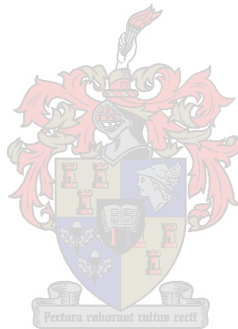


**ASPECTS OF ECOSYSTEM FUNCTION IN A WOODLAND SAVANNA
IN SOUTH WEST AFRICA**

by

MICHAEL CHARLES RUTHERFORD



**Thesis presented for the degree of Doctor of Philosophy
at the University of Stellenbosch**

Promoter

Dr. J.G. Smith

Stellenbosch

November 1975

Frontispiece (on following page). Omuverume Plateau from the south-east. (Photograph by E. Joubert)

ABSTRACT

A study was made of certain relations operating within a South West African woodland savanna ecosystem which was characterised by simplification within most of its basic components. Main attention was given to the relatively unexplored field of spatial and structural organisation of the primary producer component in relation to its quantified intra-seasonal functional changes including its phenology. Simple mathematical model descriptions of seasonal mass change of the herbaceous parts of the primary producer component were derived. Various parts of the primary producer component were also evaluated in terms of some of the main climatic driving forces of the ecosystem, decomposition relations in the form of disappearance rates, soil-vegetation mineral relations and consumer (mainly insect) relations. Gross effects of manipulation of the ecosystem type by fire and management is included.

CONTENTS

1	INTRODUCTION	1
2	STUDY AREA	5
2.1	Physiography	5
2.2	Climate	5
2.3	Soils	11
2.4	Vegetation	19
2.5	History	20
3	GENERAL SAMPLING LAYOUT	34
4	VEGETATION STRUCTURE	38
4.1	Introduction	38
4.2	Spatial and numerical structure	39
4.2.1	Density and frequency	39
4.2.2	Species-area curve	42
4.2.3	Distribution of frequency and density	43
4.2.4	Aggregation	44
4.2.5	Species density and richness	48
4.2.6	Species-associations	50
4.2.7	Mounds	52
4.3	Physiognomic structure	55
4.3.1	Vegetation profile	55
4.3.2	Tree growth forms	56
4.3.3	Frequency of tree heights	58
4.3.4	Vertical distribution of materials in trees	60
4.3.5	Heights of herbaceous layer species	64

4.4	Basal cover	65
5	PRODUCTION	95
5.1	Productivity	96
5.1.1	Field method	97
5.1.2	Processing of results	100
5.1.3	Results	108
5.1.3.1	Changes in total biomass	108
5.1.3.2	Decrease of previous season's material	111
5.1.3.3	Growth and decrease of new material	112
5.1.3.4	Changes in generative material	114
5.1.3.5	Relation of biomass increase to climate changes	115
5.2	Biomass	116
5.2.1	Herbaceous layer biomass	116
5.2.2	Tree biomass	118
5.2.2.1	Method	119
5.2.2.2	Results	122
5.2.3	Energy	123
5.3	Chemical analysis of plant material	124
6	PHENOLOGY	156
6.1	Introduction	156
6.2	Methods	161
6.3	Results	163
6.3.1	General aspects	163
6.3.2	Expression of results	167
6.3.3	Results in species groups	169
6.3.3.1	Grass species	169
6.3.3.2	Other herbaceous layer species	173

6.3.3.3	Shrub species	175
6.3.3.4	Tree species	178
6.3.3.5	Rarer species	181
6.3.4	Phenology of species groups and communities	186
6.3.5	Phenology in relation to climatic factors and productivity	188
6.3.5.1	Relation of phenological phenomena to some climatic factors	188
6.3.5.2	Relation of phenology to productivity	189
6.3.6	Other seasonal changes in the ecosystem	191
7	FIRE	209
7.1	Introduction	209
7.2	Results of fire	209
7.2.1	General effects	209
7.2.2	Regeneration and mortality after fire	210
7.2.2.1	Herbaceous layer	212
7.2.2.2	Tree layer	213
7.2.3	Vegetation dynamics after fire	217
8	VEGETATION UTILIZATION	222
8.1	Nutritive value of the vegetation	222
8.2	Effect of clipping time on regeneration	223
8.3	Effect of intensive grazing and frequent fires	225
9	GENERAL CONCLUSIONS AND RECOMMENDATIONS	230
	SUMMARY	232
	OPSOMMING	237
	ACKNOWLEDGEMENTS	242
	LITERATURE CITED	244
	APPENDIX 1 Species list	250

1 INTRODUCTION

Injudicious utilization of the natural biological resources of an area has in the past often greatly disturbed the biological balance in nature and resulted in decreased productivity. Recently, this disturbance of biological equilibrium has increasingly been the subject of scientific research. It has become clear that for correct utilization a thorough knowledge of the structure and operation of the ecosystem(s) of an area was needed.

a Type of study

Early in 1970, an ecological project was conceived that would attempt to record quantitatively some of the functional aspects of a terrestrial South West African ecosystem, paying particular attention to the seasonal changes in the vegetation over a period of one year.

The first aspect to be considered was productivity, determinations of which are central to the functioning of the system since it offers, firstly, a reliable and absolute measure of the general vigour and performance of a species and secondly, it indicates the seasonal fixation of energy in the system. Economically, the growth rate and timing of production under field conditions is of direct significance for the effective budgeting of grazeable material by stock-farmers. In South West Africa, the seasonal rates of production of herbaceous species, within their natural communities and under field conditions, have rarely been quantitatively analysed. The biomass, which is the total amount of living matter present at a given moment in a biological system, is an indication of the fixation of energy in the system, and can be a useful parameter in determining the functional status of a species in the system. Furthermore, relatively little attention has been paid to the determination of the biomass of all the vegetational components in a savanna or woodland ecosystem. Phenology, which is usually the qualitative recording of the more readily observable seasonal changes of function in plants or plant communities, is an important framework within which other functional data should be viewed. Systematic qualitative recordings of phenology and quantitative description of the phenological reaction to climate are exceedingly scanty for South West Africa. Some data of this type exist for the Southern Kalahari (Leistner, 1967).

b Requirements

To study these various aspects most effectively in South West Africa, a relatively simple and stable terrestrial ecosystem was needed to facilitate the correct interpretation of correlations between recorded sets of data. An area was thus sought that was, firstly, subject to as few external complicating factors as possible. In particular, the area should have a more or less level surface to minimize the differential effects of gradient, in the form of water run-off and exposition, on the vegetation. It should also be strictly protected from grazing and should not have been subject to an unknown history of various selective grazing pressures. Secondly, the vegetation should have attained a relatively stable successional stage with a clearly demarcated active growth season and the rainfall should, as far as possible, be relatively reliable. Thirdly, the area should have as homogeneous a vegetation and soil as possible to reduce sample variation. Vegetational components should be equally aged to reduce variation of growth due to differing ages of the individual plants. Sampling function would also be simplified if the kinds of growth form of the dominant species were well-known and well-researched. Finally, the ecosystem chosen should be large enough to withstand destructive sampling without significantly changing its character, and should be representative of other larger areas.

c Properties of study area satisfying requirements

In South West Africa, the region of least variable rainfall and the most clearly demarcated active season, is that north and east of the town Otjiwarongo (Fig. 1.1). The only area in this large zone that was found to be level yet have no history of grazing by domestic stock animals was, not unexpectedly, a rather inaccessible remnant of the Great Waterberg Plateau situated east of Otjiwarongo. This isolated remnant, called the Omuverume Plateau, contained a fairly homogeneous sandy soil over an area of about 175 ha in extent. The savanna vegetation was as homogeneous as could be expected, that is, usually homogeneous on a scale of about 1 ha but becoming more heterogeneous in smaller areas. Due to an overall fire the previous season, the above ground parts of the herbaceous layer of the savanna were all of approximately equal age. The growth forms of the dominant species were mainly bunch grasses and deciduous tree forms. From the distribution of the

dominant tree species, Burkea africana, it appeared that the vegetation was related to that of the north-eastern parts of South West Africa (Volk, 1965 - 66). Later, from the analysis of the species composition of the area, it became clear that the vegetation was a peripheral representative of the large "Tree savanna and woodland" vegetation-type (Giess, 1971) which covers the north-eastern sector of South West Africa (Fig. 1.1). This basic vegetation type appears to occur in many areas outside the borders of South West Africa, for example, through many parts of the Kalahari and in some sandy areas in the central and northern Transvaal (Van der Schijff, 1971). Certain typical species of the Omuverume Plateau sand area, for example, Andropogon gayanus and Securidaca longepedunculata are apparently associated together as far afield as West Africa (Bowden, 1964).

Since the sand area vegetation of the Omuverume Plateau appeared reasonably representative of much larger areas and to be suitable for the envisaged study, a part of this area was selected as a study area despite the difficulties of access.

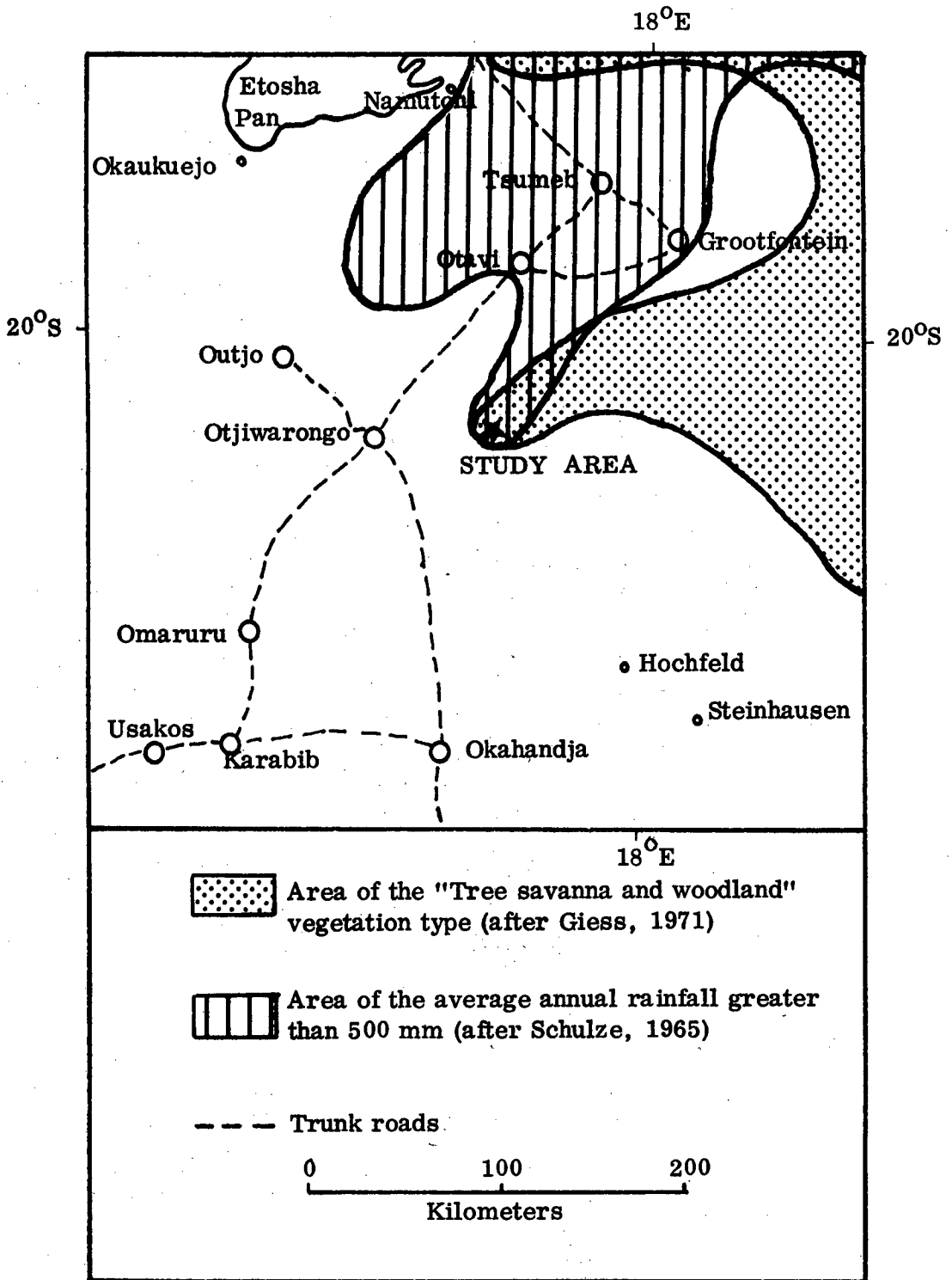


Fig. 1.1 Map showing the region within a 200 km radius of the study area

2 STUDY AREA

2.1 Physiography

A short description of the general features of the topography and vegetation of the Omuverume Plateau-Mountain has been given (Rutherford, 1972).

The Great Waterberg Plateau is roughly 50 km long, rising gradually out of the eastern sandveld plains of the Grootfontein District to its maximum height in the Omuverume and Klein Waterberg Plateaus in the west, above the central thorn bush plains of the Otjiwarongo District. The attenuated triangular shaped Omuverume Plateau is separated from the Great Waterberg Plateau by a high saddle-break about half a kilometer wide at its narrowest point (Fig. 2.1). The Omuverume Plateau-Mountain is made up of the Etjo series and is capped by deep pink vertically fissured aeolian sandstone (Gevers, 1937) which forms a line of cliffs 15 to 60 m high, completely circumscribing the mountain (Figs. 2.2 and 2.3). Below this line of cliffs is an almost continuous terrace from which descends a fairly even slope to the base of the mountain. A few fountains occur on the sides of the mountain. Above the cliff line is a rather broad, often rocky, summit perimeter belt enclosing a sandy area without surface rock in the central part of the plateau.

An area of approximately 13 ha, regarded as typical of this 175 ha sandy area, was selected as the general study area (Fig. 2.1), within which 8 ha were intensively studied. The study area was situated at the intersection of the co-ordinates of $20^{\circ}35\frac{1}{2}'S$ and $17^{\circ}07'E$ and was about 365 m above the surrounding plains at the base of the mountain, and 1847 m above sea level.

2.2 Climate

a Introduction

The climate of the study area was an important factor in selecting the area best

suited to the type of study. The region from around the Waterberg toward the north-eastern part of South West Africa has been classified as the climatic unit BShgw after Köppen and been referred to as "warm, subtropical steppe" by Barnard (1963 - 65).

Schulze (1965) has indicated various climatic characteristics of the Waterberg region. The total radiation is about $600 \text{ cal. cm}^{-2} \cdot \text{day}^{-1}$ in December and somewhat greater than $400 \text{ cal. cm}^{-2} \cdot \text{day}^{-1}$ in June. The average annual duration of bright sunshine is relatively high, that is about 80% of possible sunshine, with the average annual number of days with no sunshine (overcast days) only numbering about one. The area lies roughly between the mean annual isotherms of 20,0 and 22,5°C with a relatively low range of temperature (less than 10°C). In the study area frosts would appear to seldom occur. Winds are not common and are light to moderate mainly from the eastern to north-eastern sector and are usually strongest in late winter and spring. High gusts are, however, normal during the onset of thunderstorms throughout the rainy season. The relative variability of the annual rainfall is low (about 30%) compared to that of most of South West Africa. Rain falls in summer and, from records of nearby rainfall stations, almost all (about 97%) of the average annual rainfall falls from the 1st of October to the 30th of April. The annual rainfall of the area is about 500 mm, most of which is from thunderstorms and instability showers. Hail is rare and snow has never been recorded. During the study year, most of the rain appeared to fall in the late afternoon or early evening.

b Method of study

Records of rainfall, temperature and relative humidity were made throughout the study year (September, 1970 - August, 1971).

i Rainfall

Two rain gauges were positioned at 80 cm above ground in a slight clearing near the centre of the study area (Fig. 2.4). Readings were taken when possible every day at about 8 am. Since they could not always be taken daily, the one rain gauge was modified so that rain was fed through a waxy surfaced plastic tube into a storage receptacle underground and shaded to reduce evaporation of accumulated

so that the rainfall records of Okosongomingo were used to roughly indicate the rainfall of the study area for the periods immediately preceding and following the study period.

The average rainfall of the study area (taken from the Waterberg rainfall station) first becomes effective in October (14,8 mm) and November (43,3 mm) and then rapidly increases in December and January to a maximum of 117,7 mm in February which amounts to 23% of the annual rainfall (Fig. 2.6). The months of high rainfall are January (114,7 mm), February (117,7 mm) and March (100,3 mm). About 97% of the annual average falls between the 1st October and the 30th April. Rain occurs very rarely in the winter months of June, July and August.

The rainfall of the season preceding the study season is very important to the present study as it is this rainfall that was largely responsible for the amount of plant material as well as for the state of the plant material at the start of the study period. The rainfall of the previous season (1969 - 1970) as well as that of each month (Fig. 2.7) was very much below the average rainfall. Okosongomingo recorded a total of 342,7 mm which is about 71% of the average rainfall. A fire in the study area and surrounding area was started by lightning at the beginning of the previous season's rains. The first rains were later than usual: they only started on the 5th November, 1969. From the 5th to the 7th November 24,5 mm was recorded followed by 17,2 mm on the 22nd and 25th November. The fire of this period probably occurred before or just as the new ground layer growth was starting. In the month following the fire (December) a relatively low rainfall of 31,0 mm was recorded. Only in January and February did near-average rains fall (115,3 mm and 103,5 mm respectively). In March 36,6 mm was recorded. The last rain of this season (6,0 mm) was recorded at Okosongomingo on the 26th April, 1970. The growth of the previous season, although probably stimulated by a fire at the beginning, was thus relatively short. The period without recorded rain between this season and the study season was more than 5 months.

The first rains of the study season fell in the study area on the 17th October, 1970

(Fig. 2.6). The rains started relatively slowly in October and November but then increased rapidly in December and January to a maximum of 295,5 mm in February. In March, however, the rainfall was below average (34,2 mm) increasing to above average in April (63,7 mm). A few late light showers were recorded in May and June. The rainfall of the study year on this site was 807,3 mm, which is 157,1% of the Waterberg station's average (Fig. 2.6) or 235,6% of the previous year's rainfall recorded at Okosongomingo (Fig. 2.7). A rough indication of the availability of water in the study season, using the Gaussen proportion of 1:2 for temperature in degrees centigrade to rainfall in millimetres, shows a brief water surplus in October, 1970 followed by a slight deficit in November (Fig. 2.8). From December to February an abundant excess of water is indicated but in March a brief deficit, followed by an excess in April occurred, after which the severe water deficit of winter set in by May.

The rainfall of the season following the study season was much below average, 325,1 mm being recorded at Okosongomingo from November, 1971 to April, 1972. The first effective rains only occurred in January, while in February no rain was recorded.

The above average rainfall of the study season is in distinct contrast with the much below average of the preceding and following seasons' rainfall. The value of 807,3 mm is not the maximum recorded for the Waterberg area and has been exceeded, for instance, in the season 1953 - 54 when 880,8 mm was recorded at Okosongomingo, although, only 807,0 mm was recorded at the Waterberg Rainfall Station for this period.

ii Temperature

Estimate of mean temperature.

Schulze (1965) shows that the Waterberg area lies roughly between the 20,0 and 22,5°C mean real isotherms. The Omuverume Plateau is, however, elevated 365 metres above the surrounding plains which probably brings its average monthly temperature down to about 20,0°C or slightly lower.

The average monthly temperature of the study year was calculated at 18,7°C from the

monthly averages of the daily maxima and minima. Since maxima usually last shorter than minima, this method of calculation overestimates the average temperature. Using Schulze's (1965) correction for the averages at Maun and Windhoek, the calculated average of $18,7^{\circ}\text{C}$ was converted to a corrected $18,4^{\circ}\text{C}$. The monthly temperature means are also corrected by the same amount. From the analysis of the inverse relationship between rainfall and temperature for Windhoek (Schulze, 1965), it appears that a relatively high rainfall, as that of the study year, might depress from average the temperature of that year by about $1,0^{\circ}\text{C}$. If this is so, the average temperature of the study area is therefore about $19,4^{\circ}\text{C}$ which corresponds well with the estimate of about 20°C or slightly lower.

Temperatures of study year.

The highest average monthly temperature ($23,0^{\circ}\text{C}$) during the study year was attained in November (Fig. 2.9). Although solar radiation reaches a maximum in summer, the average monthly temperatures were depressed by the above-average rains of this period. After November, the average monthly temperature decreased steadily to a relative minimum in February ($18,3^{\circ}\text{C}$), followed by a relative maximum in March ($19,7^{\circ}\text{C}$), but then decreased to a minimum average in July ($13,9^{\circ}\text{C}$). The highest temperature ($33,0^{\circ}\text{C}$) was measured in October, while the lowest ($0,5^{\circ}\text{C}$) in August. The monthly maximum (average of daily maxima) varied from $29,8^{\circ}\text{C}$ in November to $20,0^{\circ}\text{C}$ in June, while the monthly minimum (average of daily minima) varied from $16,8^{\circ}\text{C}$ in November to $8,0^{\circ}\text{C}$ in July (Fig. 2.9). The range of temperature between average monthly maxima and average monthly minima was $9,1^{\circ}\text{C}$, which is a low range of temperature relative to the average range in the interior of Southern Africa (Schulze, 1965). The minimum range occurred in February ($8,0^{\circ}\text{C}$) and the maximum in August ($14,7^{\circ}\text{C}$).

In the study year no hot days ($>35^{\circ}\text{C}$) but 44 warm days ($>30,0^{\circ}\text{C}$) were recorded. There were 54 warm nights ($>16,7^{\circ}\text{C}$), ten of which, were tropical nights ($>20,0^{\circ}\text{C}$). No frosty nights ($<0,0^{\circ}\text{C}$) and no cold days ($<10,0^{\circ}\text{C}$) were recorded. The coldest day was $15,0^{\circ}\text{C}$, while the warmest night was $22,0^{\circ}\text{C}$. According to Schulze (1965), the number of warm nights and days are greater for the Waterberg area than were recorded. Although the temperatures of the study year were depressed by the

above average rainfall, this discrepancy is probably due mainly to the study area lying at more than 1 800 m above sea level.

In the previously mentioned relation of monthly rainfall and temperature (Fig. 2.8), the high November temperature assisted in bringing about a "water deficit" in this month.

iii Relative humidity

The average relative humidity of the monthly values was 40% with an average minimum of 26% and an average maximum of 54%.

The pattern of average monthly relative humidity (Fig. 2.10) followed the rainfall pattern closely. There was a strong increase in relative humidity from a low average of 10% in September to a maximum average of 76% in February. After this, there was a sharp decrease to the average relative humidity of 12% in August. The very low relative humidity of September, 1970, was confirmed by the recording of the average relative humidity of 12% in September, 1971.

