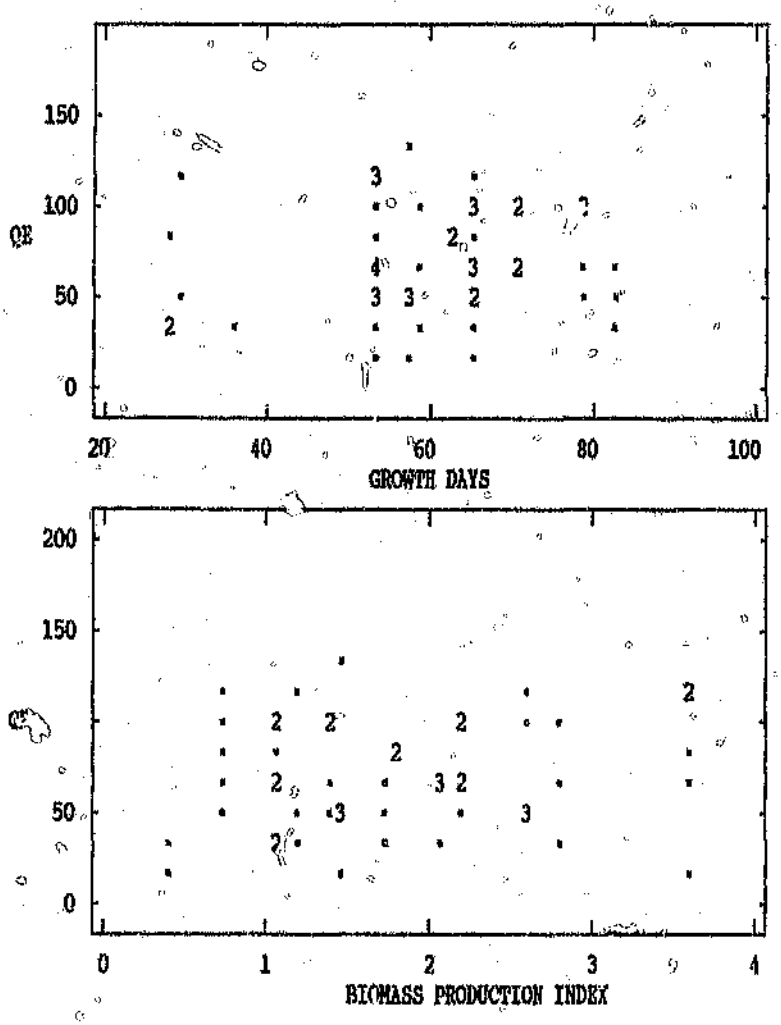


Figure D 4 Direct gradient analyses for light compensation point (CP : $\mu E \cdot m^{-2} \cdot s^{-1}$) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

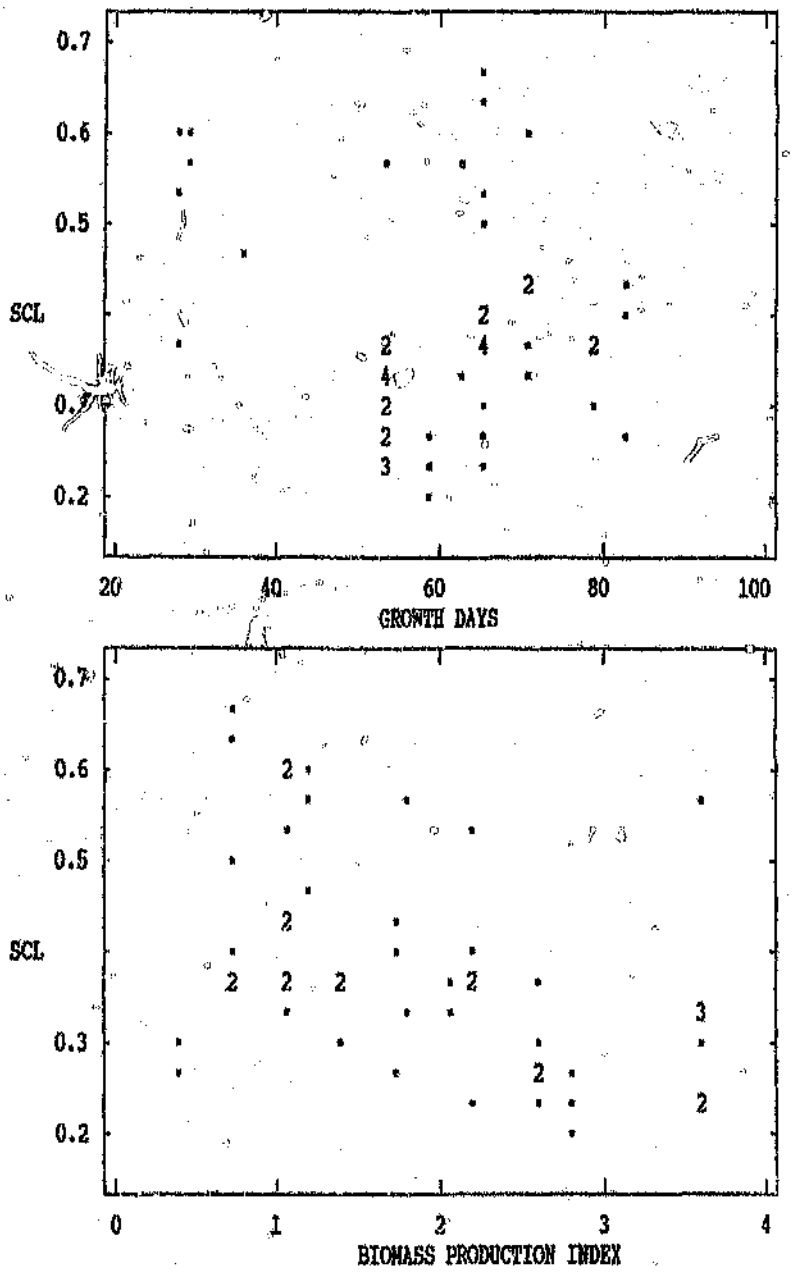


Figure D 5 Direct gradient analyses for sclerophylly (SCL : $g \cdot d^{-2}$) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

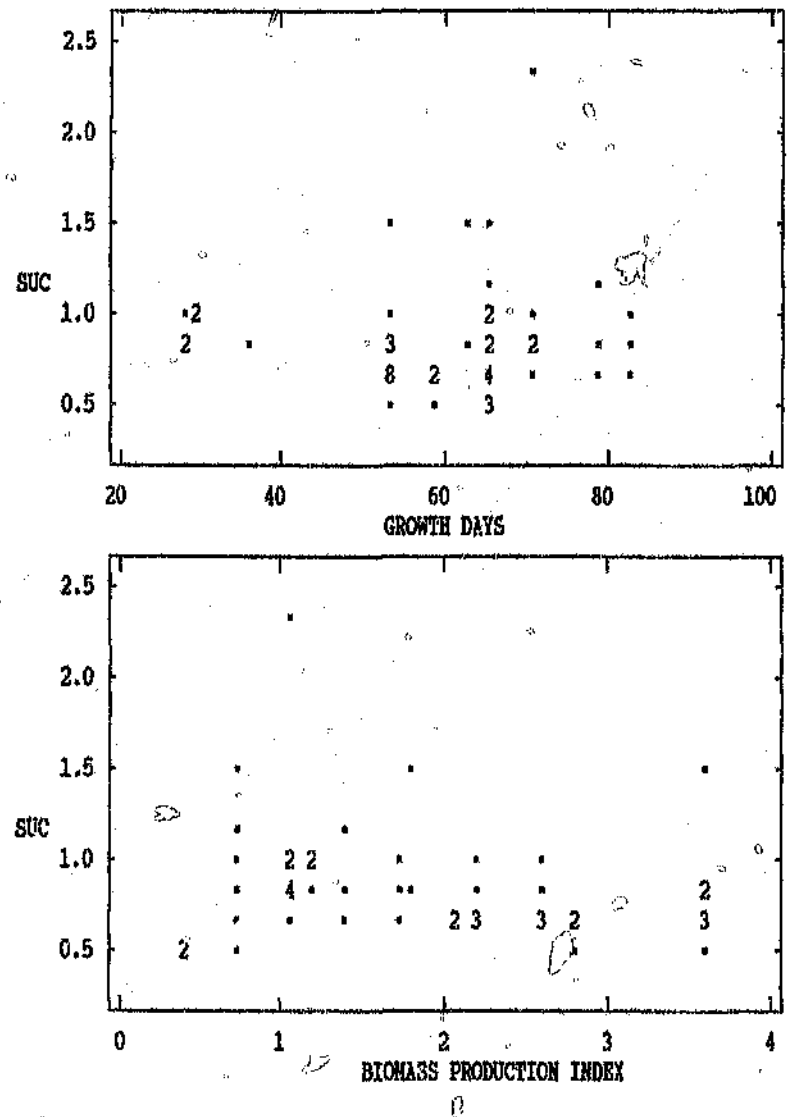


Figure D 6 Direct gradient analyses for suculence (SUC : $g \cdot d^{-2}$) of the grass component along inferred moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