2.3 Soils

a Introduction

The study area was limited to part of the sandy flats in the central area of the Omuverume Plateau. The area is not used agriculturally and has had no history of cultivation or any other evident human influence. The soil is thus a natural undisturbed soil. The gradient varies from evenly flat to slightly sloping down toward the north. The gradient is so slight that no sign of water erosion was seen. A few irregularly shaped mounds of soil up to about 50 cm high and a maximum of 20 m in diameter are scattered in the area. Due to the established perennial grass cover, little wind erosion occurs although leaf bases, such as those of some Brachiaria nigropedata individuals, are raised above the general soil surface. This phenomenon can, however, be a protective adaption to recurring fires.

b Morphology

Two pits were dug in the open flat areas and one in the centre of each of two larger mounds, all within the study area. Each pit was excavated down to bedrock. The depth of soil was 3,0 and 2,9 m on the mounds and 2,0 and 2,2 m on the flats. The difference between the soil depth on the mounds and on the flats is thought not to be significant since the surface of bedrock is very irregular due to the vertical fissuring of the sandstone cap of the plateau (Fig. 2.3). The profiles were observed when the soil was dry.

On the flats there is a reddish brown soil layer 20 to 30 cm thick, below which is an uniform red layer down to bedrock. The soil profile below the mounds (Fig. 2.11) is more developed with an approximately 2 m reddish brown layer, underlaid by a uniform red layer down to bedrock. The transition between the 2 layers in each case is clear (within 1 to 5 cm). The reddish brown upper layer (A) has a hue of 5YR, value of 5 and a chroma of 3 and the red lower layer (B) has a hue of 2,5YR, value of 5 and a chroma of 8 (Munsel Color Chart, 1954).

The texture of both profiles is on average a loamy sand. There is very little variation in the distribution of particle size in the various profiles and between mound areas and flats. From texture analyses of all soil samples (Appendix 2 and Fig. 2.12), about 75% of the soil is made up of fine sand (0,2 to 0,02 mm diameter particles), about 10 to 11% of medium sand (diameter 0,5 to 0,2 mm), about the same percentage of clay (diameter less than 0,002 mm), and about 3% of silt (diameter 0,02 to 0,002 mm), with only about 0,2% of rough sand (diameter greater than 0,5 mm). There is, however, a slight difference in particle size between the surface layer (10 cm deep) and the soil below (Fig. 2.12). The main difference is in clay content, that is, a mean of 7,85% with range of 6,97 to 9,53% of the surface layer soil is clay compared to a mean of 12,39% with range of 9,34 to 14,83% of the soil below the surface layer.

The structure of the A horizon is weakly developed, structureless, and a strongly diffuse dark brown and black fleck is present. The structure of the B horizon is

structureless-massive, and weak diffuse black flecks are present. In both layers the consistency is soft but not loose and there is thus some measure of cohesion. There are no concretions and no stones except a few round laterites near the surface of the bedrock. The bedrock consists of pink aeolian sandstone of the Etjo series (Gevers, 1937) which also forms the plateau capping.

The profile of the flats is similar to that of the mounds except that the relative thicknesses of the layers are different and only the mound profiles had tree roots of, for example Combretum collinum, and some disused termitaria cavities one half to one metre below the surface (Fig. 2.11). There appears to be a slightly higher clay content on the mounds (mean of 12,54% and range of 8,69 to 14,83%) than on the flats (mean of 8,67% and range of 6,97 to 11,11%). On the flats there is a higher percentage of medium sand material in the surface layer (mean of 14,52% and range of 10,45 to 18,76%) than below the surface (mean of 6,91% and range of 5,80 to 8,42%). This difference was not seen in the mound profiles.

c Drainage

Drainage appears to be exclusively internal as no surface run-off of rain water was seen during thunder-storms. During intense thunder-storms, short-lived and isolated ponding occurred in some areas. Surface conditions are mainly soft but in a few patches the soil tends to compact and seal at the surface, which results in very little plant growth, if any. The soil is well drained. Saturation with rain water was usually limited to a few days in the case of the mounds, while on the flats it usually lasted for only a few hours.

On a typically flat area with a slightly below average vegetation cover within the study area, narrow pits were dug daily after the first rainfalls of the season and the depths of the wet front and following dry fronts recorded. Each day's hole was filled, packed and marked to avoid digging in the area of disturbed soil. The progression of these fronts is given (Fig. 2.13) for the first 10 days following the first rain period of 2 days. The first rains fell upon dry sand that had not received rain for 5 months. Additional rainfalls are indicated on the appropriate day. The wet front was easier to define for the first 10 days but thereafter became less

defined as wet fronts overlapped previous fronts. In the first 4 or 5 days after the first rains, the internal soil drainage rate exceeded 5 cm a day, while afterwards, the rate was less than 5 cm a day. The dry front was never particularly well defined. The upper parts of the soil started to dry 4 days after the initial heavy rainfall, or two days after subsequent smaller showers. This rapid drying is assisted by maximum temperatures at this time of the year. From the first rains (in October) till almost the end of April, the surface layer never dried out to a depth of more than about 12 cm, except in one period in March, when it was dry to a depth of about 20 cm

d Chemical analysis of the soil

Samples of soil were taken at various systematic depths (specified in Appendix 2) in the profile pits of both flats and mounds. Some additional samples of the surface layer were taken on the flats. All samples fell within either one of the two horizons present and samples at 0,2 m depth all came from the upper horizon. The surface layer is the top 10 cm of the upper horizon. For each sample a 5 cm vertical section was taken except for the surface layer in which a 10 cm section was taken. Roots were sifted from the samples and the analyses were carried out by the Department of Soil Science at the University of Stellenbosch. The pH (in 1 N KCl) was determined in a paste; read with a "Metro" pH-meter. The percentage carbon was determined using the Walkley-Black dichromate sulphuric acid method. Resistance was determined using a saturated soil paste in a standard soil cup with cell constant 0,25. Calcium, magnesium, sodium and potassium were determined by first leaching with 0,5 N ammonium chloride unbuffered at the pH of the soil. The calcium and magnesium were determined in the leachate by EDTA titration and the sodium and potassium by flame photometry. Results of each determination are listed in Appendix 2.

i pH (in 1 N KCl)

On the typical open vegetated flats, all 5 samples in the surface layer (10 cm deep) have a pH equal to or less than 4,5 averaging 4,0. The pH of all 4 samples below the surface layer down to bedrock is also less than 4,5 averaging 4,08. The entire profile of the flats is thus very acidic with all samples lying close to an average of 4,03. The surface layer (10 cm deep) of a bare area with a slight crust is extremely acidic (pH 3,70). On the mounds the 2 samples of the surface layer lie within the class intervals of pH 4,5 to 5,5, with an average pH of 4,88. In the remainder of the reddish brown layer from 20 cm down to 200 cm, 5 of the 6 samples fall between pH 5,5 and 6,5 (the remaining one of the 6 has a pH of 6,65), all 6 samples

averaging 6,19. In the lighter red sand layer below 2 m depth, all three samples have a pH falling between 6,5 and 7,5 with an average of 6,98. The mound profile, in contrast to the almost constant pH of the flats profile, changes from a fairly acidic surface layer through a thick slightly acidic layer to almost neutral above the bedrock.

The pH values for the profiles of the flats and mounds may be summarised as follows with the number of samples in brackets:

	<u>pH intervals</u>	<u>Flats</u>	<u>Mounds</u>
Very acidic	3,5 - 4,5	Whole profile (9/9)	-
Fairly acidic	4,5* - 5,5	-	Surface layer (2/2)
Slightly acidic	5,5 - 6,5	-	Rest of reddish brown layer (5/6)
<u>+</u> Neutral	6,5 - 7,5	-	Red layer (3/3)

ii Percentage carbon

The organic content of the soil of the flats is lower than that of the mounds for each depth interval down to about 2 m. Only below a depth of 2 m does the organic content of the soils become more or less equal.

The average percentage carbon of the surface layer of the flats is 0,82% compared to 1,32% for the surface layer of the mounds. The percentage carbon drops rapidly to between 0,50 to 0,40% at 20 cm depth in the flats but drops more gradually to the value of about 0,40% at about 200 cm depth in the mounds. Both these depths correspond roughly to the transition from reddish brown horizon to underlying red horizon. The red horizon in both areas thus contains a very low percentage of carbon (less than 0,40% and reaches a minimum of about 0,10% in both cases just above bedrock.

The relationship between soil depth and the percentage carbon for mounds and flats is given in Fig. 2.14. It is clear that throughout the profiles the carbon content of the mounds is greater than that of the flats.

iii Resistance

The resistance of the soil is expressed as ohms at 20°C and is measure (within limits) of the amount of soluble salts in the soil. The usually accepted limit of saline danger to vegetation is where the resistance of the soil is less than 500 ohms (Russel, 1968). Soil of all samples was above 1000 ohms, indicating no high degree of salinity. This

*In all cases, in this thesis, where a common class limit is used between classes, the stated limit value falls in the class upwards of this value.

was to be expected since there is good internal drainage and a relatively high rainfall which does not easily permit accumulation of soluble salts.

On the mounds, the resistance of the soil is highest in the surface layer with an average of 2720 ohms (range of 2290 to 3150 ohms), a lower average of 1648 ohms (with a range of 1280 to 2100 ohms) for the remainder of the reddish brown horizon, and a still lower average of 1240 ohms (range of 1050 to 1400 ohms) for the underlying red horizon. On the flats, the surface layer soil has a relatively high resistance averaging 7360 ohms (with a range of 3300 to 11500 ohms) but in the remaining soil down to bedrock a still higher resistance is found, that is an average of 9500 ohms (with a range of 7100 to 12700 ohms). It is clear that the flat's soil has a much higher resistance than that of the mounds, indicating less soluble salts in the soil of the flats.

The resistance values for the profiles of the flats and mounds may be summarised as follows with the number of samples in brackets:

<u>Resistance (ohms)</u>	<u>Flats</u>	<u>Mounds</u>
> 3270	Whole profile (9/9)	-
3270 - 2270	-	Surface (2/2)
2270 - 1270	-	Rest of reddish brown layer (6/6)
< 1270	-	Red layer (2/3)

iv Calcium

In all the mound samples, the calcium content is higher than in all the samples of the flats. Samples throughout the profile on the flats vary from 0,12 to 1,37 me/100 g with an average of 0,52 me/100 g. The reddish brown horizon on the mounds has an average of 5,92% ranging from 2,22 to 8,75 me/100 g. The underlying red horizon of the mounds has a high average of 12,04 me/100 g ranging from 11,62 to 12,25 me/100 g. The mound soils thus have a calcium content which is at a maximum concentration below 2 m depth in the red sand. There are higher concentrations of calcium in the red sand below the mounds than in the red sands of the flats which may account for their differences in pH. In the texture analyses, free chalk was reported as occurring only in the red sand at the bottom of the mounds profile.

The calcium values for the profiles of the flats and mounds may be summarised as follows with the number of samples in brackets:

<u>Ca content (me/100 g)</u>	<u>Flats</u>	<u>Mounds</u>
< 2,00	Whole profile (9/9)	-
2,00 - 10,00	-	Whole reddish brown layer (8/8)
> 10,00	-	Red layer (3/3)

v Magnesium

The concentration of magnesium in the soils of the mounds is greater than that in the flats. The amounts appear to be fairly variable throughout each profile. The average value for the flat's soil profile is 0,23 me/100 g ranging from 0,04 to 0,44 me/100 g and there is an average of 1,16 me/100 g for the mound profile, ranging from 0,60 to 1,60 me/100 g.

The magnesium values for the profiles of the flats and mounds may be summarised as follows:

<u>Mg content (me/100 g)</u>	<u>Flats</u>	<u>Mounds</u>
< 0,50	Whole profile	-
> 0,50	-	Whole profile

vi Sodium

The sodium values are very low. The flats appear to have lower concentrations of sodium than the mounds. Of the values above trace amounts, the average for the flats is 0,01 me/100 g (with a range of 0,01 to 0,02 me/100 g), but for the mounds it is 0,03 me/100 g (ranging from 0,01 to 0,10 me/100 g). There are 3 trace samples out of 11 samples on the mounds and 6 out of 9 on the flats. For both areas 6 out of 7 samples have trace amounts in the surface layer against only 3 out of 13 samples below the surface layer. This indicates lower concentrations in the surface layer. The distribution of sodium through each profile appears to be fairly variable with perhaps a higher concentration of sodium in the red sand of the flats than in the upper reddish brown layer.

vii Potassium

The distribution of potassium is similar to that of sodium. The flats profile has a

lower average of 0,13 me/100 g (ranging from 0,06 to 0,24 me/100 g) compared to the mounds with an average of 0,29 me/100 g (ranging from 0,11 to 0,65 me/100 g). In the flats profile the average concentration is higher in the reddish brown soil than in the underlying red sand.

e Conclusions

Both profiles can be classified according to the South African soil classification system (Van der Eyk, Macvicar and De Villiers, 1969, revised by the National Institute for Soils and Irrigation, Department of Agricultural Technical Services, Pretoria in 1972) as the Mangano series of the Hutton form because both have an orthic A horizon on a red apedal B horizon. The lower horizon is classified as red apedal B because (i) the hue is 2,5 YR and values and chromas are more than 3 and 6 respectively, (ii) its structure is more weakly developed than a medium developed soil and (iii) it occurs beneath a diagnostic surface horizon. The upper horizon is classified as orthic because it has no properties which classify it as organic, humic, vertic or melanic, namely it (i) has less than 10% organic carbon, (ii) is structureless, (iii) has less than 15% clay and (iv) has light colours with values and chromas more than 3.

In the mounds, the main chemical differences between the 2 horizons are that, in the orthic A there is a lower pH and lower calcium content but higher resistance and percentage carbon than in the red apedal B. The concentrations of magnesium, sodium and even potassium are almost the same in both horizons. In the flats, the only clear chemical difference between the horizons is the higher percentage carbon in the orthic A. Calcium concentrations may be slightly higher in the orthic A and sodium concentrations slightly higher in the red apedal B. Concentrations of magnesium and potassium appear very similar in both horizons of the flats.

The relatively high fertility of the mounds soil is probably closely related to the distinctive species and dense vegetation of the mounds.

The 2 to 3 m deep soil is of great effective depth since it does not have any horizon

which physically or chemically limits root penetration and since roots were observed to low levels.

The reddish colour of both soils, support the earlier statements that the soil is well drained and has a high porosity, since, according to Maignien (1964), reddish colour is due to the weathering of ferro-magnesium minerals and the oxidation of the products.

2.4 Vegetation

The central part of the plateau contains a relatively uniform deciduous woodland savanna. The vegetation structure is simple (Fig. 2.4), consisting of a tree canopy layer, usually from about 3 to 7 m high, and a herbaceous layer with some grass culms up to about 2,5 m high. Only one species of shrub is common and is present in the lower part of the herbaceous layer. The more common trees belong to the species Burkea africana, Terminalia sericea, Combretum psidioides subsp. dinteri, Ochna pulchra and Securidaca longepedunculata (Figs. 2.4, 2.5 and 2.15). The only common shrub species present is the approximately half-metre high Grewia avellana, while Grewia deserticola is the only larger shrub species that is at least infrequently scattered in the area. Combretum collinum commonly forms thickets 3 to 4 m high (Fig. 2.16) usually positioned on low mounds of darker more fertile soil irregularly scattered through the area. The dominant herbs present belong to the grass species Digitaria polevansii and Brachiaria nigropedata, followed by Andropogon gayanus and Andropogon schirensis.

The partial tall grass aspect, provided by Andropogon gayanus in the herbaceous layer (see Fig. 6.1), as well as a definite stratification of tree and herbaceous layers, is similar to that observed in many areas well to the north-east in South West Africa. However, the height of the individuals of the tree species in the study area is lower than the height of the same species in areas well to the north-east. This is probably partially due to the considerable elevation (1847 m) of the study area above sea level, and to the relative shallowness of the soil compared with the great soil

depths of the Kalahari basin itself. Almost all the members of the flora of the study area are typical representatives of the woodland savanna vegetation type (Giess, 1971) of the north-eastern sector of South West Africa. This is remarkable since the study area is situated on the periphery of this vegetation type (Fig. 1.1), and is in close proximity to other localised rock-associated flora. The separateness of the vegetation of the study area from that of the adjacent areas is possibly due to the homogeneous sand covering of the study area.

2.5 History

References to the early history of the Waterberg area are made in the comprehensive work on the history of South West Africa by Vedder (1938). The reported visits of Gao-karib and Tjiponda to the Waterberg, possibly in the 16th and early 18th centuries, respectively, indicate that from these early times the Saan Bushmen and Bergdamaras were settled at the Waterberg. According to Vedder, these non-pastoral tribes practised extensive grass-burning to facilitate hunting. Vedder further indicates that, at the beginning of the 19th century, the Waterberg was still unoccupied by Hereros, although the Hereros were steadily increasing in other parts of the future Hereroland. Only later did the pastoral Hereros entirely dominate the Waterberg area. After the Battle of Waterberg in 1904, European-owned cattle increasingly supplanted those of the Hereros. It appears reasonably certain that most of the human history of the Waterberg was concerned with the areas around the fountains on the lower parts of the mountain, and not with the isolated and waterless summit of the Omuverume Mountain itself. The plateau, which until recently fell under the jurisdiction of the Monuments Commission, now falls under the Department of Nature Conservation and Tourism of South West Africa.

The Waterberg Plateau was originally referred to as the "Omuveroume" (= Gate) Plateau (Schinz, ca. 1891) and in 1904 Hartmann still called the entire Waterberg Plateau (excluding the Klein Waterberg Plateau) the "Omuweroumwe" Plateau. This name was replaced by the name Great Waterberg Plateau and the name "Omuverume" Plateau was then applied to the small insular south-western part of the Great Waterberg Plateau (Jäger and Waibel, 1921).

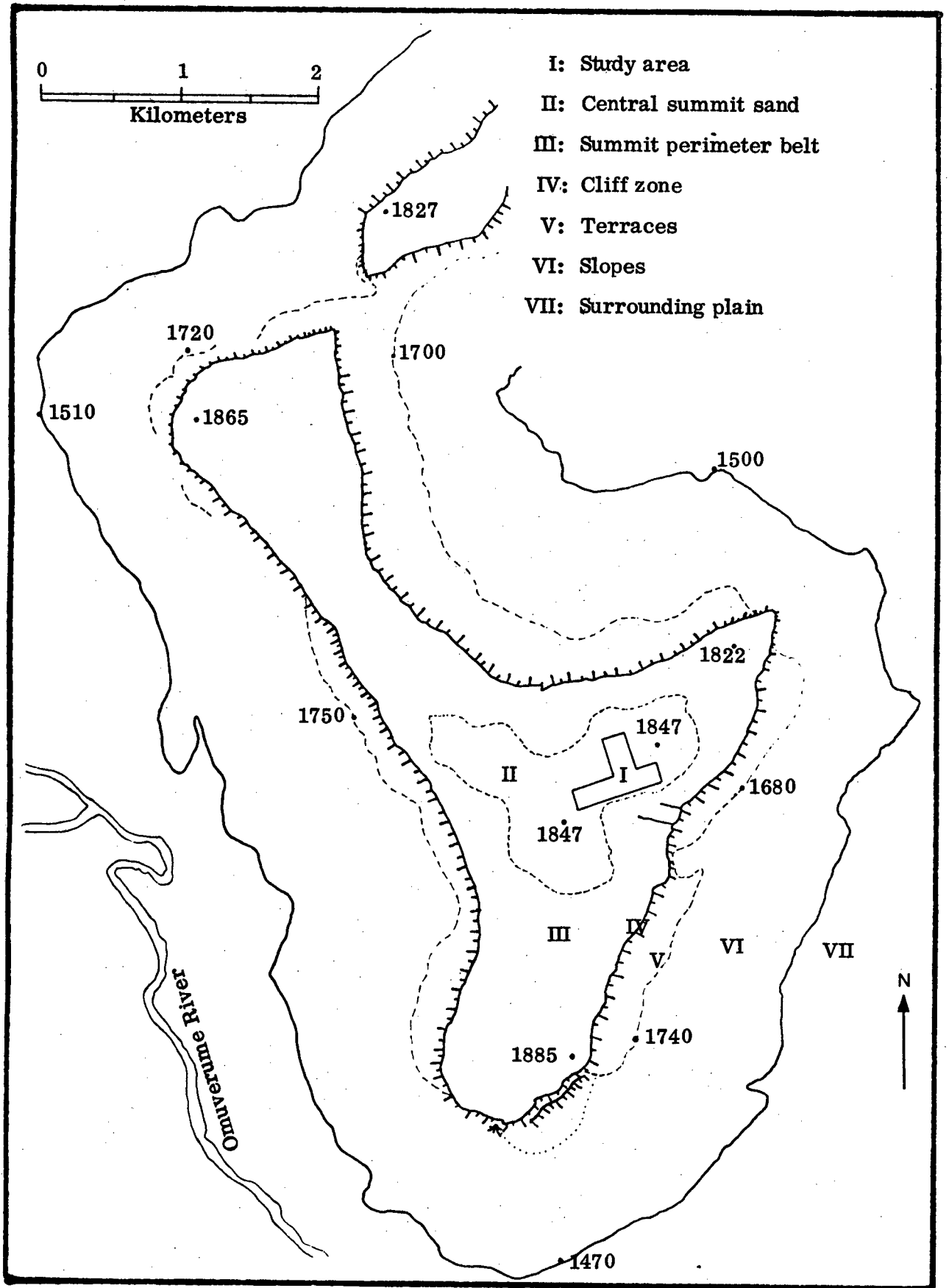


Fig. 2.1 Map showing position of the study area on the Omuverume Plateau-Mountain (Arabic figures are heights (m) above sea level)

Fig. 2.2 (on following page) The south-eastern side of the Omuverume Plateau-Mountain showing the sandstone capping that forms an encircling line of cliff that protects the plateau from larger herbivours.

Fig. 2.3 (on following page) The aeolian sandstone capping, showing its mode of vertical weathering. This capping forms the bedrock of the study area.