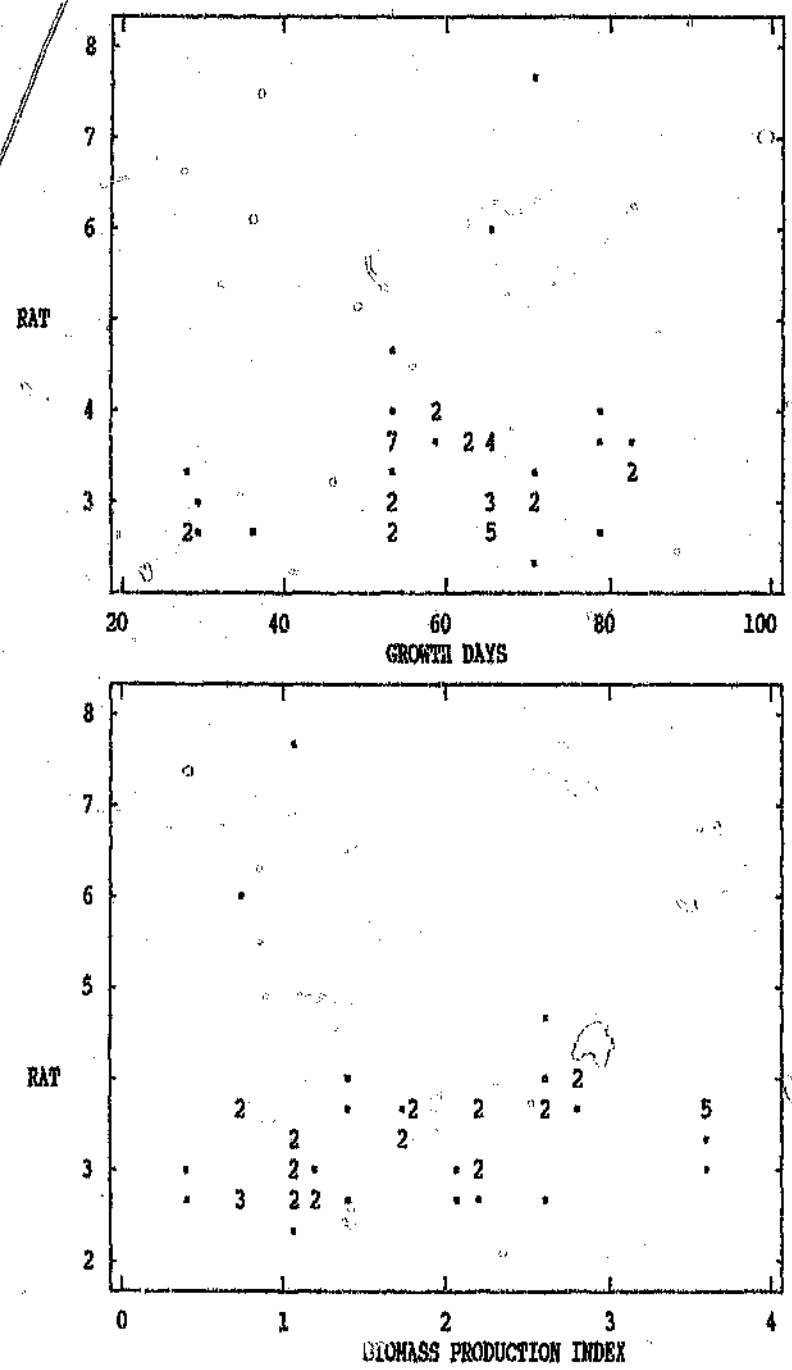


Figure D 7 Direct gradient analyses for leaf turgid : dry weight ratio (RAT) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

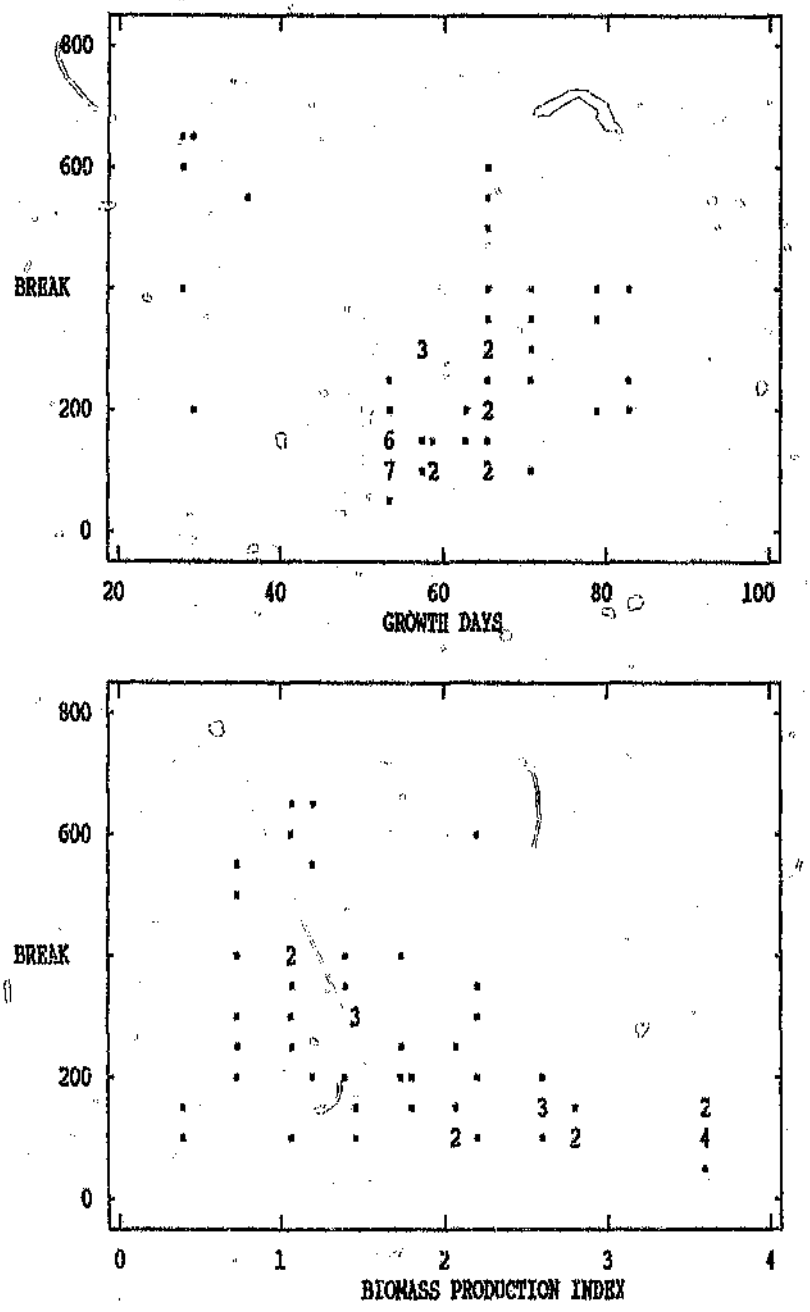


Figure D 8 Direct gradient analyses for herbaceous lamina breaking strength (BREAK : dyne·cm^{-1}) of the grass component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

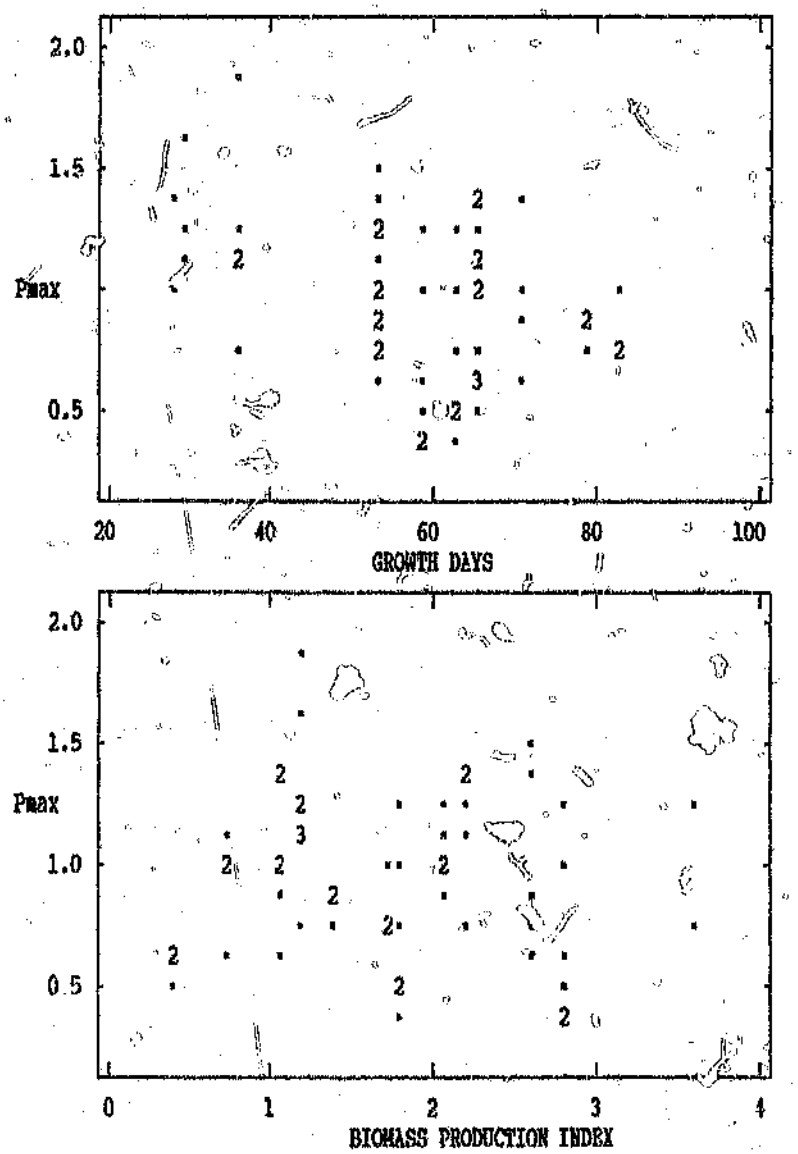


Figure D 9 Direct gradient analyses for maximum photosynthetic rates (Pmax : mg CO_2 $m^{-2} \cdot s^{-1}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