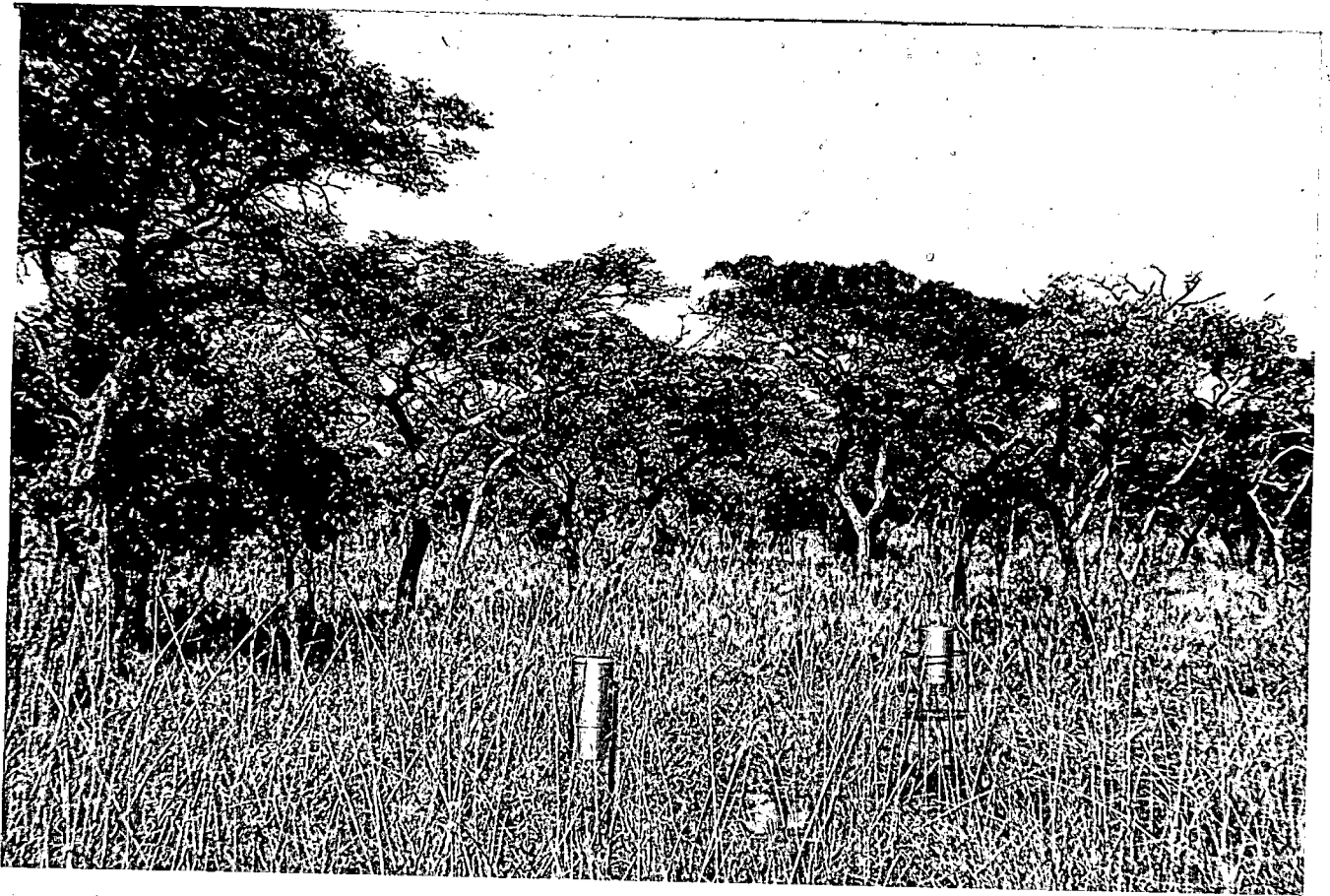


Fig. 2.4



Fig. 2.5

Fig. 2.4 (on following page) View of the Omuverume woodland savanna vegetation from an opening in which 2 raingauges were positioned. Burkea africana individuals are visible on the middle left and Combretum psidioides on the right.

Fig. 2.5 (on following page) Part of the Omuverume woodland savanna vegetation with a Stevenson screen in which the thermo-hygrographs were placed. Burkea africana is visible in middle, Terminalia sericea at right and a branch of a rare tree individual of Ozoroa paniculosa on the left.

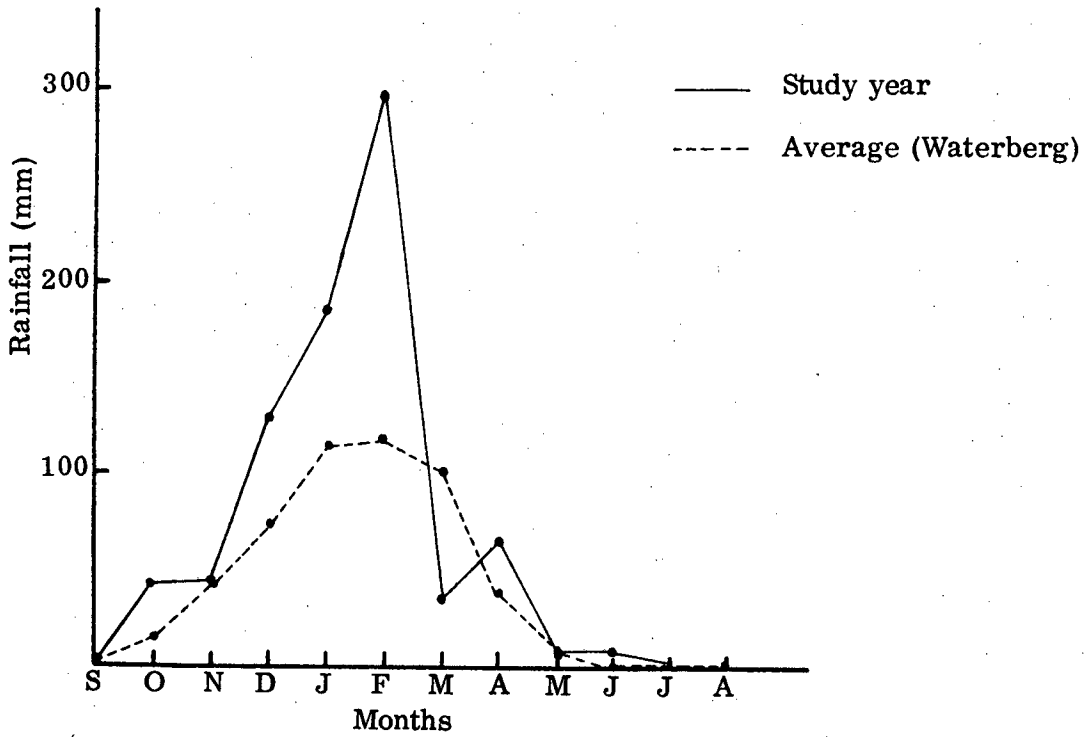


Fig. 2.6 Distribution of monthly rainfall for the study year (1970-71) on Omuverume and the average monthly rainfall distribution for Waterberg

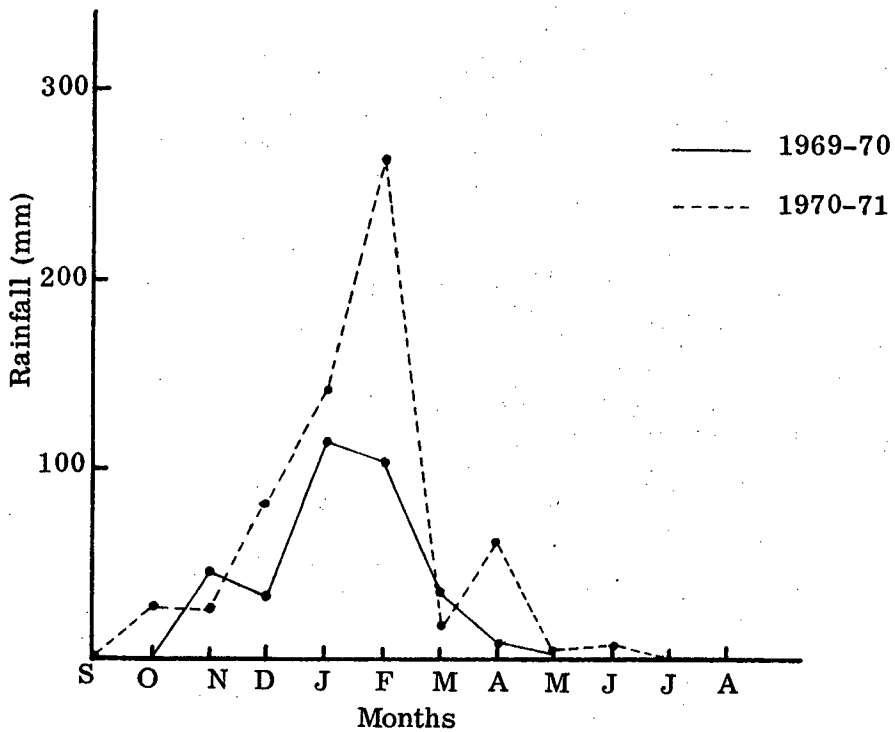


Fig. 2.7 Distribution of monthly rainfall at Okosongomingo during study year (1970-71) and previous year (1969-70)

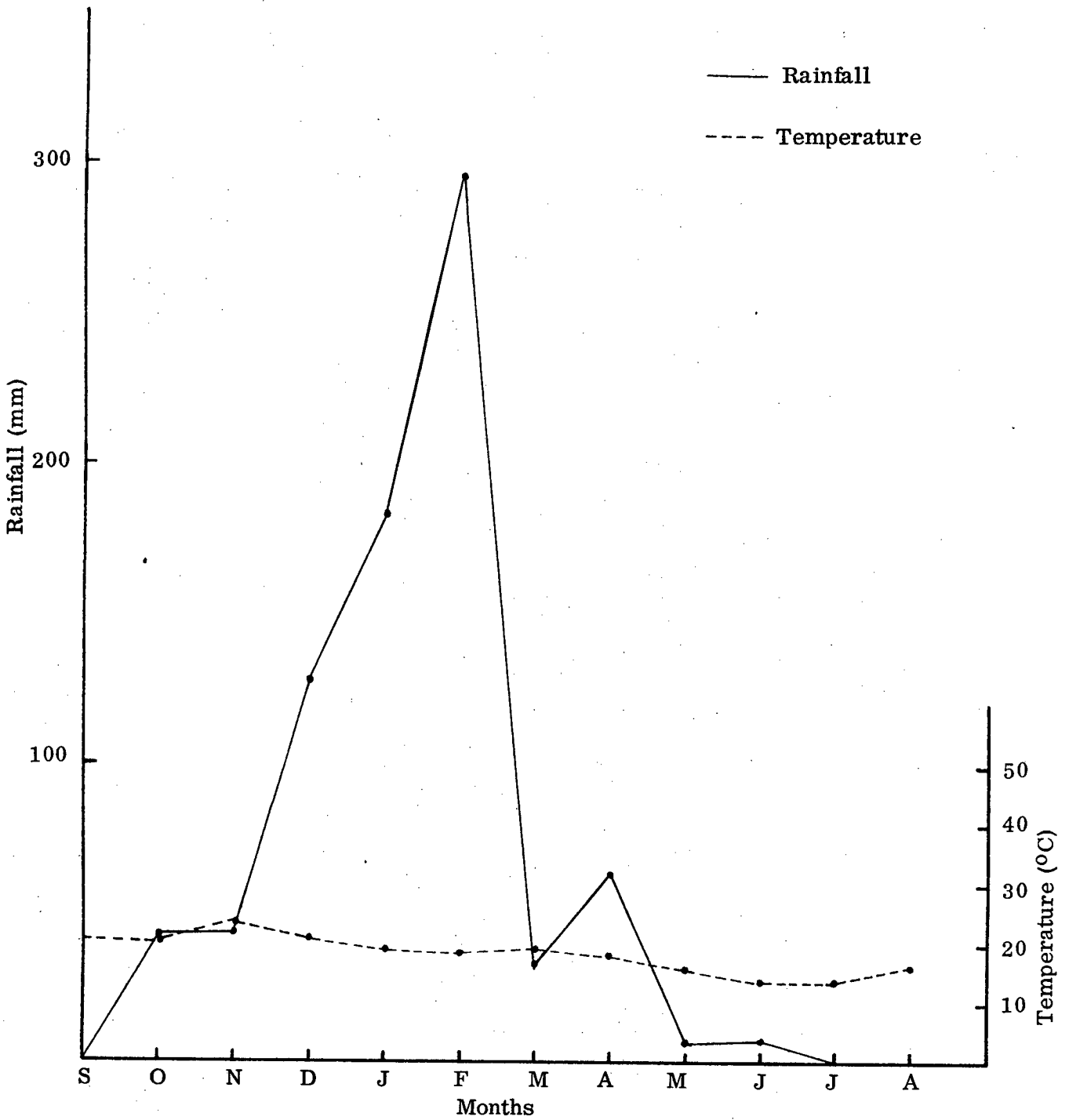


Fig. 2.8 Climate diagram (after Walter, 1962) for the study year (1970 - 71) on Omuverume showing the relation of monthly rainfall to monthly temperature

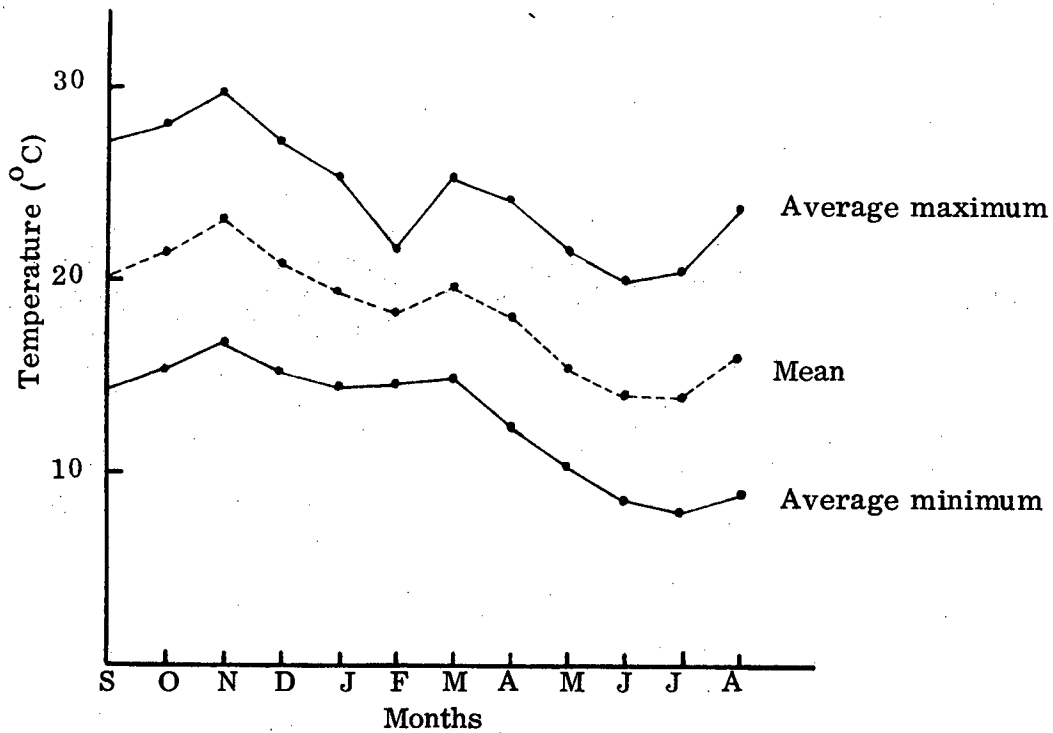


Fig. 2.9 Average monthly temperature during the study year (1970-71) for Omuvurume

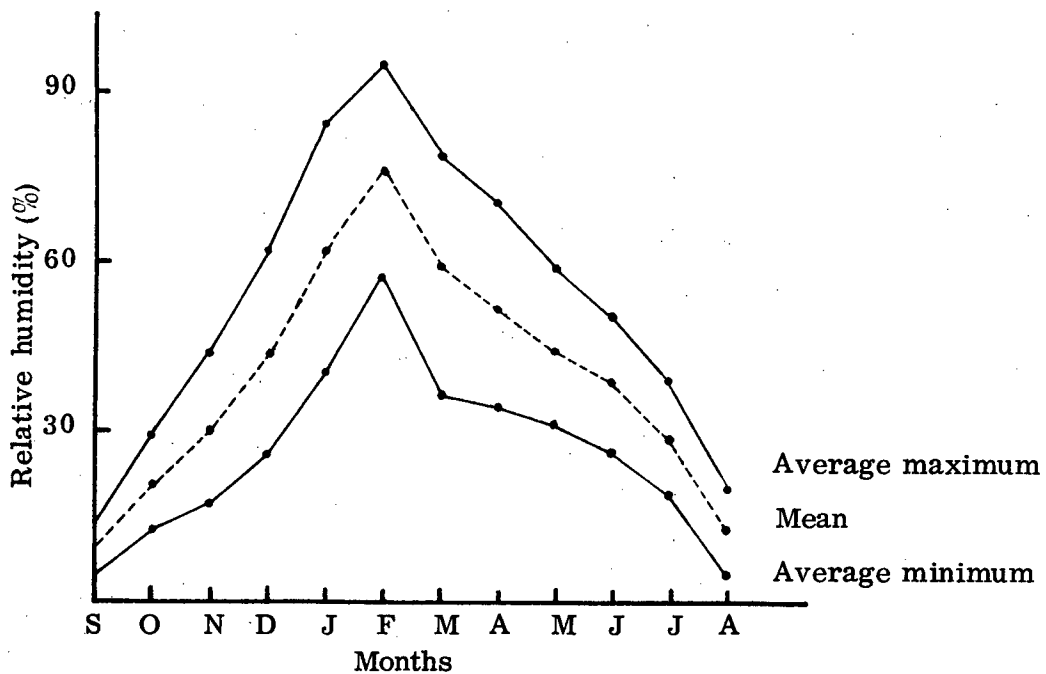


Fig. 2.10 Average monthly relative humidity during the study year (1970-71) for Omuvurume

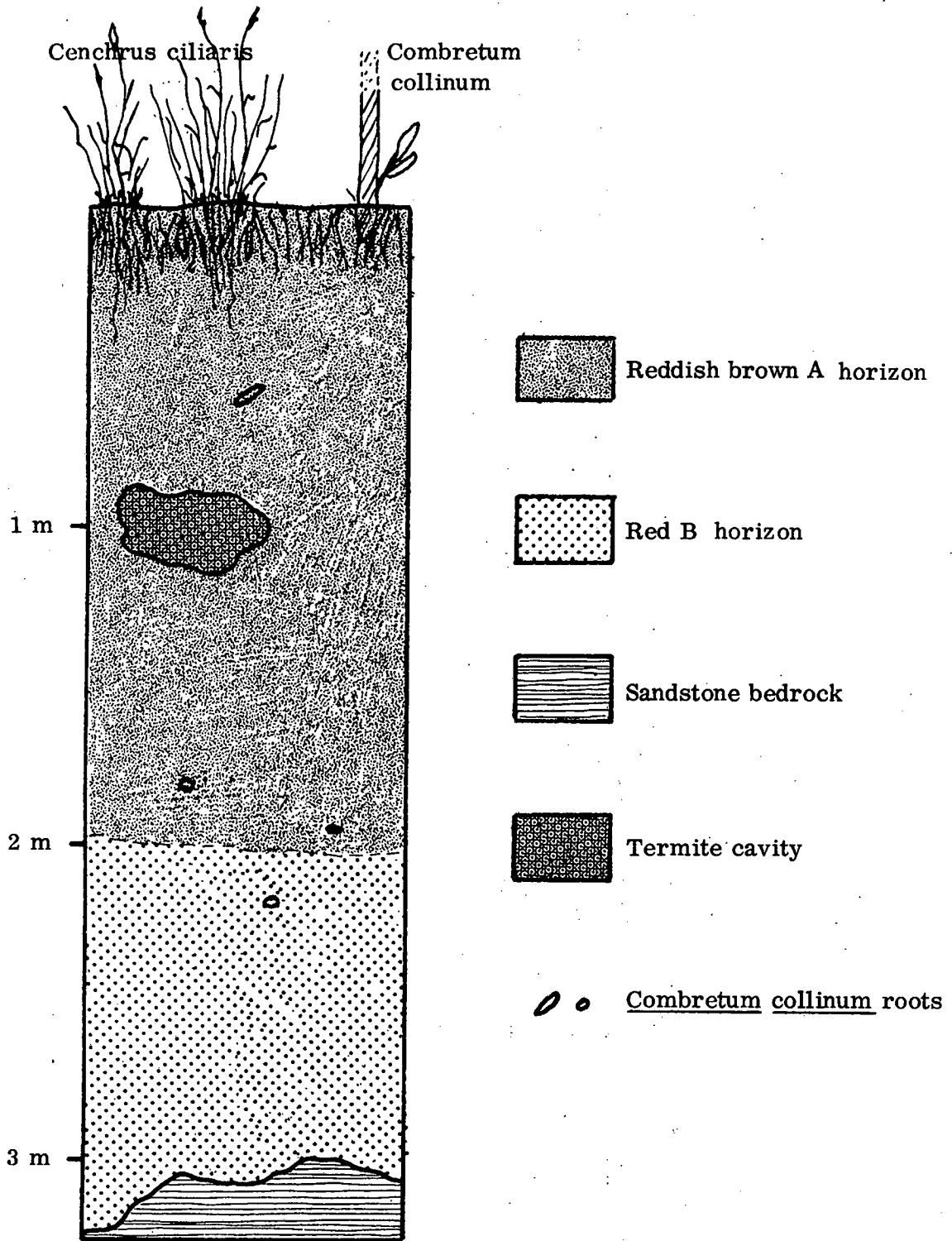


Fig. 2.11 Soil profile of a well developed mound on Omuverume

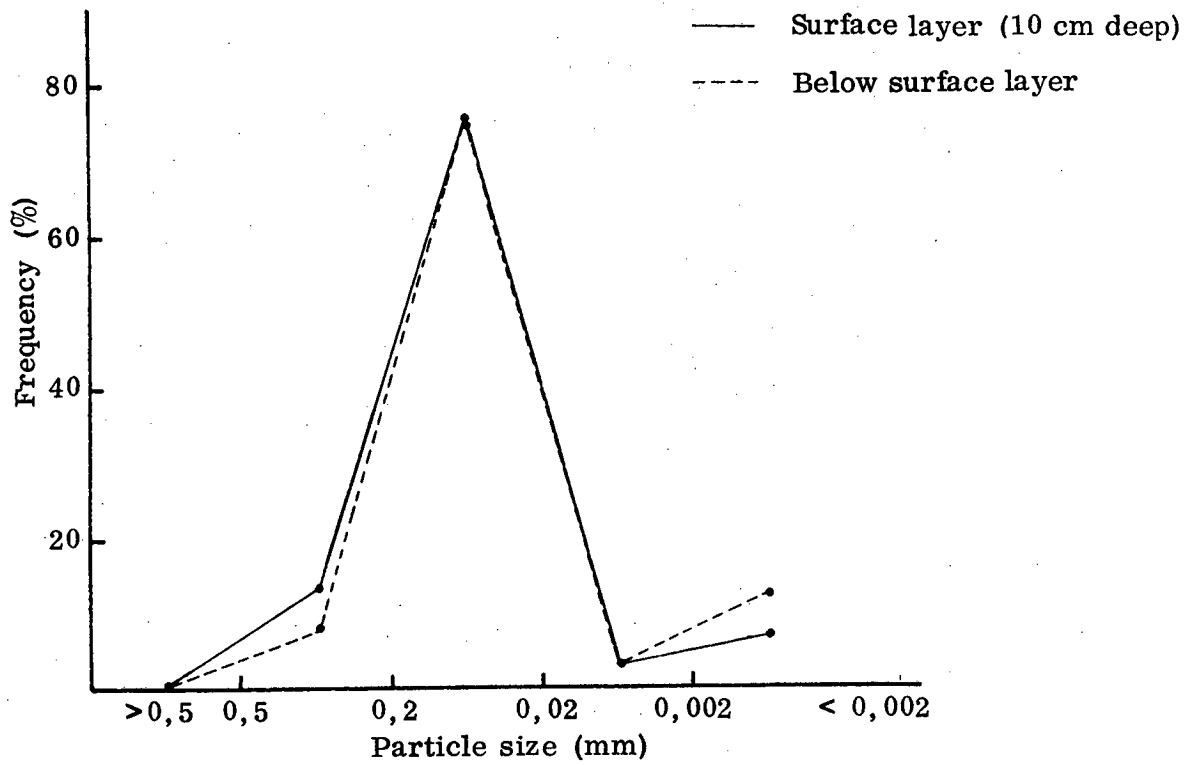


Fig. 2.12 Distribution of particle size for soils of the surface layer and that of below the surface layer

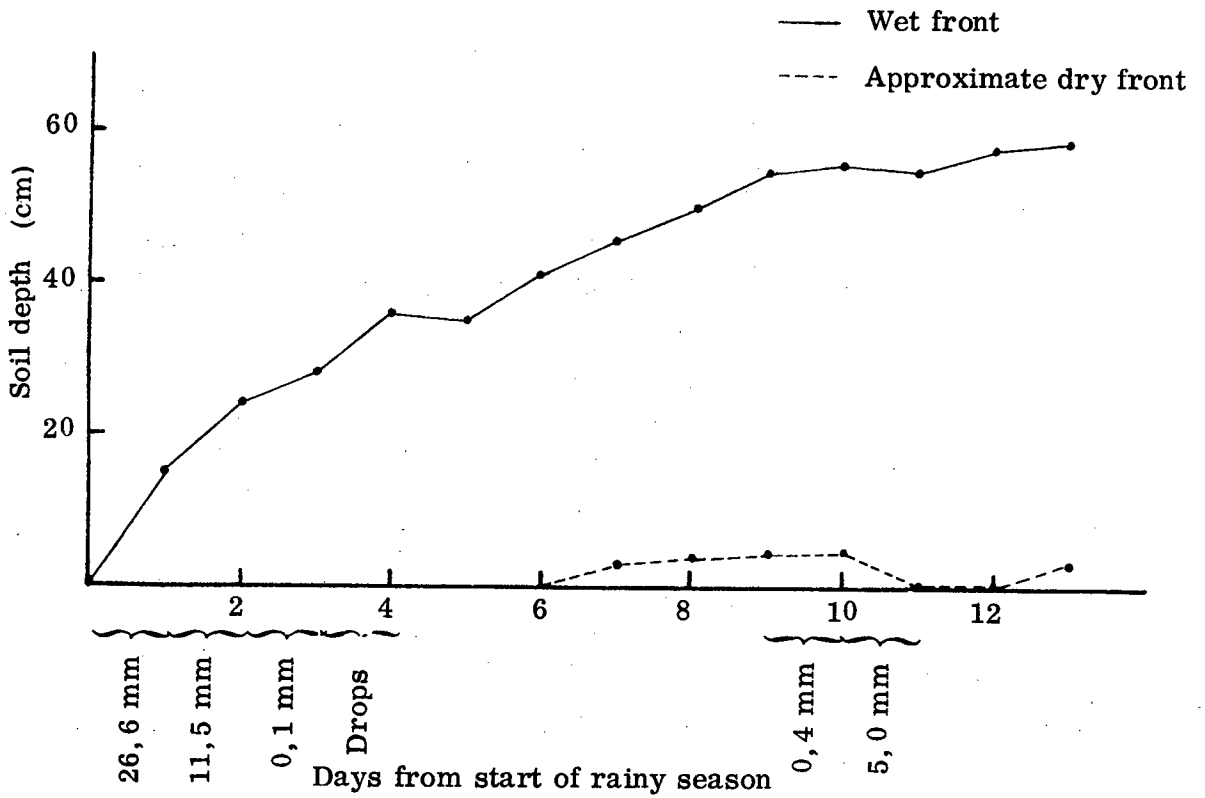


Fig. 2.13 Internal soil drainage pattern immediately after first rains of the rainy season showing the development of both wet and dry fronts and the periods and amounts of rainfall

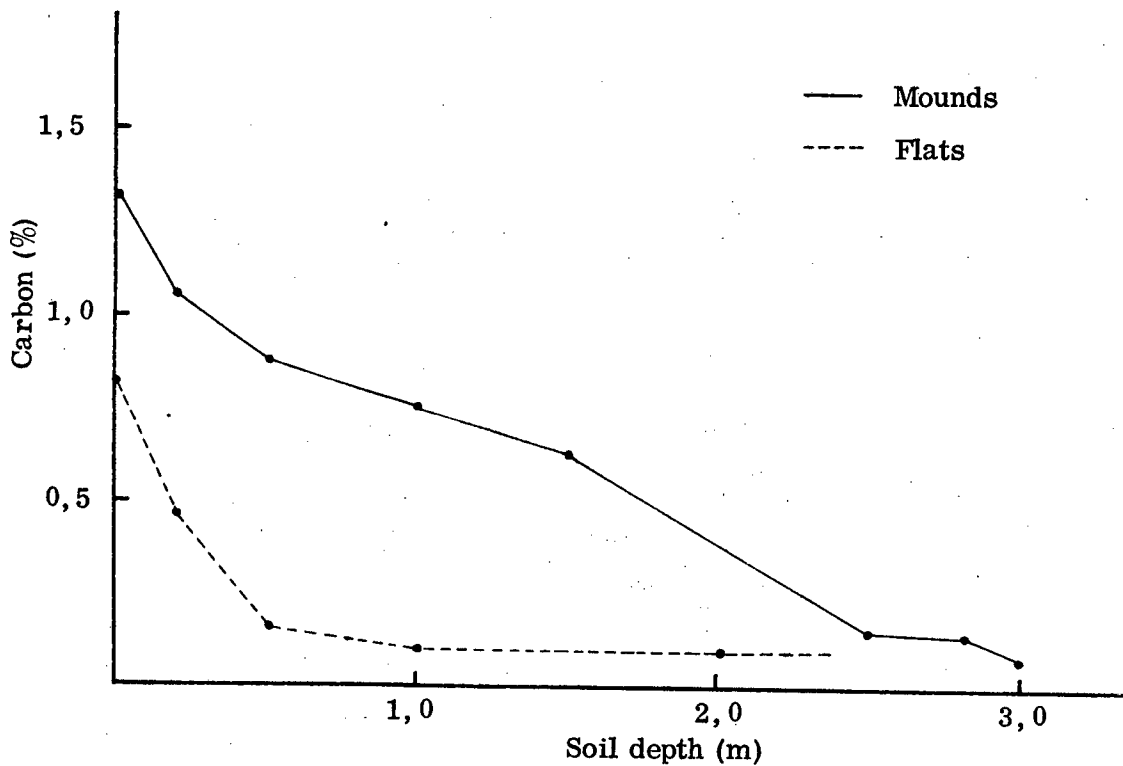


Fig. 2.14 Relationship between soil depth and the % carbon averaged per sampling depth for mounds and flats

Fig. 2.15 (on following page) An Ochna pulchra individual about 1,4 m high, just after appearance of new leaves.

Fig. 2.16 (on following page) A smaller thicket of Combretum collinum on a low mound. Burkea africana is seen in the background and Andropogon gayanus and Digitaria polevansii in the foreground.

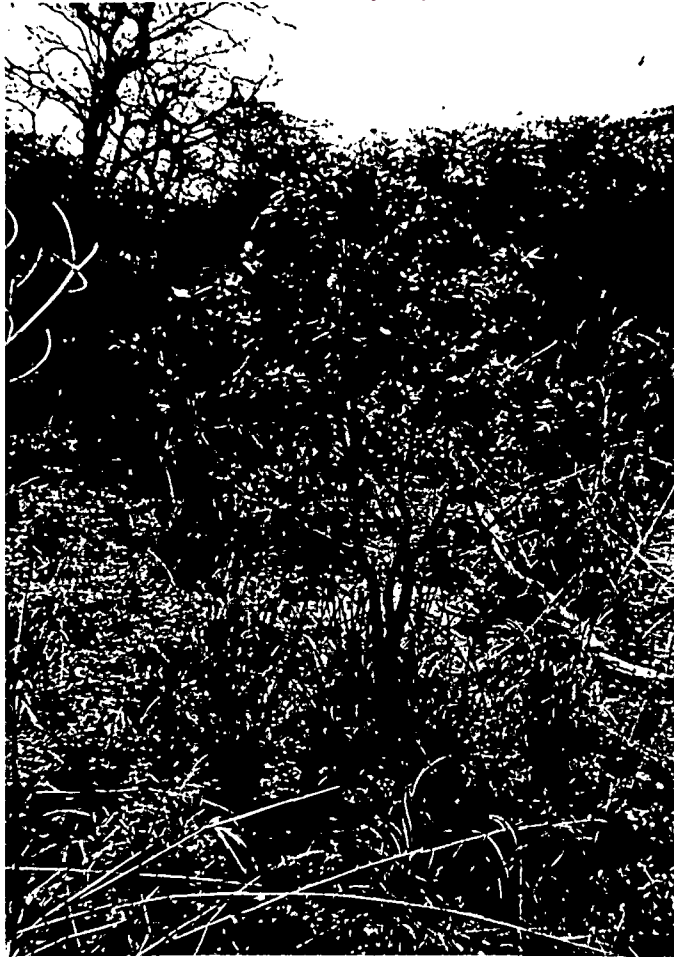


Fig. 2.15



Fig. 2.16

3 GENERAL SAMPLING LAYOUT

A T-shaped study area was selected to cover possible variation in vegetation composition more effectively in relation to the size of the study area. The study area was divided up in essentially the same way as that recommended by Newbould (1967) and endorsed by Milner and Hughes (1968).

The study area of 13 ha was divided into 4 sub-areas (Fig. 3.1) consisting of:

- (1) A small plot for stationing meteorological instruments, situated roughly in the centre of the study area.
- (2) A narrow buffer zone surrounding the meteorological plot.
- (3) Eight square ha blocks scattered throughout the remaining portion of the study area, each subdivided by grid-lines to facilitate reference to positions. These blocks constituted the measurement area for most of the systematic sampling.
- (4) The remaining land surrounding and lying between the above-mentioned areas. In this area, surveys were carried out that could not easily be fitted into the systematic sampling areas.

The large undisturbed region, surrounding the study area, provided an ample buffer zone against possible external disturbing factors.

Since the sampling methods used were usually specific to each study aspect, they are described separately in each section. However, a central programme of layout of sample quadrats existed for the monthly recording of production and some structural characteristics. Since these quadrats were used to obtain data for several different sections, the layout of the quadrats is described here, but the actual method of sampling in the quadrats is reserved for the appropriate sections.

As there was no opportunity for the extensive preliminary trials required to indicate the minimal sample size needed each month for significant differences in monthly growth of species to become apparent, it was decided that only from inspection of the data at the end of the study could the number of species which

provided adequate growth curves be related to the size of the sample taken. The largest-sized sample that could be analysed within a reasonable amount of time each month was thus taken. The sampling period each month should not exceed about 5 days, since with longer sampling periods, significant errors would probably occur due to growth and development of the vegetation during this period. Since, apart from the clipping of herbage-layer material and the density counts of individuals, the sampling period also included time-consuming sorting into species, old and new material, and generative and vegetative material, the maximum monthly sample size that could be considered, even with extra assistance in the active season, was 100 m^2 .

All the positions of the 1200 quadrats required for the monthly recording of production, density and frequency of species over one year were laid out according to a method of restricted randomisation. To avoid possible trampling during the study of quadrats not yet sampled, all the quadrats required were laid out and marked in advance. The first three ha blocks were divided as a whole into 75 equal square sub-blocks in each of which a marker-point was centralized. The position of each quadrat was laid out at random distance (read from random tables) along each of 8 equidistant radii from every marker point, making up a total of 600 quadrats. No quadrat was positioned at less than 2 m distant from the marker point or beyond the boundary of the particular sub-block. Thus no overlapping of quadrats was possible and buffer zones of at least 2 m wide were provided between the quadrats. In laying out the remaining 600 quadrat positions in the other 5 ha, the same procedure was followed, although a wider distribution of the 75 marker points resulted, since the 75 sub-blocks were now distributed over a wider area.

Each quadrat position was marked by an erect metal pole to which an index letter to a month of the year was affixed. The months were taken in a continuous series and assigned in clockwise direction around the marker points. When all 8 quadrat positions in a sub-block were marked in this way, the series was continued in the adjacent sub-block, each sub-block being completed in systematic rows across each of the 8 ha blocks. Quadrats for the sampling of data each month were thus randomly distributed in between the quadrats of the other months, and throughout the study area.

Each month, a quadrat frame was placed in position in a constant compass direction, at all the poles bearing the index letter relating to that month. The square aluminium quadrat frame had an inside dimension of 1 m². One side of the frame was hinged to include tree trunks. Another side was extended by about 0,5 m and terminated in a clasp that engaged with the base of the quadrat position marker-pole, thus avoiding sampling the vegetation which might have been affected by the long-term proximity of the marker-pole.

- I Meteorological recording area
- II Narrow buffer zone
- III Measurement area (hectare blocks)
- IV Surrounding area

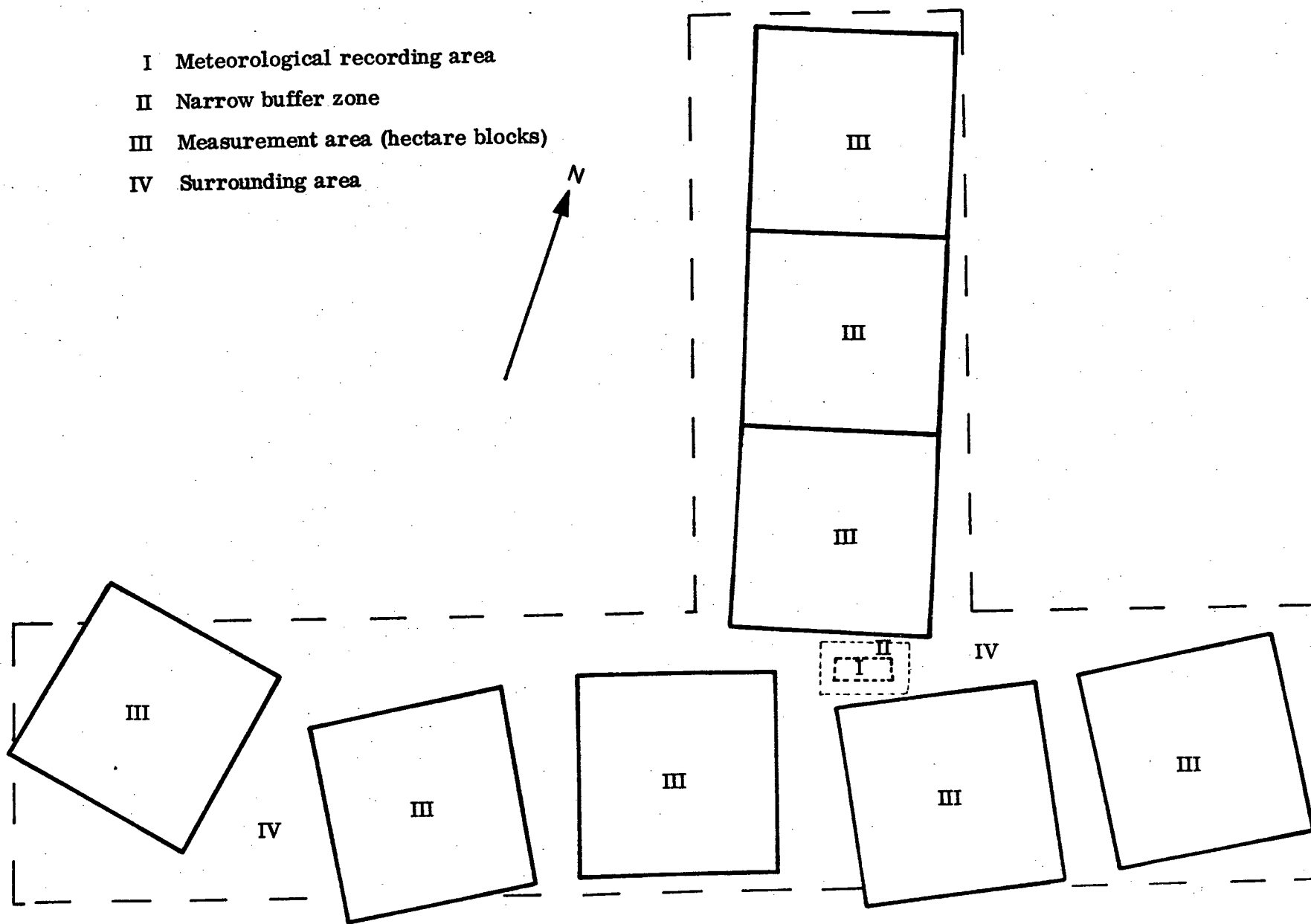


Fig. 3.1 Map of sampling layout of study area

4 VEGETATION STRUCTURE

4.1 Introduction

The extension of measured functional aspects from the vegetation of the study area to other similar areas, depends primarily upon accurate recording of vegetation structure as a basic form of reference.

Vegetation structure includes spatial distribution of species, numbers of individuals, physiognomy and cover.

A table of species giving structural and other data may be arranged according to an index of ecological importance values, instead of in taxonomic sequences based on relations of origin that are not necessarily eco-functionally significant.

Importance values such as the DFD index of Curtis (cited Greig-Smith, 1964) where relative density, frequency, and basal cover are added together, seriously underestimate, for example, the importance of the functional status of tree species relative to the herbaceous species. The functional significance of importance indices such as these appears to be limited. Hurlbert (1971) points out that "despite its past use in more static senses, the term 'importance' connotes ecological function". He quotes Whittaker as stating that "the best single measure of a species' importance ... is its productivity". On the study area, the entire herbaceous layer was razed to ground level by fire one season before the period of study. Thus, in the study period, the average aerial biomass of the herbaceous layer species may be regarded as loosely related to the average rate of production in the period from the time of burning to the time of study. This is commonly applicable in most tropical grassland areas (Bourlière and Hadley, 1970). Although biomass, as an importance value, was thus only strictly applicable to herbaceous layer species, it would for want of other comprehensive functional data, provide a reasonable measure of functional importance relative to the energy input and energy fixation in the ecosystem for all the species present. For this reason the species listed in Table 4.1 were arranged according to their respective biomass. As the nature of the tree and herbaceous layers is very different, the member species of these layers are listed separately.

4.2 Spatial and numerical structure

4.2.1 Density and frequency

a Method

In each of the 1 200 m square quadrats sampled for biomass throughout the year, the density of each species was recorded and the frequency of occurrence in these quadrats computed. The quadrat size of 1 m², governed by biomass sampling requirements, was not necessarily optimum for obtaining frequency data of each species. Data on the frequency of species was, however, in the light of the entire study considered less essential than the biomass data. Furthermore, although the quadrat size used for sampling the frequency of tree species was probably below optimum, for comparison of frequency and frequency dependent data between tree and herbaceous species, the quadrat size used for trees could not be different to that used for the herbaceous species. Frequency of a species, unaccompanied by further qualification, refers to the frequency of the occurrence of that species in quadrats of stated size and is expressed as a percentage. All other use of the word frequency pertains to the number of occurrences (as a percentage) of a defined object in a stated class and applies to statistical frequency distributions. The number of individuals, that is density, of each species, was counted by method of removal (Van Dyne, Vogel and Fisser, 1963) where the species growth form permitted, and was performed in conjunction with the clipping of the quadrats for the production study. By counting the individuals as they were clipped and removed, errors due to counting the same individuals twice were eliminated and the accuracy of counts was improved since no well hidden individual, for example in the base of a thick grass tuft, was overlooked. All individuals rooted in the quadrats were counted. Where only part of the base of an individual was present in the quadrat, it was recorded as half an individual for the density data, but as present for the frequency data, so avoiding recording a species with a positive density and no accompanying frequency. The error introduced by treating all parts of individuals as half-individuals was reduced for the more common species. Where the difference between live and dead individuals was clear, these two were counted separately.

Various difficulties arose in the density counts.

In some species, individuals were difficult to distinguish although a working definition of an "individual" could be made. In Ancylanthos bainesii and Grewia avellana it was convenient to define the closely grouped stems as an individual, although several adjacent groups were joined below the soil surface (Fig. 4.2). In some grass species,

especially Brachiaria nigropedata and Panicum kalahareense, with old tufts, dead and burned regions intervened between the live parts of the original tufts. These were treated as one individual except where a living part was more than about 5 cm from the other living parts, in which case two individuals were recorded. For the purposes of comparison, especially between months, these arbitrarily defined individuals appeared satisfactory.

In one species, it was difficult to distinguish individuals and also found very difficult to define an individual. This was the dominant grass species Digitaria polevansii which is a non-tufting species with occasional runners. Here counting was very subjective and data based on the density of this species should only be regarded as approximate. All other grass species present were tufting species and usually easy to count.

Individuals of Oxalis purpurascens were so numerous in one quadrat that the count was only approximate.

All creeper species were only included if rooted in the quadrat. In 2 quadrats with Pentarrhinum abyssinicum, and where the vegetation was very tangled, the count was approximate. (The clipping only included those parts of the individuals of this species that were in the quadrat.)

Regeneration shoots, if clearly part of a tree individual, were not recorded as separate individuals. Multistemmed trees were recorded as single individuals (Fig. 4.1) for production purposes.

In the count of dead individuals, only those still firmly fixed in the ground were counted. Fixed and loose individuals were not easily distinguished from each other in some representatives of Aristida meridionalis and Polygala kalaxariensis.

Unidentifiable species, usually seedlings, were counted and lumped separately. Counts of Basidiomycetes (fruiting bodies), Hepatics and mosses, although very rare, were recorded separately.

b Results

The tabulated density (living and dead individuals) and frequency figures (Table 4.1) are both averages of the monthly sets of data covering the natural seasonal fluctuation in density and frequency of each species population. Due to fluctuating numbers of individuals in some species, it is clear, that at no single time of the year, is a

determination of density a valid reflection of the comparative density status of those species. For example, the apparent density of some annuals, only present for half of the year, is not strictly comparable to the density of the other perennial species. By taking the average densities over the whole year, however, a statistically valid comparison may be made. Data of the individuals of tree or larger shrubs species occurring within the herbaceous layer is added to the data of the tree layer. It is clear that although density and frequency of species is roughly related to the importance (biomass) of the species, there are several exceptions, for example, where Cenchrus ciliaris, which is the 9th most important herbaceous layer species, is relegated to an inferior position when only density and frequency are considered.

With a density which exceeds 20 000 individuals per ha and a frequency of 90,33%, Digitaria polevansii is by far the most common (and dominant) species of the herbaceous layer. The 9 species with the next highest densities per ha are Tephrosia cephalantha (23 208), Grewia avellana (11 258), Brachiaria nigropedata (10 217), Cyperus margaritaceus (9 883), Andropogon schirensis (9 650), Aristida stipitata (8 825), Aristida meridionalis (5 342), Rhynchelytrum species (4 950) and Andropogon gayanus (3 075), and those with the next highest frequencies are Brachiaria nigropedata (48,42%), Cyperus margaritaceus(42,17%), Tephrosia cephalantha (41,58%), Andropogon schirensis (35,33%), Aristida stipitata (33,17%), Grewia avellana (30,75%), Aristida meridionalis (28,42%), Rhynchelytrum species (20,42%) and Andropogon gayanus (19,75%). Despite the variation in the sequence of density and frequency of species it will be noted that the same 10 species occur in both.

Unimportant species that have a relatively high density are Fimbristylis exilis (2 200 individuals per ha) and Oxalis purpurascens (1 300). These species are both made up of very small sized individuals. F. exilis also has a relatively high frequency (2,83%) although the O. purpurascens has not (0,33%). Due to the relatively high density and the relatively low frequency of O. purpurascens one expects that the distribution of individuals of this species is localized (aggregated). Other suspected aggregations occur in several other species with relatively high densities and low frequencies, for example in Eustachys paspaloides.