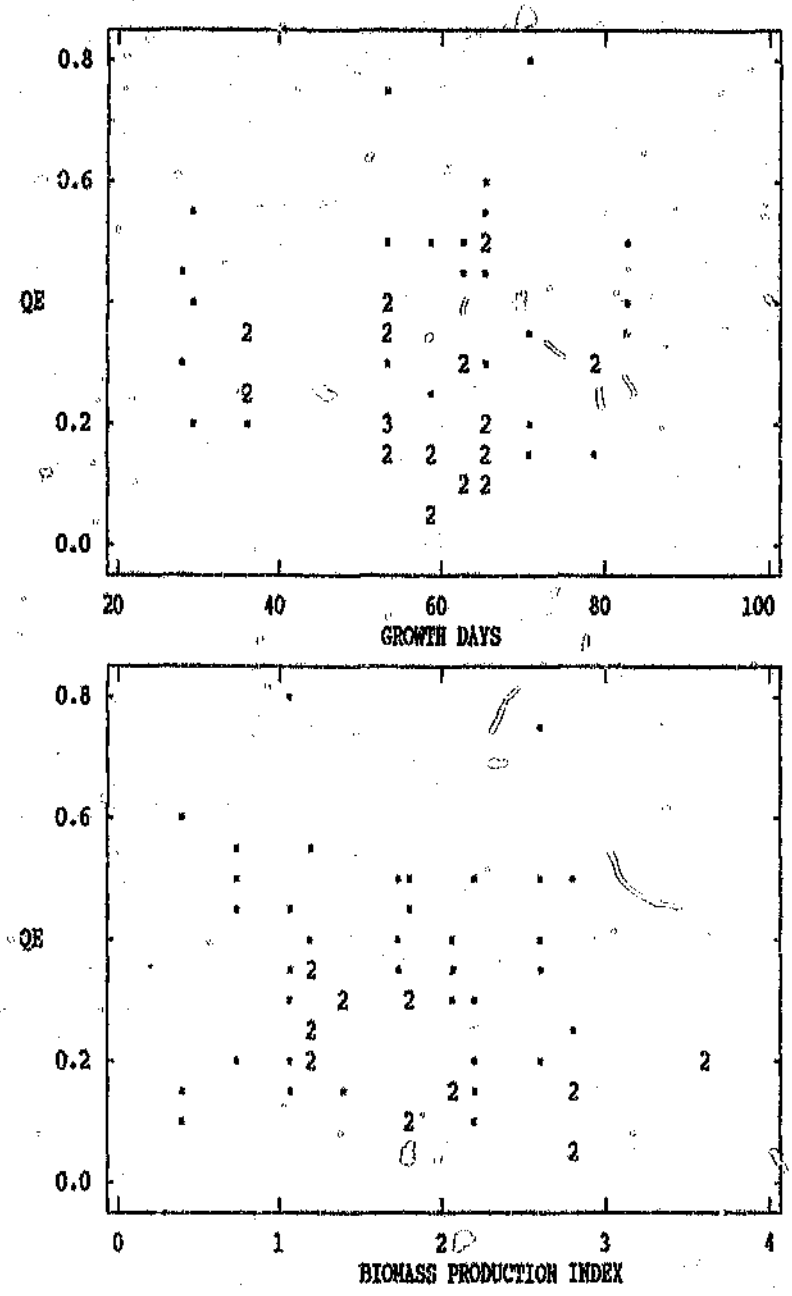


Figure D 10 Direct gradient analyses for quantum efficiency (QE : $\mu E \cdot mg\ CO_2^{-1}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

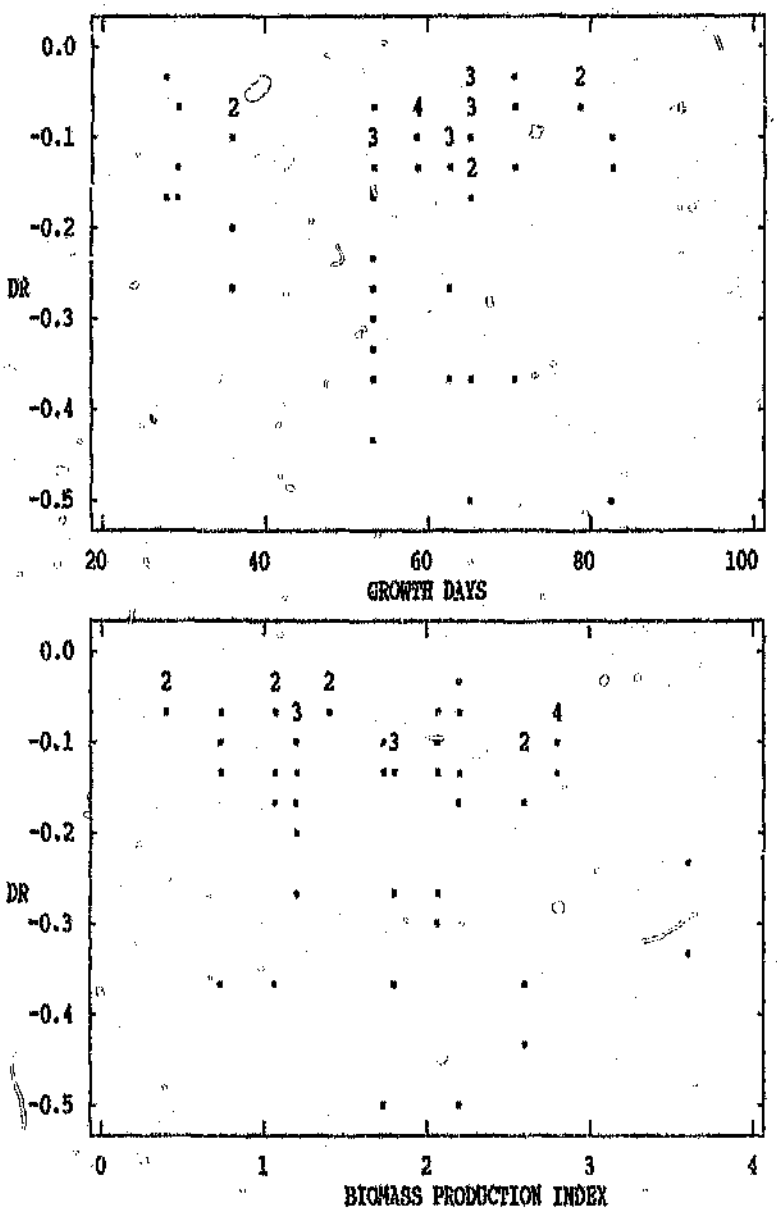


Figure D 11 Direct gradient analyses for gross dark respiration (DR: mg $CO_2 \cdot m^{-2} \cdot s^{-1}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

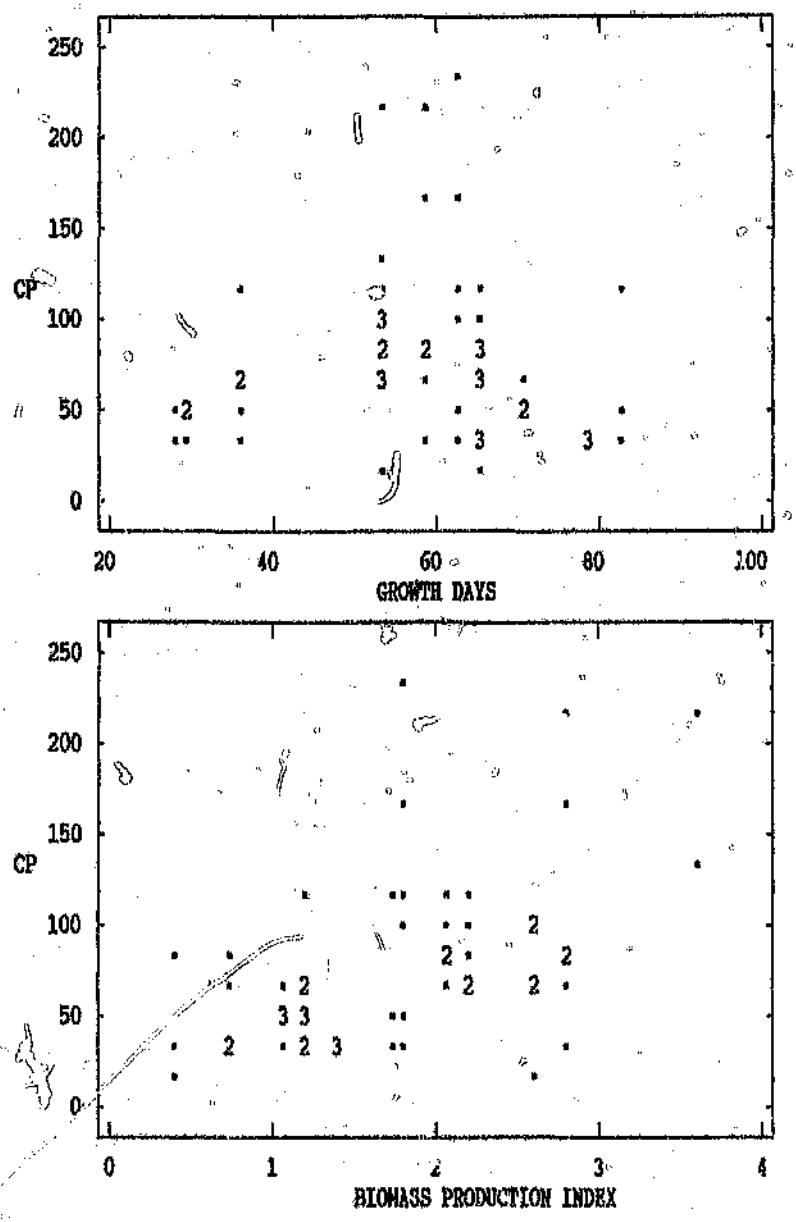


Figure D 12 Direct gradient analyses for light compensation point (CP : $\mu E \cdot m^{-2} \cdot s^{-1}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

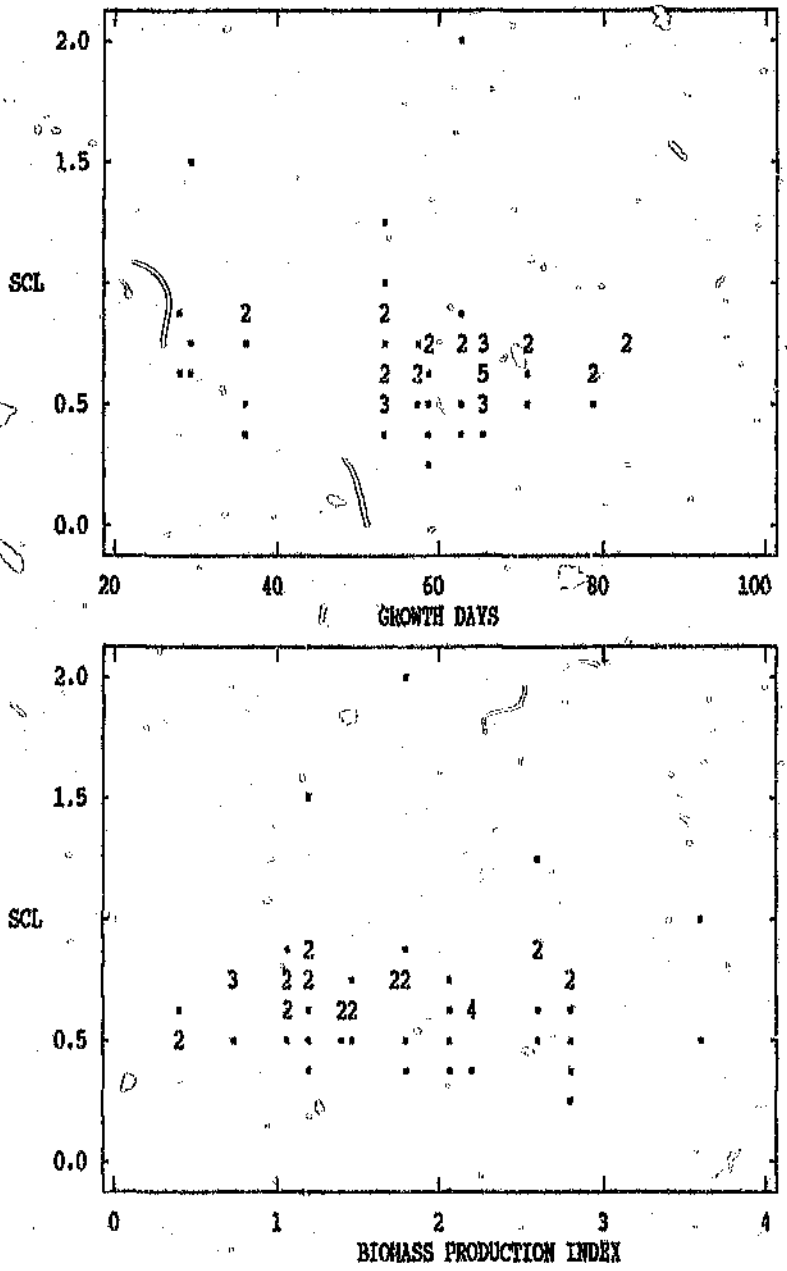


Figure D 13 Direct gradient analyses for sclerophylly (SCL : $g \cdot d^{-2}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