4.2.2 Species-area curve

a Method

Of all the 1200 m² quadrats laid out for sampling at the rate of 100 m² plots each month, only the samples of the 4 months of March to June were considered to include the maximum number of species for the curve of the cumulative frequency of species per number of quadrats (species-area curve), since before this period, some late annual aspect species were not readily recognisable, and after this period, some species were already shrivelled and unidentifiable, or absent. For this reason, the maximum size area for which the species-area curve (Fig. 4.3) could be accurately drawn was 400 m² that was made up of separate and randomly distributed quadrats which was a requirement for this curve (Greig-Smith, 1964). The quadrats were taken arbitrarily from March through to June, although the form of the curve is basically the same if taken from June to March. To facilitate the plotting of the curve, the quadrats were taken consecutively in groups of ten.

b Results

The species-area curve revealed that the 100 quadrats taken each month sampled all but rare and sporadic species. Although interpretation of the adequacy of sampling from this curve is limited since the exact form of the curve depends on the relative scales of the axes of the graph (Goodall, 1952), it is nevertheless an indication of 2 characteristic aspects of the vegetation of the study area.

The first characteristic becomes apparent from the gradient of the curve. As shown in Fig. 4.3, 60 different species had been recorded by the 400th quadrat. By expanding the sample size to cover the whole year's data, that is a sample of 1200 m², the number of species had risen slowly to 67. The 8 ha study area was very thoroughly inspected throughout the study year and was found to contain 95 species. It seems probable that in nearing the 80 000th quadrat, the number of species present would have risen to about 95. From the first quadrat sampled until virtually the entire study area was "sampled", the curve continues to rise and thus

no sample smaller than the whole study area will include all species. To include only about 70% of the species, a relatively large 1,5% of the study area must be sampled. Many of the rare species are "escapes" from the distinctive adjacent floras. Although totally unimportant to the function of the system (as far as energy fixation is concerned), the large group of rare species can provide a serious bias in any ecological expression based upon the percentage of total number of species present in the system, for example in Raunkiaer's (1934) "Biological Spectrum".

The second characteristic is seen in noting that the 2 most rapid relative rises in the 50 to 60 and to a lesser degree in the 90 to 100 quadrat intervals, are due, in each case, to a quadrat falling upon a mound. These rises indicate some heterogeneity in the vegetation of these mounds and the study area. Although the mounds have a very distinctive floristic composition, they constitute a very small part of the study area (about 2%), and they did not influence the lay-out of sample quadrats.

4.2.3 Distribution of frequency and density

A distribution of species in 5 frequency classes was drawn up to compare with Raunkiaer's (1934) "normal" distribution. Raunkiaer's J-shaped distribution, or "law of frequencies", states that in 5 equal frequency classes the lowest frequency class of 0 - 20% contains most species and is followed by a general fall in the next 2 or 3 classes. However, in the 5th class with the highest frequencies of 80 - 100%, a rise critical to the basic shape of the distribution, occurs. A common conclusion arising from this J-shaped distribution was that, apart from the usual decrease in number of species in the higher frequency classes, there are more "high frequency" (dominant) species in the community than there are those species with a frequency which is almost as high (sub-dominant) (Oosting, 1956).

As expected from the species-area curve, where a large number of rare species was indicated, the number of very infrequent species in the first class of the distribution was very high (Fig. 4.4a). Most species of this class had very low

frequencies (Fig. 4.4b). The sizes of the other classes also conform roughly to Raunkiaer's distribution and although only one species occurs in the 5th frequency class, the size of this class still exceeds the 4th class (with a frequency of 60 - 80%) in which there are no species.

This J-form distribution, with a 5th class strongly depressed compared to that of Raunkiaer's "normal", is indicated by Greig-Smith (1964) to be caused by, and indicative of pronounced aggregation in vegetation. A subsequent analysis (following section) confirmed that strong aggregation was present in much of the vegetation of the study area.

The J-form distribution has been shown to be theoretically misleading since the frequency classes include unequal density classes. For example, the 5th frequency class covers a potential range of density exceeding that of the remaining classes put together so that more species fall into this class than into, for example, the 4th frequency class (Greig-Smith, 1964; Kershaw, 1964). To test, in the light of these misgivings, the conclusion that there are more dominant species than sub-dominant species, a histogram of the distribution of species in equal density classes was drawn up (Fig. 4.5). This showed a slight but clearly evident J-form distribution, thus indicating at the end of the J-form distribution a larger group of species with a higher density than the group of species with a somewhat lower density.

It appears that, had the vegetation been less aggregated, the 5th frequency class would have been larger, indicating a greater number of dominant species than sub-dominant species. Despite misgivings, this interpretation was found to still hold true in the study area when dominance is measured in terms of density.

4.2.4 Aggregation

Since the frequency distribution of species suggests that aggregation of individuals of species is a characteristic of the spatial organization of the vegetation on a 1 m^2 scale, a short analysis of aggregation at this scale was undertaken.

Apparent aggregation occurs when more than one individual of a species is frequently recorded in a quadrat. As a species becomes more common however, this apparent aggregation may be due entirely to the increased number of individuals which may be randomly or evenly distributed. This apparent aggregation is thus only indicative of the average density or proximity of the individuals in the quadrats where they occur, and not necessarily indicative of aggregation as Daubenmire (1968) appears to have assumed. For example, Brachiaria nigropedata is shown to apparently "aggregate" slightly more than Ochna pulchra (2, 1 individuals per quadrat in which they occur as opposed to 2, 0), whereas Ochna pulchra actually aggregates considerably more than Brachiaria nigropedata (a ratio for aggregation of 1, 9 against 1, 5). Although 2 species are differently aggregated, as far as possible interaction between the numbers of their respective individuals is concerned, they are equivalent.

a Method

Determination of aggregation in a species entails detection of non-randomness in the distribution of its individuals, that is, where expected densities in random distributions are exceeded by actual densities in the field. When individuals tend to clump or aggregate together more than is expected had the same individuals been randomly distributed, the term overdispersion has been used (Greig-Smith, 1964). The theoretical case where individuals are more evenly spaced than is expected from a random distribution, has been referred to as underdispersion. Greig-Smith (1964) has pointed out that these 2 terms are confusing, and suggests the term "contagion" for aggregated distributions, and "regular" for evenly-spaced distributions.

Since the number of individuals of all the study species occurring in a one metre square quadrat does not usually approach the maximum number possible, the Poisson series may be applied as a basis of random distribution. It should, however, be noted that several species, such as tree species, are possibly aggregated on a larger scale than that of 1 m^2 while some species, for example Ochna pulchra, may be aggregated at both a 1 m^2 and at a larger scale. Aggregation, as given below, is only valid at a scale of 1 m^2 .

To indicate the degree of aggregation of each species, the method of ratio of observed density to calculated density as outlined by Greig-Smith (1964), was followed. The observed density is the total count of individuals of a species divided by the total number of sample quadrats. The calculated density is the expected density of a random distribution, and was estimated by using the known frequency of a species and Table 6 of Appendix B in Greig-Smith (1964), where the relation of observed frequency (F) to density (m) is given by $F = 100(1 - e^{-m})$. The ratio of observed density to calculated density is a measure of the degree of non-randomness in a population and is greater than 1 for contagious distribution, less than 1 for regular distribution and in the region of 1 for random distribution.

b Results

Ratios for aggregation in the study area are given in Table 4.1, column 5. The only species that was omitted from the analysis was Digitaria polevansii due to the aforementioned difficulty in density counts. Very rare species were also omitted. There were no regularly distributed species present. The ratio of less than 1 for Eragrostis pallens was due to the many half-individuals recorded. All distributions are thus random or of differing degrees of contagion, which corresponds well with Kershaw's (1964) observation that "little evidence has appeared to suggest that regular distribution of individuals (underdispersion) is of more than rare occurrence in vegetation".

The 22 random or almost random species with an arbitrary range of ratio for aggregation of 1,0 to 1,2 include the tree species - inclusive of one large woody shrub species - but with the exception of Ochna pulchra. A larger scale of about 25 m² would probably have contagion for the tree species Combretum collinum, Combretum psidioides, Terminalia sericea and Dombeya rotundifolia. The other 16 more or less randomly distributed species are herbaceous and generally rare, that is all have a frequency of less than 4%. The most frequent species which was more or less randomly distributed was Turbina oblongata with a relatively low frequency of 3,67%. However, most of the other rare species, with a frequency of less than 4%, have definite degrees of contagion. Most of these can be grouped

into (i) pioneer species, for example, Kyphocarpa angustifolia, Pygmaeothamnus zeyheri, Nidorella resedifolia and Fimbristylis exilis; (ii) mound associated species, for example Cenchrus ciliaris, Oxalis purpurascens, Panicum maximum, Rhynchosia sublobata and Pentarrhinum abyssinicum; and (iii) distinct patches of single species, for example Eustachys paspaloides or Panicum kalaharensense. The last group would also include Eragrostis pallens if the scale for contagion was increased slightly.

Of all the more common herbaceous layer species under consideration in the study area, that is all 15 species with a frequency of more than 5%, none approach a random distribution (ratio 1,0 to 1,2). Although 3 of these species (Andropogon gayanus, Triraphis schinzii and Commelina africana) occur in an intermediate class of contagion (ratio 1,3 to 1,4), all the other 12 species are clearly aggregated (ratio \geq 1,5). Ancylanthos bainesii and Grewia avellana both have a high ratio of 3,1 due to the mode of vegetative growth where underground parts connect defined "individuals".

To contrast the aggregation of rarer (frequency less than 5%) and more common (equal to or more than 5% frequency) herbaceous layer species (Table 4.2) the 2 groups are tabulated as percentage of total (56) species present - Digitaria polevansii excepted. The majority of species (71,4%) have some degree of aggregation at a scale of 1 m². Since many of the non-aggregated remaining 28,6% of the species are aggregated at a larger scale or are only present as one individual and cannot show aggregation, it appears that aggregation of species in the study area is a common characteristic. It is particularly evident that none of the more common species are randomly distributed, almost all being clearly aggregated. This is in general accordance with the popular observation (reported by Greig-Smith, 1964) that in contrast with the various aggregations possible in rare species the "commoner species are usually not randomly distributed".

To investigate the level of significance of aggregation of the majority of more common species with ratios for aggregation equal to or greater than 1,5, a species with the lowest ratio in this group was chosen as a test species. Aristida congesta was selected and had a ratio of 1,5 and was also the species with the lowest frequency in the group (5,42%). As the mean density of the Aristida congesta population was very low,

the X^2 (= chi squared) test to compare the terms of the Poisson distribution with the observed data could not be carried out since only 2 adequate classes of numbers of individuals (0 and ≥ 1) were obtained which provided no degree of freedom required for the X^2 test. Greig-Smith's (1964) advice that "when the mean is very low we are ... dependent on the variance: mean ratio test for lack of a better one" was followed.

$$\sum(x)^2 - \frac{(\sum x)^2}{N}$$

The variance was calculated as $\frac{\sum(x)^2 - \frac{(\sum x)^2}{N}}{N - 1} = 0,1976$

and thus the ratio of the variance to the

$$\text{mean} = \frac{0,1976}{0,0867} = 2,2791$$

To test the significance of this ratio, a t-test was carried out where

$$t = \frac{\text{observed variance/mean} - \text{expected variance/mean}}{\text{standard error}}$$

where the standard error of this ratio is $\sqrt{\frac{2}{N - 1}}$

Since expected variance/mean = 1 for the Poisson distribution then

$$t = \frac{2,2791 - 1}{0,0412} = 31,05, \text{ which for } 1\ 199 \text{ degrees of freedom, is extremely significant.}$$

As the other members of this group of common species have ratios for aggregation higher than that of this extremely significantly aggregated test species, it appears likely that most species of this group are highly significantly aggregated. The ability and opportunity to aggregate appears, therefore, to be a fundamental characteristic of species that successfully control the community. The high incidence of aggregation is also of fundamental importance to the interpretation of density-frequency relations (c.f. Brown, 1954) and of sampling errors when compiling growth curves.

4.2.5 Species density and richness

In all the 1 200 m² quadrats sampled, the average number of species per quadrat

was 5,12. A distribution of this species density per quadrat is given in Fig. 4.6. No quadrat was empty. The percentage of quadrats with only one species present was very low (1,42%), but the percentage of quadrats increases rapidly for higher numbers of species until there are 5 species per quadrat (21,17% of the quadrats). Thereafter the percentage of quadrats drops rapidly for increasing number of species until about 9 species per square metre is recorded in 2,50% of the quadrats. Quadrats with more than 9 species are relatively rare, although the maximum number of species per quadrat is 13. The species density in a quadrat varies with the species present.

For all the Aristida congesta quadrats, the distribution of species density per quadrat (Fig. 4.6) is essentially the same as that of the total number of quadrats, except that it is uniformly displaced to the right due to an overall increased species density. The average species density of these Aristida congesta areas is thus, not unexpectedly, higher than the average for the whole area, and is 6,94 species per square metre. In these Aristida congesta areas there is a clear tendency for preference for high density extremes (about 6 species above average) rather than for low density extremes (about 4 species below average).

The average number of species per Dicliptera eenii quadrat is about 5,75 and the distribution conforms roughly to that of the total number of quadrats.

Species density per square metre does not, however, convey any information on species richness, that is, there is no indication of how many different species are concerned in the Aristida congesta and in the Dicliptera eenii areas. Hurlbert (1971) points out that since species richness tends to increase with the size of the collection of organisms, comparisons of species richness are meaningful only when all "collections" are adjusted to a common size. A rough comparison of species richness of the Aristida congesta and Dicliptera eenii areas can be made by recording the species in a random selection of the quadrats which make up the larger Aristida congesta area. This random collection should be equal in number to the quadrats which make up the smaller Dicliptera eenii area. In the 30 m² Dicliptera eenii area, 24 species were recorded whereas in the randomly composed

area of 30 m² of the Aristida congesta area, 34 species occurred. It thus appears that Aristida congesta quadrats do not only have a higher species density per quadrat than the Dicliptera eonii quadrats but also a higher species richness.

4.2.6 Species-associations

An analysis of species associated with the 2 species (Aristida congesta and Dicliptera eonii) with different species density and richness was undertaken. These 2 species were selected as representing areas of probable dissimilar functional status on the flats (that is mounds excluded). Aristida congesta (Fig. 4.7) was typically represented on certain small bare-surfaced, potentially unstable, and unshaded patches, and is a well-known and recognised pioneer or seral species (Rattray, 1960; Jones, 1968). Dicliptera eonii (Fig. 4.8) was a typical representative of more stable, relatively densely vegetated areas, often in the shade of trees. Randomly selected individuals of these species (for phenological observation) had 9 out of 10 Aristida congesta individuals on relatively bare soil, and 6 out of 10 Dicliptera eonii individuals on soil with a thin tree-leaf litter layer, 5 of which also with a layer of decomposing organic matter. Although Dicliptera eonii individuals are later shown to be significantly associated with the mounds relative to the flats, only the individuals on the flats were considered here.

Both the above 2 areas, each with their respective species, were analysed for significantly associated species. The presence or absence of each species in the quadrats concerned was placed in a 2 x 2 contingency table and a X² test carried out to determine significant association with Aristida congesta and Dicliptera eonii areas.

A relatively large number (10) of species was found to be highly significantly associated with the Aristida congesta blocks. These were Anthospermum ericoideum, Aristida meridionalis, Cassia biensis, Cyperus margaritaceus, Fimbristylis exilis, Ochna pulchra, Pogonarthria squarrosa, Polygala kalaxariensis, Rhynchelytrum species and Turbina oblongata. The instability of this area is clearly shown since

apart from Aristida congesta, some of these species, for example, Fimbristylis exilis, Pogonarthria squarrosa and Rhynchelytrum species, are also pioneer species (c.f. Rattray, 1960). Four species were significantly associated with the Dicliptera eonii blocks. These were the herbaceous species Commelina africana and Mariscus laxiflorus and the tree species Combretum psidioides and Terminalia sericea.

An illustrative diagram (Fig. 4.9) showing these two functionally distinct associations of species, is given. The associated species are arranged around each of the selected species on radii, the length of which is a measure of the strength of association, that is, the shorter the radius line the stronger the association, where the radius $r = \frac{1}{X^2}$. The dotted circle around each association represents the limits of 95% confidence. The associated species with the highest frequencies have been placed toward the centre of the diagram as it is these species that have the greatest probability of being associated with other species intermediate to these 2 groups of functional distinctiveness. Also shown are the few negative associations which could be calculated.

It is clear that the Aristida congesta quadrats contain a closely-associated group or "node" of species, whereas the Dicliptera eonii quadrats contain a laxer association of fewer species.

Due to the statistical inefficiency of the X^2 test for indicating significant association of a species with a large area in contrast to one with a small area (for example, in the case where Ochna pulchra is common in the large area outside the Dicliptera eonii quadrats but is absent within these quadrats, no significant difference is indicated), only a few negative associations (that is positive association with non-Aristida congesta or non-Dicliptera eonii quadrats) were indicated at a probability level of greater than 90%. The species which significantly avoid Aristida congesta quadrats are Grewia avellana and Tephrosia cephalantha, while those avoiding Dicliptera eonii quadrats are Tephrosia cephalantha and Aristida meridionalis. Tephrosia cephalantha had the most rapid increase of density of individuals during the study season. It is not unexpected that its new individuals avoid the relatively densely covered Dicliptera eonii quadrats but the avoidance of the relatively open

Aristida congesta quadrats is of particular interest. Areas with Aristida congesta are not, however, the only relatively bare and open parts of the study area.

These two associations, each distinguished by one typical species, will subsequently be shown to be functionally different in several respects. In the unstable areas with Aristida congesta, the soil is bare and relatively poor in nutrients, and the biomass of plants per square metre less than average. However, as previously seen, the number of individuals per square metre is higher, the species richness is relatively high and the associated species are those that aggregate significantly. In the relatively more stable areas of Dicliptera eeni, the characteristics of the above area are reversed, that is the soil is usually covered and has higher concentrations of nutrients and it has a relatively higher biomass per square metre than average, while, the number of individuals per square metre is relatively lower, the species richness is lower, and the associated species are species that aggregate only to a slight degree, although many of the other species present here may be aggregated.

4.2.7 Mounds

Irregularly scattered in the 13 ha study area were 7 areas which were slightly raised above the surrounding ground. The mounds constituted only about 2,3% of the 8 ha measurement area. No mound was less than 50 m or more than 170 m from another. The mounds were roughly circular in shape and varied in diameter from about 4 to 20 m and in height from about 10 to 60 cm, usually at the centre of the mound.

Mound vegetation, with a dense herbaceous underlayer, varied from a 3 to 4 m high canopy with closely grouped tree-stems with some regeneration from their bases (Fig. 4.10c) to dead tree stems 2 to 3 m high with prolific basal regeneration.

Most species on the mounds were not found on the surrounding flats. The floristic composition of each mound was noticeably distinct from that of other mounds. To show the degree of difference between the flora of the mounds and that of the

surrounding flats, a separate survey was carried out. The 7 mounds in the study area, as well as an 8th mound on the border of the study area, were included in the survey. The close association between the mound areas and the thickets of Combretum collinum and Dombeya rotundifolia was used as a basis for delimiting these areas. The perimeter of each mound was marked by the stem bases of peripheral individuals of the above 2 species.

To sample presence of species, 155 m² quadrats were randomly distributed over the 8 mounds, the number in each mound area being determined by the size of the mound, but maintaining a minimum of 15 quadrats per mound. Altogether 514 m² quadrats were randomly placed in the intervening flat areas between the mounds.

This survey confirmed that the mounds had a very specific floristic composition relative to the rest of the study area, and were themselves different from one another. Many of the species found on the mounds were typically found on the edge and slopes of the Omuverume Plateau-Mountain (Rutherford, 1972). Only the mound defining species Combretum collinum as well as the ubiquitous Digitaria polevansii were present on all 8 mounds (Table 4.3). The ubiquitous Andropogon gayanus had a presence value of 7, Cenchrus ciliaris and Dicliptera eonii a presence of 6 and Dombeya rotundifolia a presence of 5. All other mound species presence values were low. Presence values refer to the number of mounds on which the species occurred and are not expressed as percentages since the total number is only eight.

On the mound areas, Combretum collinum had the highest local frequency (53,4%) followed by Cenchrus ciliaris (45,8%). Other species with a local frequency of greater than 2,5% are given in Table 4.3. Local frequency refers to frequency of a species on the mounds alone.

To indicate the degree of floristic difference between the mounds and the surrounding flats, X² values were computed for each species, and those species significantly different at a level of probability equal to or greater than 95%, are marked with an asterisk in Table 4.4. Fourteen species, for example, Combretum collinum, Cenchrus ciliaris, Dicliptera eonii, Rhynchosia venulosa and Panicum maximum were found significantly associated with the mounds, and 22 species, for example, Digitaria polevansii, Tephrosia cephalantha, Grewia avellana, Brachiaria

nigropedata and Cyperus margaritaceus with the flats. Since amongst the more common tree species present, Combretum collinum provides most shade throughout the year, the association of shade species, such as Panicum maximum and Dicliptera eonii with the mounds, is expected. The flora of the mounds is so significantly different to the flora of the flats that both the two most frequent species of each area, viz., Combretum collinum, Cenchrus ciliaris, and Digitaria polevansii and Brachiaria nigropedata respectively, have X^2 values of greater than 100 for 1 degree of freedom.

The ratio of the frequency of a species on the mounds to the sum of its frequencies on the mounds and on the flats (Table 4.4), indicates the relative difference in the frequencies of the 2 areas, that is a species with a ratio of 1,00 is exclusive to the mounds; 0,50 indicates a frequency equal on the mound and flats and a ratio of 0,00 exclusive to the flats. There is a relatively large group of 16 species with a relative frequency ratio of 1,00, that is, exclusively confined to the mounds, and also a large group of 39 species with a ratio of 0,00, that is, exclusively recorded on the flats. Most, that is 11, of the remaining species in the survey are very nearly exclusive to the mounds (ratio 0,99 to 0,95) or to the flats (ratio 0,049 to 0,001). The mound defining species, Combretum collinum, with a ratio 0,99 to 0,95, shows its slight occurrence on the flats. It occurs here as a few small groups of stems, and as one isolated tree about 7,5 m high. The remaining 8 species occur in the large range of ratios 0,949 to 0,050 which shows that very few species approach a more or less equal frequency in both areas. Only one common species, Andropogon gayanus, has almost equal frequencies, with a ratio of 0,54. This corresponds with findings of Andropogon gayanus on diverse soils throughout Africa (Bowden, 1964).

The origin and significance of the mounds is obscure although it appears that some of the mounds have vestigial characteristics of some termitaria described from other parts of Southern Africa. For example, there are, apart from a few old termite cavities (Fig. 2.11), similarities in soil properties such as relatively higher pH value and a greater retention of bases, as well as the occurrence of some termitaria-associated species (exclusively associated with the mounds of

the study area) such as Ziziphus mucronata in Rhodesia (Watson, 1967), Panicum maximum in Tanzania (Boaler, 1966) and Cenchrus ciliaris which is often found on "ant-hills" in Rhodesia (Ratray, 1960).

Further consideration of the origin of the mounds is given in the section on chemical analysis of plants (Section 5.3).

4.3 Physiognomic structure

4.3.1 Vegetation profile

Three non-overlapping belt-transects were laid out at random in the study area. Each transect was 40 m long and 10 m wide. All woody species with a basal stem diameter of greater than 1 cm were plotted on a map of the belt areas. Total height of individuals, height of the base of the canopies, canopy widths and height of the lowest branch of each individual were recorded by clinometer and measuring staffs, and individuals were then drawn to scale in a profile diagram (Fig. 4.10a, b, c) as viewed from one side of the transect. The form of the individuals and the canopy shape were drawn in from inspection in the field.

In all 3 transects (Fig. 4.10a, b, c) the canopy height varies greatly, although Burkea africana and Terminalia sericea usually form a roughly defined upper canopy while Combretum psidioides tends to form a somewhat lower tree layer. Ochna pulchra, a common diminutive tree, is clearly seen in Fig. 4.10a. Scattered Grewia deserticola shrubs are seen in Fig. 4.10a, c with an Ozoroa paniculosa shrub-form in Fig. 4.10b. Part of a mound, densely covered with Combretum collinum, is included in Fig. 4.10c.

There is an immediately apparent variation in canopy density which corresponds well with that of the profiles of similarly structured vegetation (which includes Burkea africana) of Ghana (Lawson, Jeník and Armstrong-Mensah, 1968) and Nigeria (Hopkins, 1962). The aggregate groupings of Terminalia sericea and

Combretum psidioides individuals are clearly shown in Fig. 4.10a, b.

Although an overall picture of the growth form and height of individuals is obtained from the profiles, the variation of these 2 aspects is considerable so that separate quantitative analyses of these were made.

4.3.2 Tree growth forms

Tree individuals were classified into 7 classes that appeared best suited to distinguish the varying growth forms which were present.

- I Tree form: Trees with a canopy of more than 2 m in height and no regeneration from the base.
- II Regenerative tree form: Trees with a canopy of more than 2 m in height as well as regeneration from the base.
- III Small tree form: Trees with a canopy of less than 2 m in height and no regeneration at the base.
- IV Small tree regenerative form: Trees with a canopy of less than 2 m in height as well as regeneration from the base.
- V Basal regenerative tree form: Trees higher than 2 m but only living at regenerative base.
- VI Basal regenerative shrub form: Tree species individuals lower than 2 m in height and only living at regenerative base.
- VII Tussock form: Suffruticose tree forms only regenerating from ground level with no dead parts present. Included here are all seedlings recorded, since it was found difficult to distinguish these 2 types especially where the seedling had grown for a period of some time or where burned back stumps had rotted and weathered away. Boaler and Sciwale (1966) also found, in similarly structured vegetation, that it is "often difficult to distinguish seedlings from suffruticoses" and that "the necessary examinations were found to be very time consuming".

In order to obtain a reasonably large sample of these tree-forms 4 sample belts were laid out which totalled an area of 2 ha (2 of 250 m x 20 m and 2 of 500 m x 10 m). In this sample area, all woody species normally producing tree individuals under favourable conditions, were recorded. Shrub species which attain more than 1 m in height were also recorded. Dead individuals were recorded separately and are referred to in a section on mortality (Section 7.2.2.2). Individuals with more than one "stem" were recorded as single individuals. The frequency of each growth form for each species is given in Table 4.5.

Burkea africana was the only species which had more than half its individuals belonging to the tree form class I, although Lonchocarpus nelsii was similar and had almost half its individuals in this class.

Terminalia sericea, Combretum psidioides and Combretum collinum had similar growth forms, each with a relatively high percentage of basal regenerative shrub forms VI (30,8%, 31,0% and 32,8% respectively) with almost as many tree forms I and somewhat fewer regenerative tree forms II especially in Combretum collinum.

Ochna pulchra and Securidaca longepedunculata both had the majority of their individuals (63,1% and 64,8% respectively) belonging to the basal regenerative shrub form VI and fewer to the tussock form VII. The other rarer larger woody species present, were similar to the last 2 species but were more or entirely restricted to one or both of the latter 2 forms. The tree species in this group thus rarely attained tree dimensions. The species here were Ozoroa paniculosa, Grewia deserticola (where the basal regenerative shrub form and tussock form were not easily distinguished from each other), Combretum apiculatum, Acacia hereroensis, Ximenea americana and Grewia flavescens. (The latter 3 are not given in Table 4.5 because of their extreme scarcity.)

Some of the rare larger woody species of the study area were not recorded in this survey, for example, Dombeya rotundifolia, Tarchonanthus camphoratus and Ziziphus mucronata.

Considering all the tree species individuals irrespective of species (Table 4.5),

the majority of the individuals (58,8%) were basal regenerative shrub forms and tussock forms (VI and VII). This was because these 2 forms were made up mainly of 62,4% of the very common Ochna pulchra individuals and 15,6% of Combretum psidioides. Apart from these 2 non-tree forms, the form which was most common (19,5%) was the tree form I which was made up mainly of Combretum psidioides (38,0%), Burkea africana (37,0%) and Terminalia sericea (15,4%) individuals. All the other tree form types were relatively infrequent.

The least frequent growth form (2,9%) was the small regenerative form IV, made up mainly of Combretum psidioides (52,7%) and Ochna pulchra (22,0%) individuals. The closely related small tree form III, also with a low frequency (5,1%) was made up mainly of Ochna pulchra (58,2%) and Combretum psidioides (19,6%) individuals.

The relatively infrequent (4,1%) basal regenerative tree form V was made up chiefly of Combretum psidioides (44,1%) and Terminalia sericea (18,1%) individuals. The remaining class of regenerative tree form II had a somewhat more frequent occurrence (9,6%) and had roughly similar proportions of constituent species as the basal regenerative tree form V, that is Combretum psidioides (61,1%) and Terminalia sericea (21,6%) individuals.

The small tree form, small tree regenerative form, basal regenerative shrub form and tussock form (III, IV, VI and VII) all had Combretum psidioides and Ochna pulchra as the most important constituent species. The regenerative tree form and basal regenerative tree form (II and V) both had Combretum psidioides and Terminalia sericea as the main constituent species, while the tree form I had, in addition, Burkea africana as a main constituent species.

4.3.3 Frequency of tree heights

In Table 4.1 the average unaffected heights of the microphanerophytes and rare mesophanerophytes are given. There was, however, a great variation around these average values which was closely related to the canopy physiognomy of parts of the community.

The heights of all individuals more than 2 m tall were measured, using measuring staffs up to 4 m high and a clinometer for trees above 4 m. Readings were taken to the nearest 10 cm. All heights were recorded of those individuals rooted in a 3 000 m² area made up of 3 representative strips, each 10 m in width and 75, 110 and 115 m in length.

Almost one third (30,3%) of the individuals of the dominant tree species, Burkea africana, were 5 to 6 m high (Fig. 4.11b). Although Burkea africana had the highest individuals of the study area (roughly 3% of its individuals above 9,0 m in height and the absolute maximum height measured 9,4 m), individuals above 7 m in height were rare (<6%). Most of the individuals (75,7%) were approximately evenly spread in the frequency height classes of 4 to 7 m, which, in areas with more Burkea africana present, resulted in a somewhat undulating canopy effect with a rare giant individual obtruding here and there. A clear feature of the Burkea africana population was the relative scarcity of individuals below 4 m in height. This was possibly related to the fairly infrequent fires killing many of the younger trees below 4 m in height. Trees above 4 m in height appeared to be not so seriously affected as evidenced by the recent 1969 fire.

42,1% of Terminalia sericea were between 6 and 7 m, and only 5,3% in a higher class (Fig. 4.11c). As this most frequent height class of 6 to 7 m included more individuals than each of the lower height classes, this particular height distribution resulted (in predominantly Terminalia sericea areas) in a more or less regular and level canopy which was in contrast with the more undulating canopy in areas of mainly Burkea africana individuals. In contrast to Burkea africana, Terminalia sericea had 31,6% of its individuals between 2 and 4 m in height but only 5,3% between 4 and 5 m in height, and its smaller individuals thus did not appear to be as seriously affected by fire. Although Terminalia sericea and Burkea africana had much the same average height, Terminalia sericea appeared to be taller due to a relatively large proportion of individuals falling in a frequency class positioned higher in the frequency distribution.

Combretum psidioides had a decreasing number of individuals with increasing height (Fig. 4.11d). Due to the presence of 3 relatively well represented frequency classes together, in areas with Combretum psidioides predominant within the normal range

of density of individuals for the area, the canopy presented a very irregular and undulating subcanopy with here and there an individual joining the Burkea africana and Terminalia sericea upper canopy. The height class in which there was the greatest frequency (42,9%) of individuals was the lowest possible class (2 to 3 m).

Combretum collinum grew socially together and presented a fairly regular canopy with 52,8% of the individuals 3 to 4 m high (Fig. 4.11e). It should, however, be noted that one of the two mounds included in this sample contained several dead upper portions which were included with the other individuals.

Of the remaining species, some of which were rarely trees, Ochna pulchra were from 2 to just over 4 m in height, Lonchocarpus nelsii and Securidaca longepedunculata were usually large and above 4 m, while Dombeya rotundifolia in height corresponded closely with its associate Combretum collinum in being always less than 5 m in height. A few individuals of Grewia deserticola occasionally exceeded 2 m in height, but about nine-tenths of them were 2 to 3 m high and one-tenth 3 to 4 m high.

Canopy stratification was more apparent on a smaller scale when one species predominated. The stratification became more diffused or even lost on a larger scale when all individuals (Grewia deserticola and the mound-associated species Combretum collinum and Dombeya rotundifolia excepted) were viewed as a whole, since the distribution of height of all species individuals showed no particular frequency class considerably better represented than the others (Fig. 4.11a). The abundance of Combretum psidioides resulted in the frequency distribution of its individuals being superimposed (Fig. 4.11d) on that of this distribution (Fig. 4.11a). There was a sudden decrease of individuals from the 15,1% which were 6 to 7 m high, to the 2,8% of 7 m height (Fig. 4.12a), indicating the physiognomic top of the canopy of the community at this point of decrease (7 m).

4.3.4 Vertical distribution of materials in trees

Although analysis of growth forms and heights of trees provide some general information on the vertical distribution of plant material in the community, a more precise indication of the vertical distribution of the plant matter of tree individuals is desirable for a background to biomass studies. Because of the great labour involved in such analyses, only the vertical distribution of mass in one metre intervals of the materials of wood, leaf and fruits in a representative mature individual of each of the 8 more common tree species, was analysed.

Using previously obtained data on height, trunk diameter and regeneration to select a representative mature tree of a particular species, a clinometer reading of the standing height of the tree was taken and the metre intervals then marked off on the fallen tree, corrections being made in the upper foliage sections for extension of tree length and distortion of branches when pressed against the ground, especially in the case of Burkea africana and Combretum psidioides. Each correction was made by measuring the difference between standing and prostrate tree height and apportioning this difference proportionately over the height intervals above the point of observed branch distortion (usually from just above the first branch). All branches or parts of branches were included in the height intervals in which they occurred. The canopy diameter was measured in the standing individual.

In the figure 4.12 (a - h), the distribution in one metre height classes of the mass of wood, mass of leaves and, where present, number of fruits is given for each of 8 species. To compare trees of different heights, each height was expressed as a percentage. The actual mass values pertain to the mid points of the class interval. The joining lines between the points are only for guidance from point to point. Joining lines for all materials are tapered in the uppermost height class to 0% of the material's mass at 100% of its height, while the joining lines are tapered to the actual height of the lowest recorded leaf or fruit, irrespective of the class limits in which the lowest leaf or fruit occurs. However, for the woody component, the joining line is not tapered to 0% of the wood's mass at ground level as this would seriously underestimate the amount of material of wood in the 0 to 1 m class.

In addition, the following information was recorded for each species and set down below the diagrams (Fig. 4.12 a - h):

- 1 Height of tree
- 2 Total dry mass of wood
- 3 Total dry mass of leaves
- 4 Number of leaves
- 5 Number of fruits (if present)
- 6 Leaf area of tree and average area per leaf
- 7 Maximum canopy diameter
- 8 Trunk diameter at stated height (wet).

In Ozoroa paniculosa some additional information on live and dead parts is given (Fig. 4.12h). Since only the shrub form of Ozoroa was sampled, it is suffice to

state that it provided a typical pyrric regeneration form, having similar regenerative shoots to Combretum collinum, but the upper portions consisting of dead and leafless material. Further discussion is limited to vertical distribution in tree forms (Fig. 4.12a - g).

a Vertical distribution of woody material (see Fig. 4.12a - g)

By far the most important part of the tree individual's mass is the woody component.

The trunk mass was virtually constant over the first third of the tree height in Burkea africana, Combretum psidioides and Combretum collinum, and the latter species did not show any relative maximum concentration of wood mass above its base. In Terminalia sericea, Ochna pulchra, Securidaca longepedunculata and Lonchocarpus nelsii, however, there was a decrease in mass from the base to roughly 20 to 30% of the individuals' height while a maximum or relative maximum mass was reached at about two-thirds height in Terminalia sericea, Ochna pulchra, Lonchocarpus nelsii and Burkea africana. Securidaca longepedunculata and Combretum psidioides also had this relative maximum mass but the former was situated at lower than two-thirds height while the latter was situated higher than two-thirds height.

The height of the maximum or relative maximum wood mass above the base of the tree corresponded closely to the interval in which the maximum number of thick branches was situated. Combretum collinum, with its weakly developed upper branching system, did not possess a higher maximum or relative maximum mass in its mass distribution. Relative to the other species, the woody component in Securidaca longepedunculata terminated least abruptly at the top of the tree.

b Vertical distribution of leaves (see Fig. 4.12a - g)

In the three dominant tree species Burkea africana, Terminalia sericea and Combretum psidioides, as well as Ochna pulchra, all the leaves occurred in the top half of the tree. In the remaining species, leaves occurred from somewhat below 50% of the tree height with the lowest leaves occurring from about 30% height in Combretum collinum. The leaves of basal regeneration shoots of Combretum

collinum extended almost from ground level to about 30% of the tree's height.

Distribution of leaves on the tree is indicative of the canopy shape of the individual. Where more than 50% of the leaves occurred above about 85% of the height of the tree, the crown was characteristically flat-topped as in Burkea africana, or secondarily a flat sub-top as in Terminalia sericea. Where the majority of the leaves were more or less evenly distributed at heights above 70 to 75% of the height of the tree, the crown had a more rounded appearance, for example, Lonchocarpus nelsii, Ochna pulchra, Combretum collinum and the more irregularly rounded crown of Combretum psidioides. The two separate peaks in the leaf distribution of Securidaca longepedunculata was evidence of the irregular and usually obscure stratification within the foliage of these tree individuals.

Only in Combretum psidioides did the maximum leaf concentration coincide with the maximum or relative maximum mass of the woody component. In all the other species the maximum leaf concentration was situated above the height of the maximum or relative maximum of the woody component. At this height relatively few leaves occurred, or in some species almost none, for example, Securidaca longepedunculata and Ochna pulchra.

Of the species analysed, those which had the smallest leaves also had the greatest number of leaves, for example Securidaca longepedunculata and Terminalia sericea, which indicated the rough inverse relationship which exists between leaf number and leaf area for the species analysed. Burkea africana was an exception due to its compound leaves.

The ratio of the leaf area to the total mass of the individual (leaf area ratio or LAR) was lower for Terminalia sericea ($0,09 \text{ m}^2/\text{kg}$) and Securidaca longepedunculata ($0,12 \text{ m}^2/\text{kg}$) compared with the higher ratio of the other species which ranged from $0,25 \text{ m}^2/\text{kg}$ in Ochna pulchra to $0,50 \text{ m}^2/\text{kg}$ for Combretum collinum. In spite of being the heaviest individual sampled, Burkea africana had as high a LAR ($0,34 \text{ m}^2/\text{kg}$) as several of the other lighter individuals.

c Vertical distribution of fruits (see Fig. 4.12b, f)

At the time of sampling (June), most of the relatively few fruits were still attached to the trees; fruits were only present in 2 species. In both Terminalia sericea and Securidaca longepedunculata the distribution of the frequency of fruits followed that of the leaf frequency very closely, although largely avoiding the lowest parts of the leaf canopies.

4.3.5 Heights of herbaceous layer species

In 10 randomly selected individuals of each species for phenological observation, the heights of the herbaceous layer species individuals were measured to the nearest cm in early May, by which time, there was no more increase in the length of culms of grasses. The average height of each species was calculated (Table 4.1), damaged heights being excluded.

A distribution in height classes of the 18 most important species of the herbaceous layer, each with a biomass greater than 2,0 kg/ha, indicated that most of the average heights of species were irregularly distributed from about 15 cm to about 130 cm in height. The herbaceous layer species with the greatest average height was Andropogon gayanus (233 cm) while the average height of the dominant species, Digitaria polevansii was 126 cm. Seven of these 18 species were more than 100 cm high and 5 were 50 to 100 cm high. The remaining 6 of these 18 species were between 0 to 50 cm average height; they constituted all the non-grass species.

4.4 Basal cover

A wheel point survey was carried out on the 19th and 20th of April, 1971 at the height of the growing season, to determine the basal cover of each of the more important species. Five thousand points were taken along straight lines

evenly spaced over the whole study area, each point at a distance of 2,86 m (one revolution of the wheel) from the next. The wheel point apparatus was similar to that designed by Tidmarsh and Havenga (1955). Each point was only recorded as a stroke if the basal area of the point ($0,4 \text{ cm}^2$) pressed down upon the ground-level area of a plant individual or would clearly have pressed down upon this part had the point not been deflected by the upper parts of the plant. If there was any doubt whether the point had touched the actual base of the plant, the point was not recorded as a strike. Therefore, when the point pressed down on soil between closely-grouped stems, for example in Grewia avellana, it was not recorded as a strike.

When a tree individual was encountered which blocked the path of the wheel, the set-line was kept to as far as possible. Although the survey of basal cover thus only applied to the herbaceous layer, the total basal plant cover is virtually unaffected by the exclusion of the trees. Most of the basal cover of the tree and large bush species was made up of the dominant species, Burkea africana, Terminalia sericea and Combretum psidioides. From the data of the ground-level stem or trunk diameters of these species (taken in addition to other measurements in 2 strips of 300 x 10 m), the basal stem or trunk diameter of a "mean individual" of each of these species was calculated, converted to area, multiplied by the respective density of each species and added together, giving a rough estimate of the total basal area of these dominant tree species. This amounted to about 0,08% basal cover, with no single species exceeding 0,03%. As a percentage of the total basal plant cover, the trees of the study area appeared to contribute only slightly more than 1,0% of the total basal cover of plants of the study area. The basal cover figures given for the herbaceous layer are thus reasonably representative of the basal plant cover of the whole area.

The basal cover values recorded are presented in Table 4.1 (column 2). The basal cover of the herbaceous layer was 7,82%. The highest basal cover was that of the

grass species Digitaria polevansii (3,92%) and secondly Brachiaria nigropedata (1,94%) which together made up 74,6% of the total basal plant cover. The species with the next greatest cover was Grewia avellana (0,40%) which was only 5,1% of the total plant cover. The basal cover was made up of 88,8% grass species, 5,9% woody species, and 5,3% other herbaceous species.

The inefficiency of the wheel point method for cover determinations of less common species was amply demonstrated here, since very few species of the large group with lower frequencies were recorded. In the 5 000 points recorded, only 21 of about 80 recordible species of the herbaceous layer were recorded. This included Burkea africana and Ozoroa paniculosa within the herbaceous layer.

There was marked variation in the efficiency of ground surface utilisation of the more common species. For those species with an April basal cover of >0,1%, the cover values were divided by the biomass values for April which were derived from the 5th degree polynomial regressions (or 4th degree in the case of Grewia avellana), for each species. These species are listed in order of descending surface area utilisation:

1	<u>Aristida stipitata</u>	39,63 g/cm ²
2	<u>Grewia avellana</u>	35,24 "
3	<u>Andropogon gayanus</u>	28,36 "
4	<u>Triraphis schinzii</u>	22,26 "
5	<u>Digitaria polevansii</u>	17,08 "
6	<u>Andropogon schirensis</u>	15,69 "
7	<u>Brachiaria nigropedata</u>	9,71 "
8	<u>Cyperus margaritaceus</u>	7,63 "

The different surface area utilisation of species explains how the relationship between cover and biomass is dependent on the species present and is one of the main reasons why cover cannot be used as a measure of biomass irrespective of species, since, for example, the biomass of species with a relatively low surface utilisation, for example, Cyperus margaritaceus, may be grossly overestimated, while the biomass of a species with a relatively high surface utilisation, for example Aristida stipitata, may be somewhat underestimated using cover values.