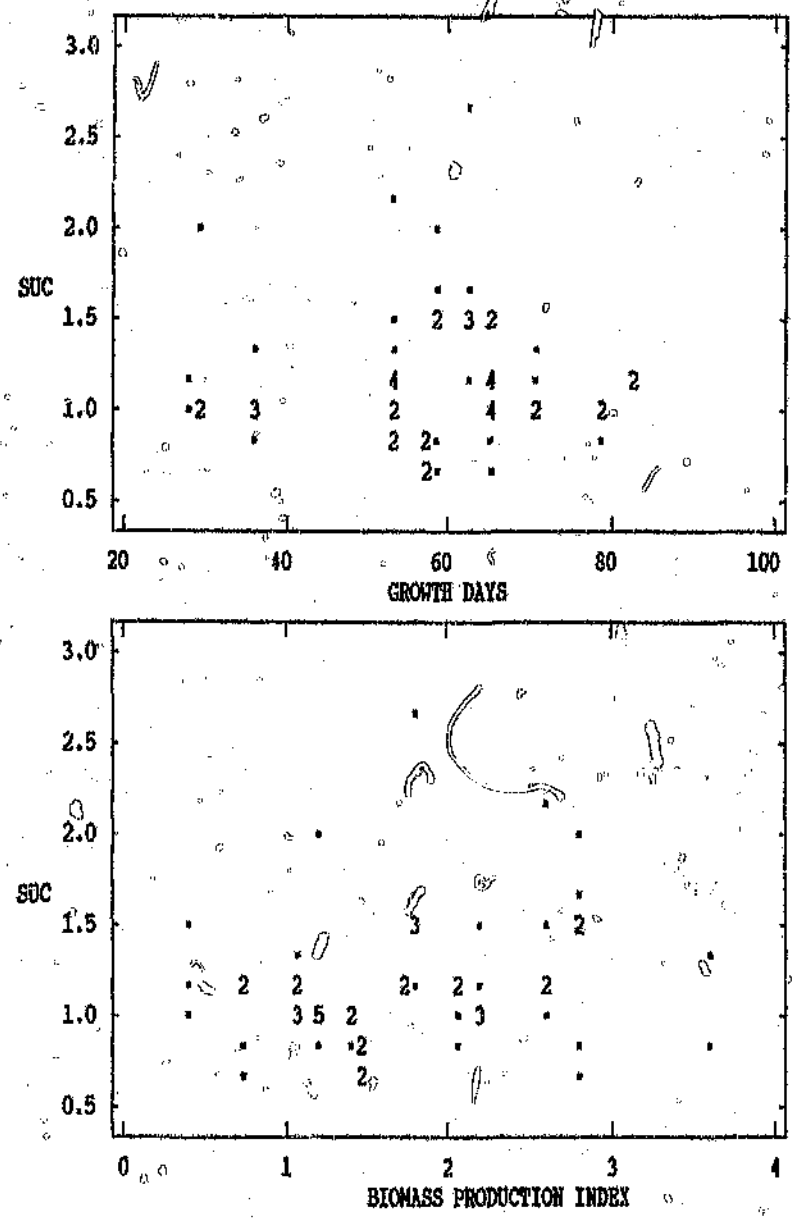


Figure D 14 Direct gradient analyses for suculence (SUC : $g \cdot d^{-2}$) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