Table 4.1 List of sampled species arranged according to average dry biomass, giving data of community structure

Symbols : * : Species significantly associated with mounds
 + : Preceeds data of tree species in herbaceous layer (Mass to nearest kilogram)
 " " : Approximate value due to sampling difficulties, dependence upon supporting plants or excessive damage
 () : Species with too low densities to be used for reliable test of aggregation
 - - : Only applies for individuals in the herbaceous layer

	Average dry biomass (kg/ha)	Basal cover (%)	Frequency in 1 m ² quadrats (%)	Density of individuals (ind/ha)	Ratio for aggregation (scale of 1 m ²)	Average unaffected height of population (cm)
TREE AND LARGE WOODY SPECIES						
<i>Burkea africana</i>	11 801 + 1	} + 0,02 "0,08"	3,58	375	1,1	511
<i>Terminalia sericea</i>	6 153 + 1		3,25	340	1,1	514
<i>Combretum psidioides</i>	3 405 + 1		3,25	360	1,1	331
<i>Ochna pulchra</i>	226 + 3		8,25	1 650	1,9	-15-
* <i>Combretum collinum</i>	195 + 1		1,17	125	1,0	315
<i>Securidaca longependiculata</i>	160 + 1		0,42	42	1,0	-66-
<i>Grewia deserticola</i>	157		1,08	125	1,2	"210"
<i>Lonchocarpus nelsii</i>	96		0,08	8	-	-
<i>Grewia flavescens</i>	31		-	-	-	-
<i>Ozoroa paniculosa</i>	22	+ 0,02	0,08	-	-	-
* <i>Dombeya rotundifolia</i>	20		0,25	-	-	-
<i>Ximenia americana</i>	15		-	-	-	-
<i>Tapinanthus oleifolius</i>	9		-	-	-	-
TOTAL	22 290 + 8					
	= 22 298					
HERBACEOUS LAYER SPECIES						
<i>Digitaria plevansii</i>	422,93	3,92	90,33	>20 000	-	126
<i>Brachiaria nigropedata</i>	119,65	1,94	48,42	10 217	1,5	66
<i>Grewia avellana</i>	89,28	0,40	30,75	11 258	3,1	41
<i>Andropogon gayanus</i>	59,29	0,34	19,75	3 075	1,4	233
<i>Andropogon schirensis</i>	42,68	0,28	35,33	9 650	2,2	101
<i>Aristida stipitata</i>	36,24	0,12	33,17	8 825	2,2	81
<i>Triraphis schinzii</i>	21,90	0,14	15,25	2 250	1,4	130
<i>Rhynchelytrum species</i>	18,61	0,02	20,42	4 950	2,2	91
* <i>Cenchrus ciliaris</i>	18,60	-	0,92	208	2,3	99
<i>Aristida meridionalis</i>	10,91	0,04	28,42	5 342	1,6	"70"
<i>Stipagrostis uniplumis</i>	10,33	0,08	5,75	900	1,5	107
<i>Tephrosia cephalantha</i>	8,02	0,06	41,58	23 208	4,3	19
<i>Cyperus margaritaceus</i>	7,59	0,18	42,17	9 883	1,8	39
<i>Ancylanthos bainesii</i>	6,28	0,02	8,25	2 708	3,1	22
<i>Eragrostis pallens</i>	5,58	0,06	1,17	100	0,9	124
<i>Panicum kalaharensis</i>	4,05	0,04	0,50	300	6,0	133
* <i>Dicliptera eeni</i>	3,87	0,02	2,67	283	1,0	39
<i>Commelina africana</i>	3,78	0,06	9,83	1 342	1,3	16
* <i>Rhynchosia sublobata</i>	1,10	-	0,58	217	3,7	"41"
<i>Eragrostis jeffreysii</i>	1,66	-	1,00	125	1,3	137
* <i>Pentarrhinum abyssinicum</i>	1,27	0,06	1,25	325	2,6	"60"
<i>Turbina oblongata</i>	1,15	-	3,67	392	1,1	5

Table 4.1 (continued)

	Average dry biomass (kg/ha)	Basal cover (%)	Frequency in 1 m ² quadrats (%)	Density of individuals (ind/ha)	Ratio for aggregation (scale of 1 m ²)	Average unaffected height of population (cm)
<i>Aristida congesta</i>	1,10	-	5,42	850	1,5	72
<i>Cissampelos mucronata</i>	1,04	-	1,50	150	1,0	17
* <i>Sphedamnocarpus puriens</i>	0,99	-	0,25	21	1,0	"65"
* <i>Rhynchosia venulosa</i>	0,95	-	2,58	333	1,3	32
<i>Schmidtia pappophoroides</i>	0,74	-	0,17	33	1,9	75
<i>Mariscus laxiflorus</i>	0,58	-	4,58	775	1,7	97
<i>Cassia biensis</i>	0,47	-	12,58	2 033	1,5	21
* <i>Oxalis purpurascens</i>	0,40	-	0,33	1 300	39,4	10
* <i>Panicum maximum</i>	0,35	-	0,08	33	4,1	"105"
<i>Dicoma gerrardii</i>	0,32	-	1,17	308	2,6	18
<i>Pavonia clathrata</i>	0,31	-	0,42	66	1,6	61
<i>Blepharis maderaspatensis</i>	0,30	0,04	4,08	692	1,7	9
<i>Dicoma schinzii</i>	0,20	-	0,50	87	1,7	14
<i>Eustachys paspaloides</i>	0,19	-	0,17	133	7,8	"41"
<i>Eragrostis stapfii</i>	0,18	-	0,33	33	1,0	50
<i>Limeum fenestratum</i>	0,17	-	1,92	225	1,2	36
<i>Pogonarthria squarrosa</i>	0,16	-	0,25	25	1,0	52
<i>Elephantorrhiza elephantina</i>	0,13	-	0,67	67	1,0	30
<i>Pentamenes zambesiacus</i>	0,11	-	0,75	108	1,4	55
<i>Indigofera daleoides</i>	0,09	-	0,92	175	1,9	20
<i>Kyphocarpa angustifolia</i>	0,08	-	0,50	133	2,7	"45"
<i>Pygmaeothamnus zeyheri</i>	0,07	-	0,42	100	2,4	-
* <i>Hibiscus fleckii</i>	0,06	-	0,17	13	(1,0)	"195"
<i>Nidorella resedifolia</i>	0,06	-	0,33	225	6,8	78
<i>Polygala kalaxariensis</i>	0,03	-	1,50	158	1,0	29
<i>Raphionacme burkei</i>	0,03	-	0,17	17	1,0	"9"
<i>Solanum delegoense</i>	0,03	-	0,08	8	(1,0)	-
<i>Tephrosia lupinifolia</i>	0,03	-	0,50	58	1,2	"66"
<i>Anthospermum ericoideum</i>	0,02	-	0,50	75	1,5	17
* <i>Gloriosa virescens</i>	0,02	-	0,08	8	(1,0)	-
<i>Phyllanthus pentandrus</i>	0,02	-	1,33	358	2,7	13
<i>Fimbristylis exilis</i>	0,01	-	2,83	2 200	7,7	"15"
<i>Felicia muricata</i>	0,01	-	0,08	17	2,1	-
<i>Hermannia tomentosa</i>	0,01	-	0,17	25	1,5	-
<i>Tragia dinteri</i>	0,00	-	0,08	8	(1,0)	-
unidentified species	0,09	-	-	"2 617"	-	-
TOTAL	904,12	7,82				
TOTAL WITH TREE SPECIES IN HERBACEOUS LAYER	912,85	7,86				
GRAND TOTAL FOR STUDY AREA	23 202,85	"8,00"				

Table 4.2 Percentage of rare and common herbaceous layer species in aggregation classes

	Random (Ratio 1,0-1,2)	Intermediate (Ratio 1,3-1,4)	Aggregation (Ratio 1,5)	Total -
	%	%	%	%
Rare species $F < 5\%$	28,6	5,4	39,3	73,2
Common species $F > 5\%$	0,0	5,4	21,4	26,8
TOTAL	28,6	10,8	60,7	<u>+100</u>

Table 4.3 Presence and frequencies of plant species on 8 mounds (determined with 155 1 m² quadrats)

Species	Presence (out of 8)	Local frequency (%)
1 <i>Combretum collinum</i>	8	53,5
2 <i>Cenchrus ciliaris</i>	6	45,8
3 <i>Digitaria polevansii</i>	8	41,3
4 <i>Andropogon gayanus</i>	7	18,7
5 <i>Dicliptera eonii</i>	6	17,4
6 <i>Rhynchosia venulosa</i>	4	17,4
7 <i>Panicum maximum</i>	2	12,9
8 <i>Sphedamnocarpus pruriens</i>	1	11,6
9 <i>Oxalis purpurascens</i>	1	11,0
10 <i>Rhynchosia sublobata</i>	1	11,0
11 <i>Dombeya rotundifolia</i>	5	9,0
12 <i>Pentarrhinum abyssinicum</i>	3	7,7
13 <i>Hibiscus fleckii</i>	4	6,5
14 <i>Gloriosa virescens</i>	3	3,9
15 <i>Commelina benghalensis</i>	3	2,6
16 <i>Maerua juncea</i>	1	2,6
17 <i>Tephrosia cephalantha</i>	2	2,6

Twenty one other plant species with frequency values of 2,5% and lower were also recorded; almost all of these had a presence of 1.

Table 4.4 Ratio of frequency on the mounds to the sum of that on the flats and mounds for each species

* indicates significant (P < 0,05) difference between mound and flat

1,00	0,99 - 0,95	0,949 - 0,800	0,799 - 0,500	0,499 - 0,200	0,199 - 0,050	0,049 - 0,001	0,000
Acacia hereroensis	*Combretum collinum	*Dicliptera eenii	Andropogon gayanus	*Digitaria polevansii	*Grewia avellana	*Andropogon schirensis	*Ancylanthos bainesii
Asparagus africanus	*Dombeya rotundifolia	*Rhynchosia venulosa	Hermannia tomentosa	Turbina oblongata	*Tephrosia cephalantha	*Aristida meridionalis	Anthospermum ericoideum
*Cenchrus ciliaris	*Hibiscus fleckii					*Brachiaria nigropedata	*Aristida congesta
Combretum apiculatum	*Pentarrhinum abyssinicum					*Rhynchelytrum species	*Aristida stipitata
*Commelina beghalensis	*Rhynchosia sublobata					*Triraphis schinzii	*Blepharis maderaspatensis
Croton gratissimus	*Sphedamnocarpus puriens						*Burkea africana
Eragrostis rigidior							*Cassia biensis
*Gloriosa virescens							Cissampelos mucronata
Heteropogon contortus							*Combretum psidioides
*Maerua juncea							*Commelina africana
Melhania acuminata							*Cyperus margaritaceus
*Oxalis purpurascens							Dicoma gerrardii
*Panicum maximum							Dicoma schinzii
Solanum delegeense							Elephantorrhiza elephantina
Sporobolus fimbriatus							Eragrostis jeffreysii
Ziziphus mucronata							Eragrostis pallens
							Eragrostis stapfii
							Eustachys paspaloides
							*Fimbristylis exilis
							Grewia deserticola
							Indigofera daleoides
							Kyphocarpa angustifolia
							*Limeum fenestratum
							Mariscus laxiflorus
							Nidorella resedifolia
							*Ochna pulchra
							Panicum kalahareense
							Pavonia clathrata
							Pentamenes zambesiacus
							Phyllanthus pentandrus
							Pogonarthria squarrosa
							Polygala kalahariensis
							Pygmaeothamnus zeyheri
							Raphionacme burkei
							Schmidtia pappophoroides
							Securidaca longepedunculata
							*Stipagrostis uniplumis
							Tephrosia lupinifolia
							*Terminalia sericea

More frequent on mounds
More frequent on flats

Table 4.5 Frequency of larger woody species in 7 growth form classes
(Symbols for growth form classes as in text)

Species	Growth form classes						
	I	II	III	IV	V	VI	VII
	%	%	%	%	%	%	%
<i>Burkea africana</i>	64,6	5,5	2,3	0,6	2,6	8,1	16,4
<i>Terminalia sericea</i>	30,5	21,0	3,3	3,0	7,5	30,8	3,9
<i>Combretum psidioides</i>	27,7	21,8	3,7	5,8	6,7	31,0	3,2
<i>Ochna pulchra</i>	1,1	0,1	7,3	1,6	0,3	63,1	26,6
<i>Combretum collinum</i>	25,9	10,3	12,1	4,3	13,8	32,8	0,9
<i>Securidaca longepedunculata</i>	5,6	4,2	2,8	7,0	0,0	64,8	15,5
<i>Ozoroa paniculosa</i>	-	-	-	-	-	51,7	48,3
<i>Lonchocarpus nelsii</i>	45,5	13,6	4,5	0,0	0,0	36,4	-
<i>Combretum apiculatum</i>	-	21,4	-	-	14,3	57,1	7,1
<i>Grewia deserticola</i>	-	11,4	-	1,1	17,0	70,5	-
All individuals	19,5	9,6	5,1	2,9	4,1	43,9	14,9

Fig. 4.1 (on following page) Illustration of a fire-induced two-stemmed Burkea africana individual amongst smaller Combretum psidioides individuals.

Fig. 4.2 (on following page) Exposed underground parts that connect several adjacent Grewia avellana "individuals".



Fig. 4.1



Fig. 4.2

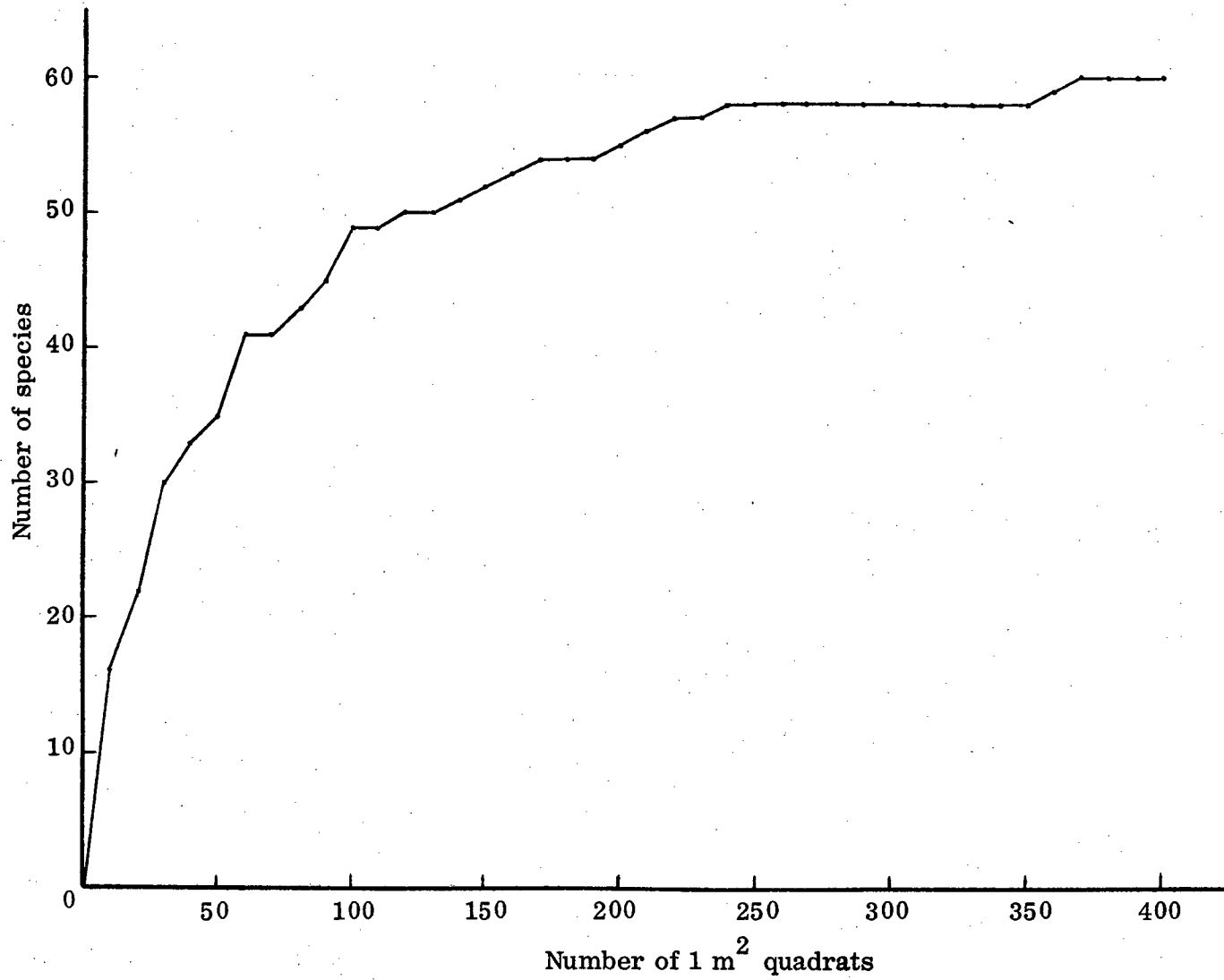


Fig. 4.3 Species-area curve: cumulative frequency of species per number of 1 m² quadrats

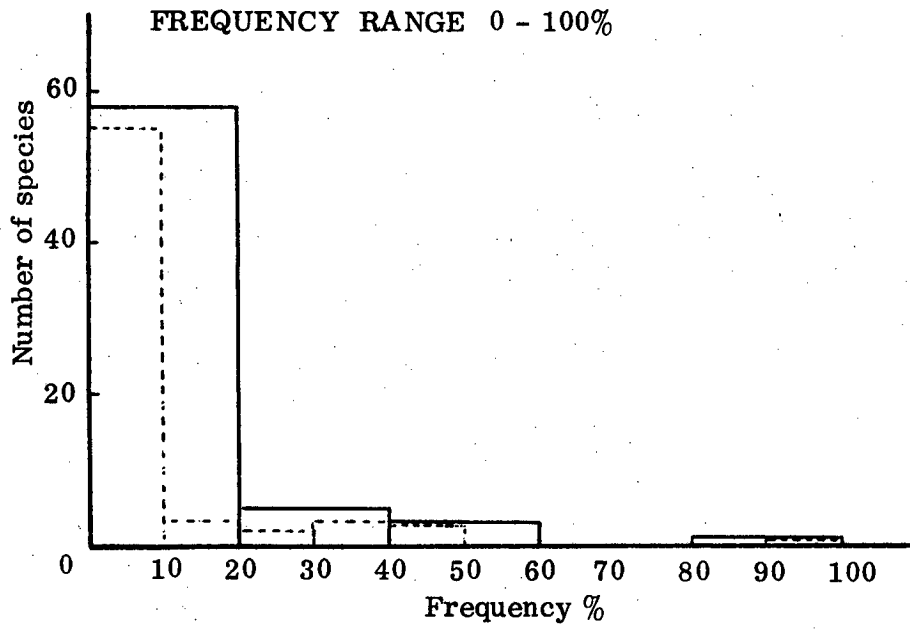


Fig. 4.4a Number of species in frequency classes

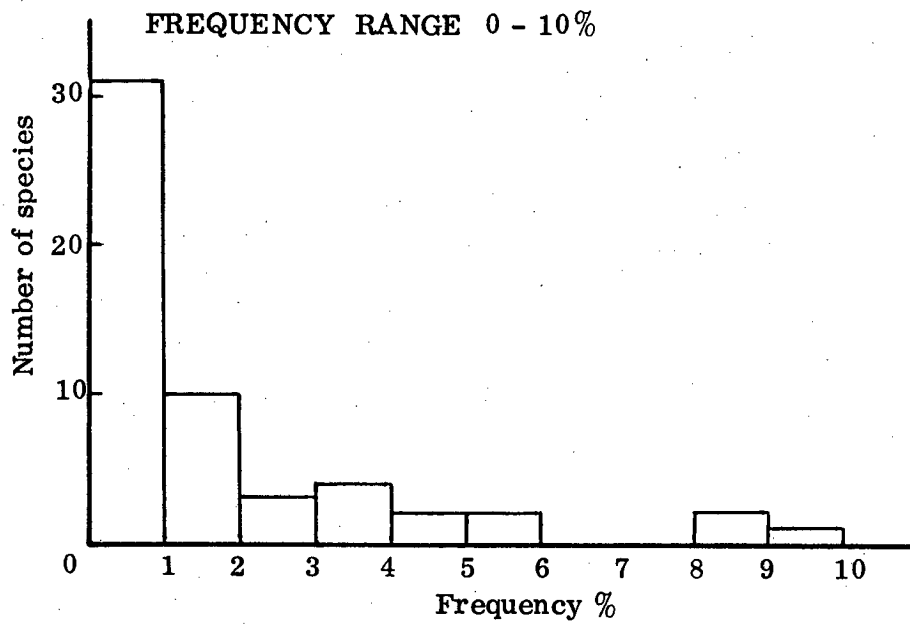


Fig. 4.4b Number of species in frequency classes

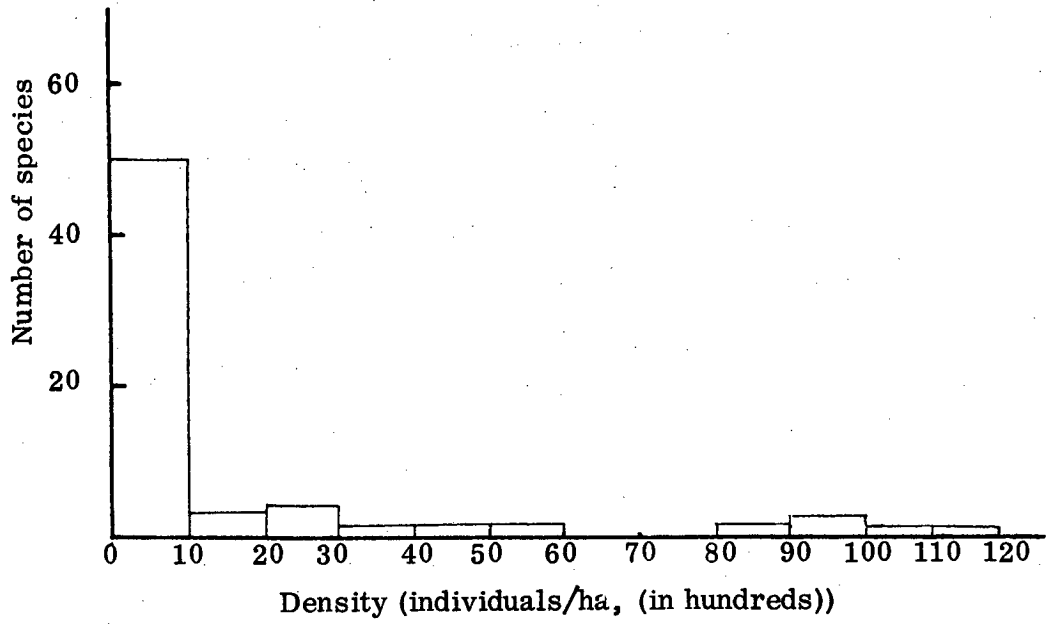


Fig. 4.5 Distribution of the occurrence of species in density classes

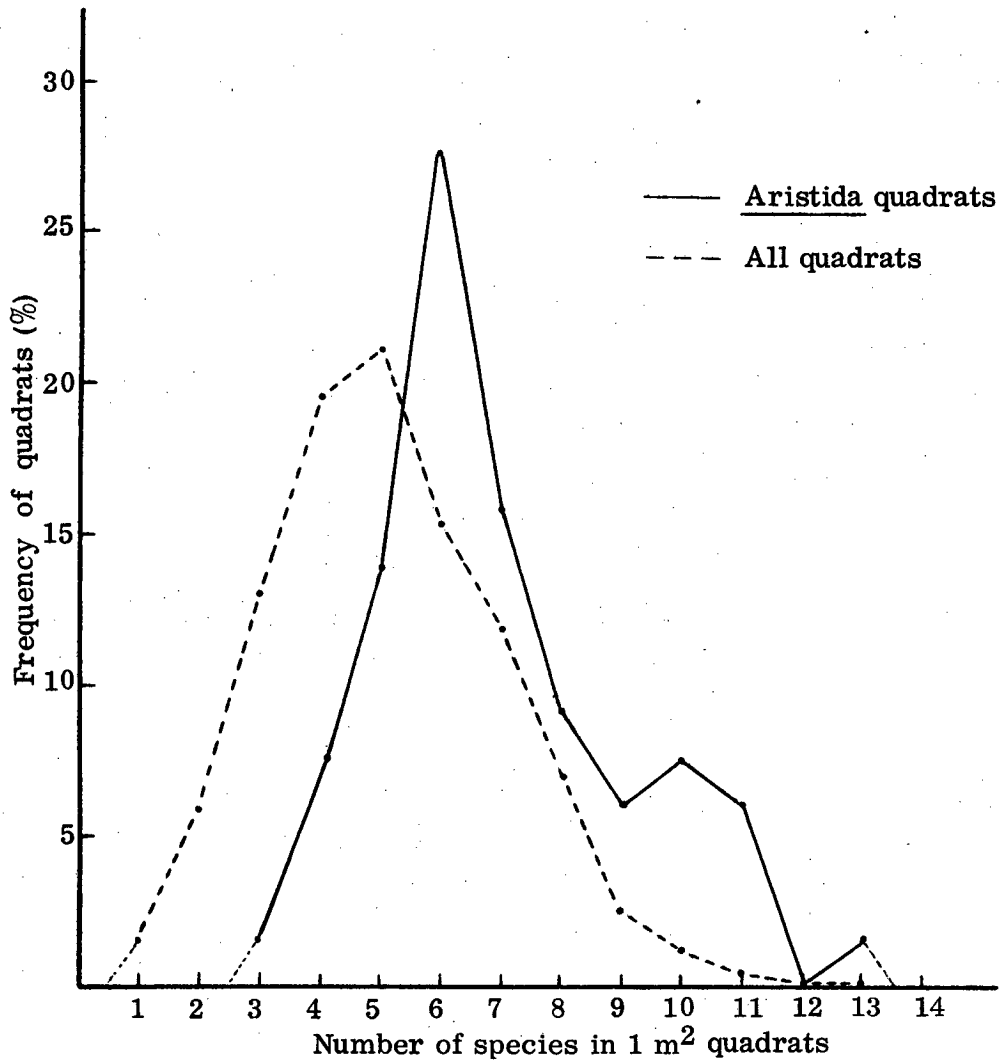


Fig. 4.6 Distribution of species density in Aristida congesta quadrats and in all quadrats

Fig. 4.7 (on following page) An Aristida
congesta individual on an open area (in winter).