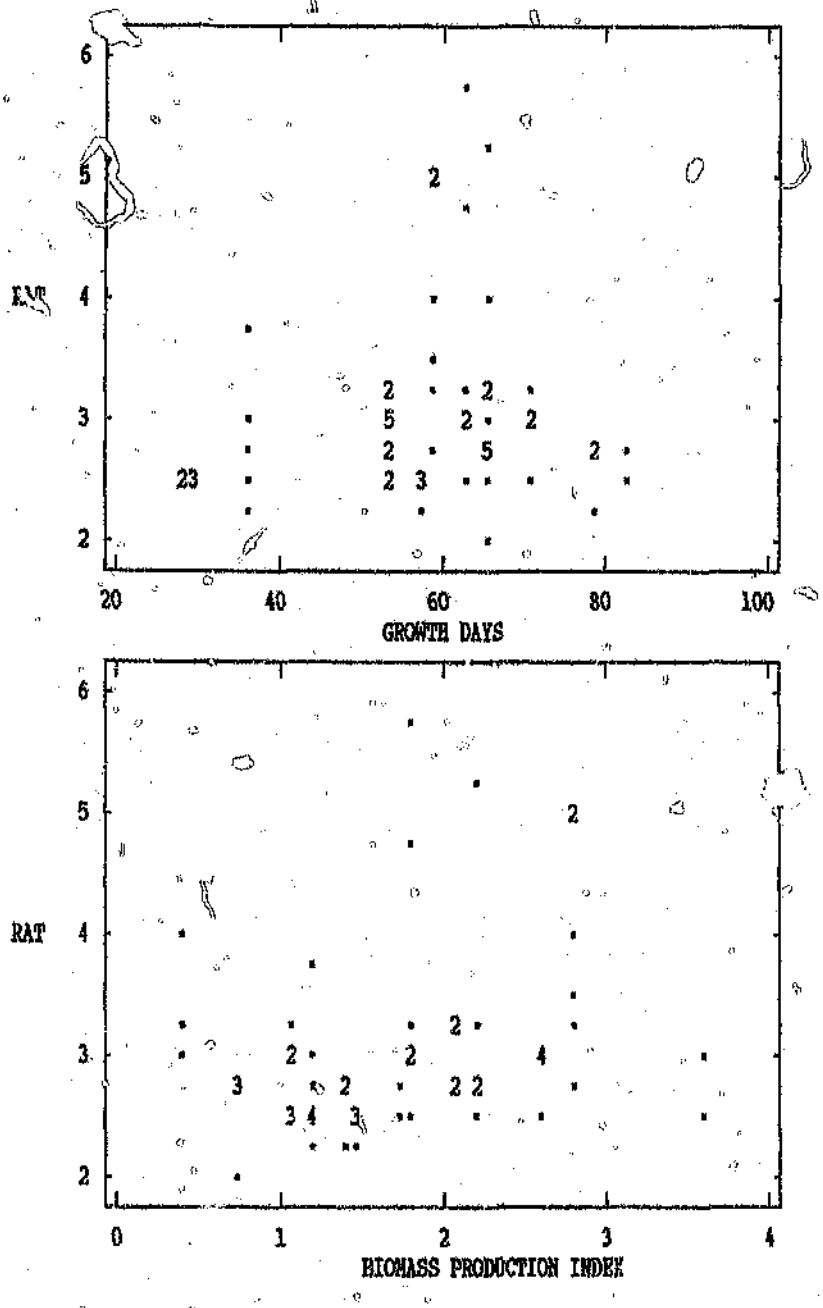


Figure D 15 Direct gradient analyses for leaf turgid : dry weight ratio (RAT) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

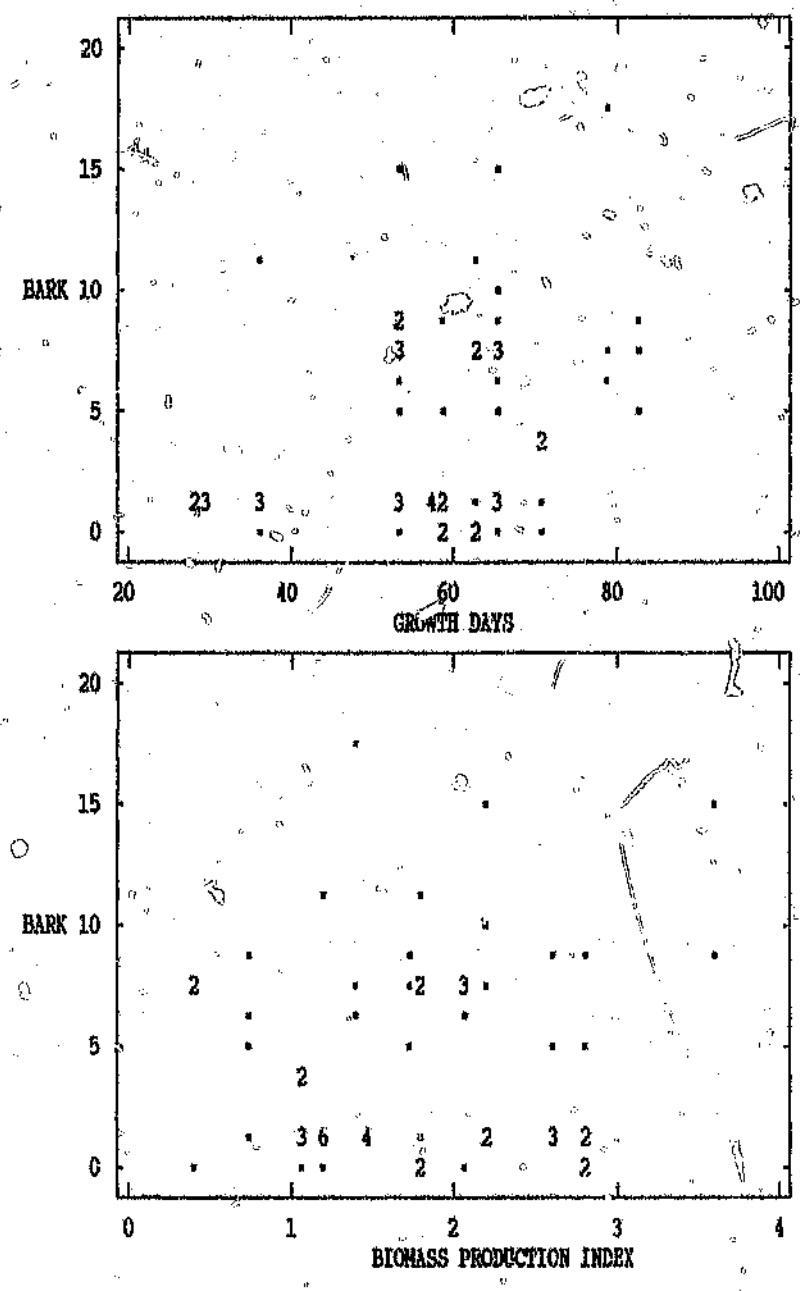


Figure D 16 Direct gradient analyses for bark thickness (BARK : mm) of the woody component along infered moisture and nutrient gradients (see sections 3.5 and 4.5 above). Intergers represent overlapping data points.

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