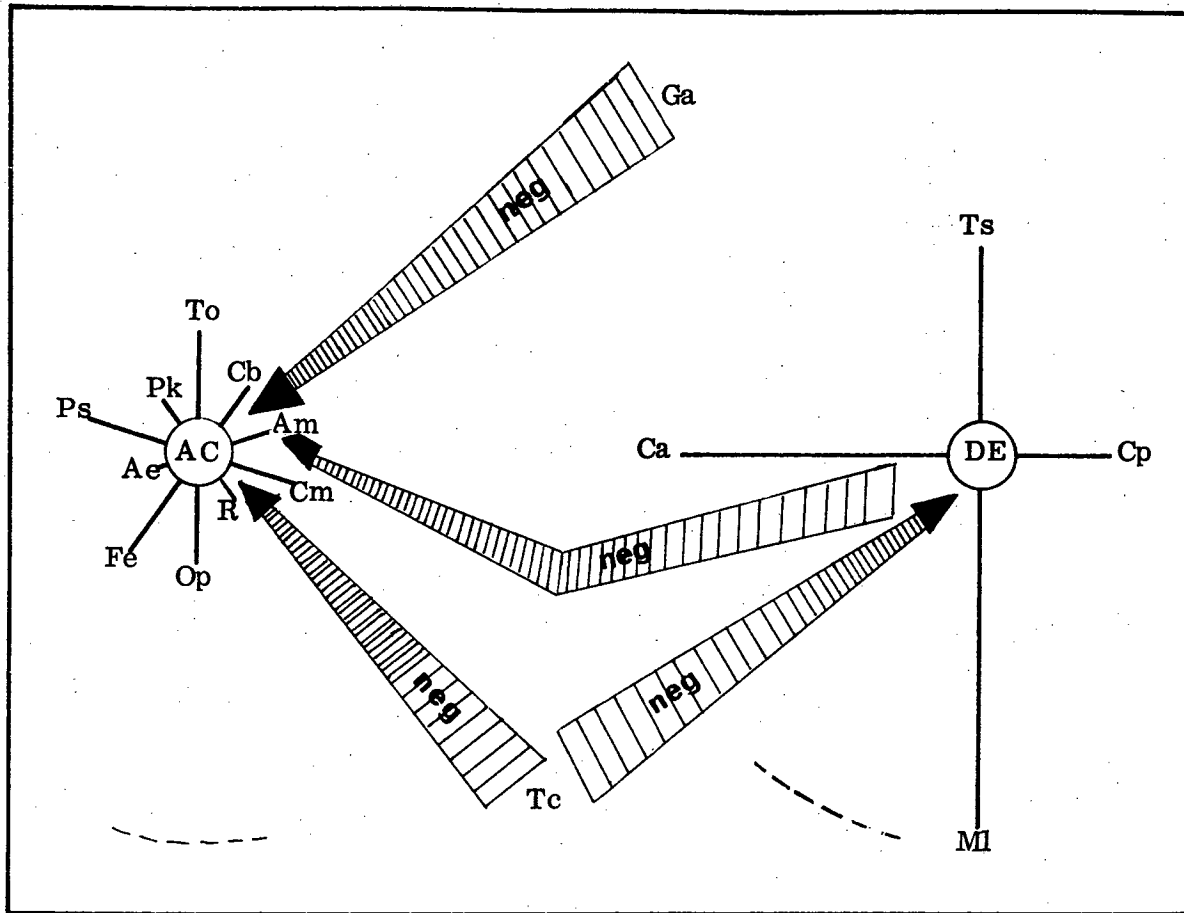
Fig. 4.8 (on following page) A Dicliptera
eenii individual in the shade



Fig. 4.7

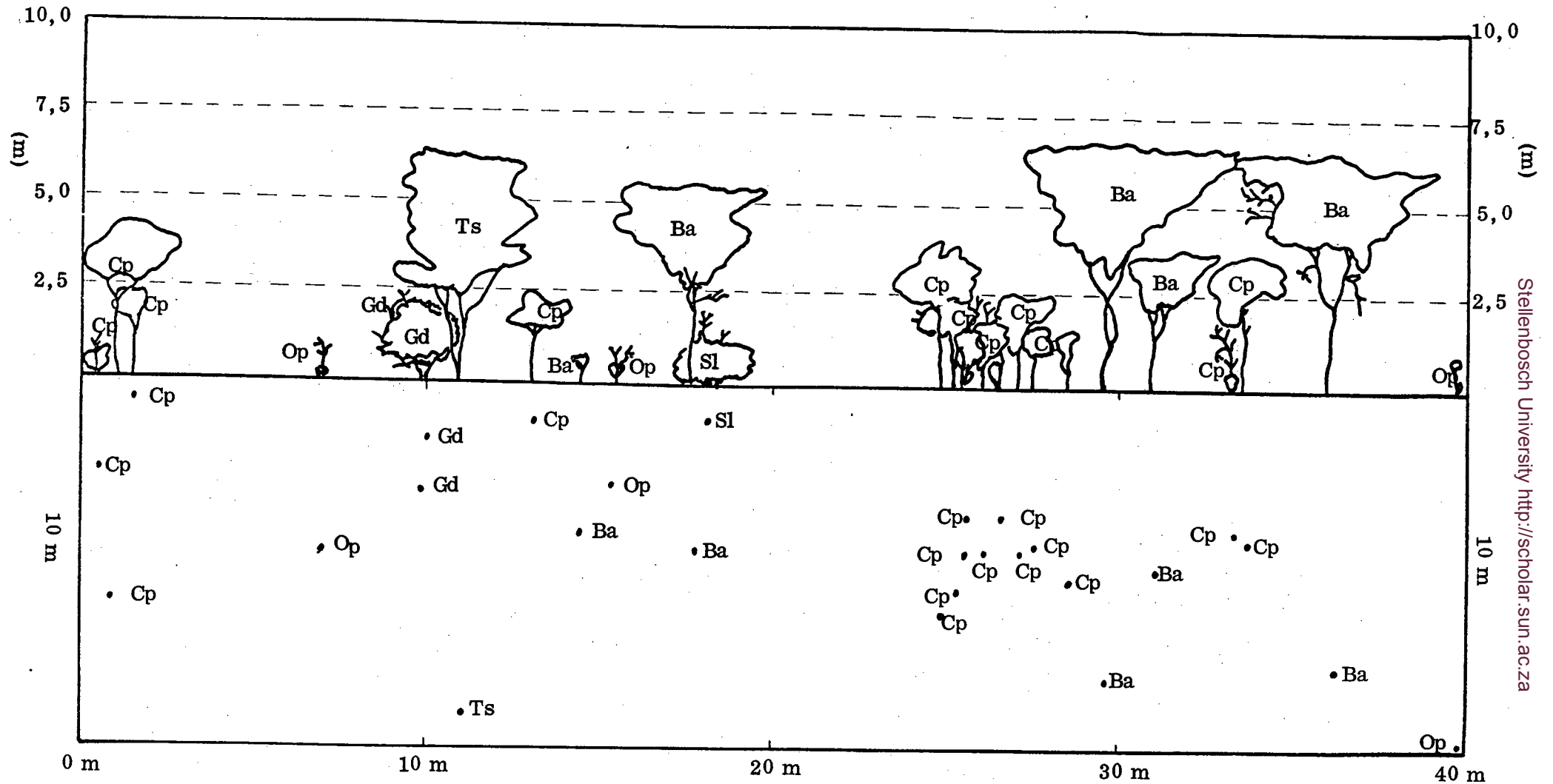


Fig. 4.8



- AC = *Aristida congesta*
- Ae = *Anthospermum ericoideum*
- Am = *Aristida meridionalis*
- Ca = *Commelina africana*
- Cb = *Cassia biensis*
- Cp = *Combretum psidioides*
- Cm = *Cyperus margaritaceus*
- DE = *Dicliptera eeni*
- Fe = *Fimbristylis exilis*
- Ga = *Grewia avellana*
- MI = *Mariscus laxiflorus*
- Op = *Ochna pulchra*
- Pk = *Polygala kalaxariensis*
- Ps = *Pogonarthria squarrosa*
- R = *Rhynchelytrum species*
- Tc = *Tephrosia cephalantha*
- To = *Turbina oblongata*
- Ts = *Terminalia sericea*

Fig. 4.9 Diagram illustrating 2 plant associations in the study community on Omuverume (Explanation in text, page 51)



Stellenbosch University <http://scholar.sun.ac.za>

Ba = *Burkea africana*; Cp = *Combretum psidioides*; Gd = *Grewia deserticola*; Op = *Ochna pulchra*; Sl = *Securidaca longepedunculata*; Ts = *Terminalia sericea*

Fig. 4.10a Vegetation profile of part of the study area on Omuverume

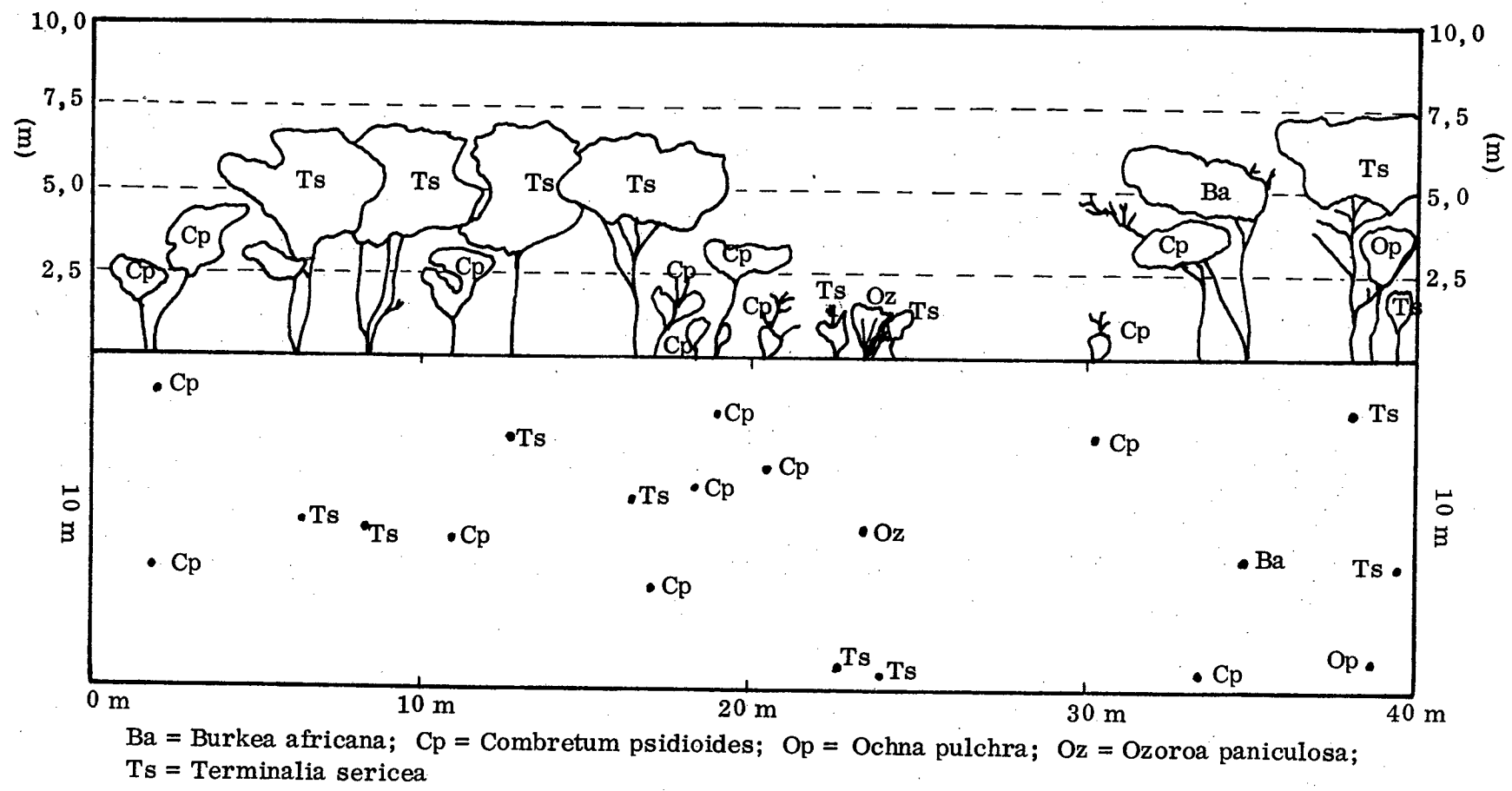
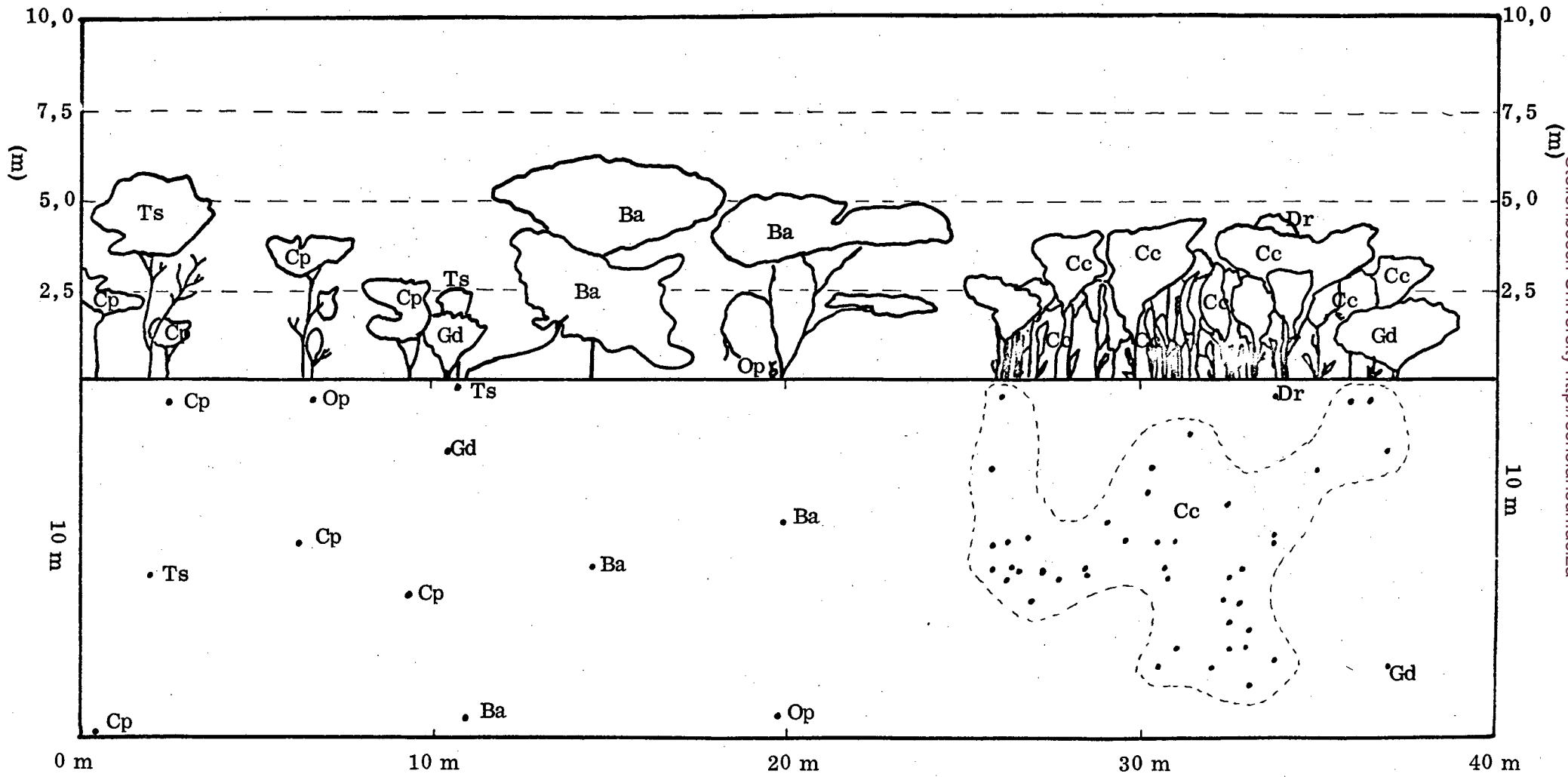


Fig. 4.10b Vegetation profile of part of the study area on Omuverume



Ba = *Burkea africana*; Cc = *Combretum collinum*; Cp = *Combretum psidioides*; Dr = *Dombeya rotundifolia*; Gd = *Grewia deserticola*; Op = *Ochna pulchra*; Ts = *Terminalia sericea*

Fig. 4.10c Vegetation profile of part of the study area on Omuverume

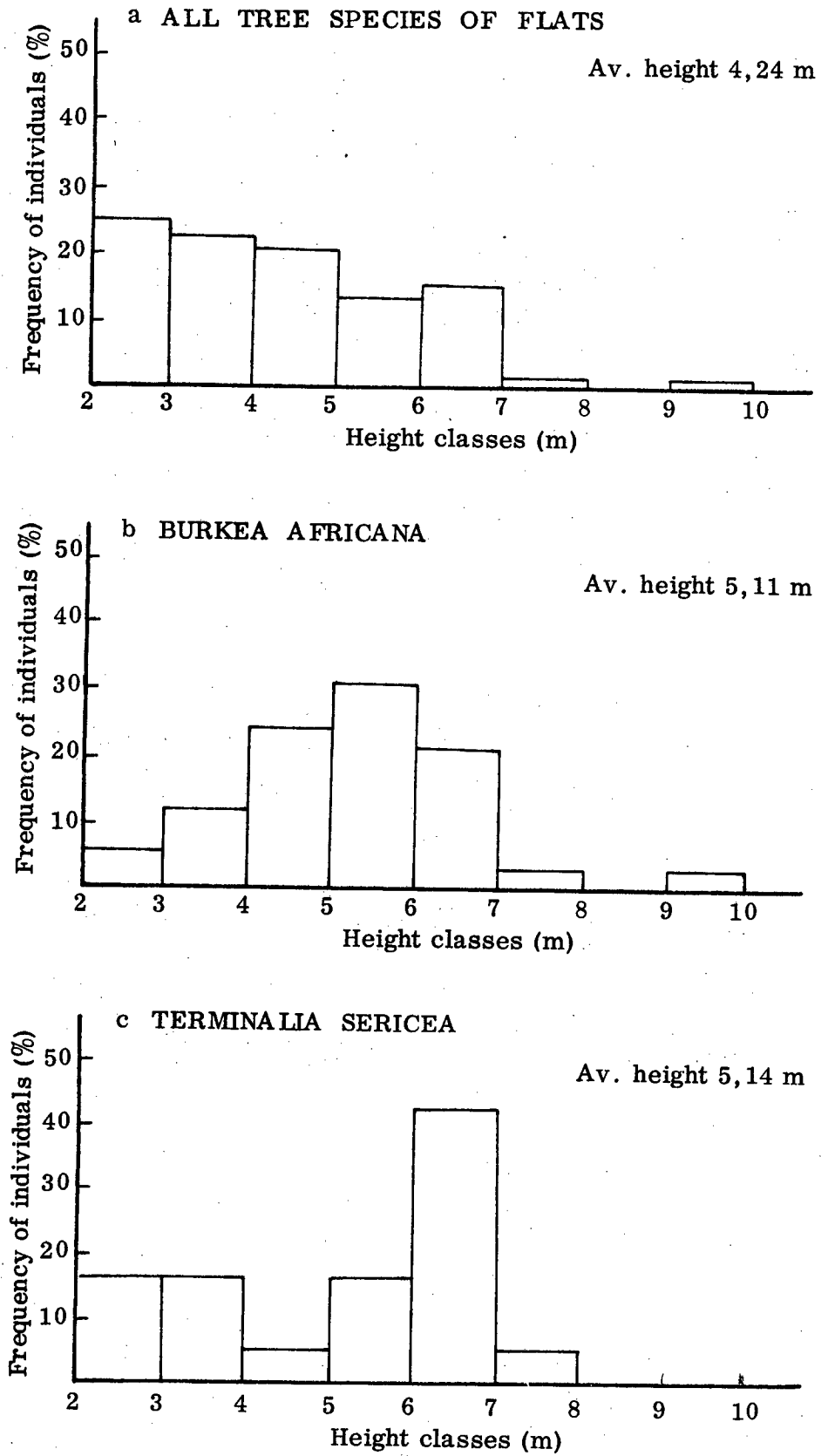


Fig. 4.11 Distribution of the frequency of tree individuals in height classes

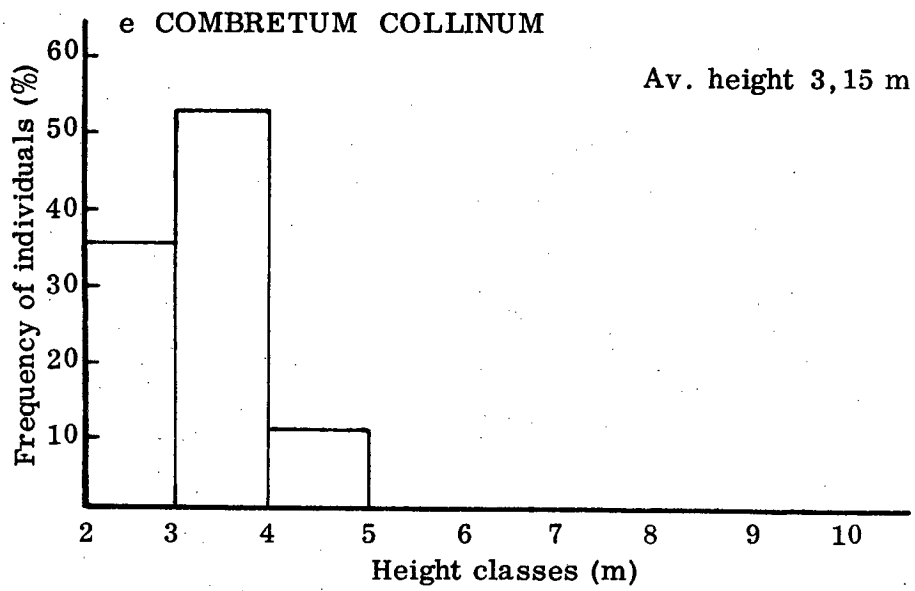
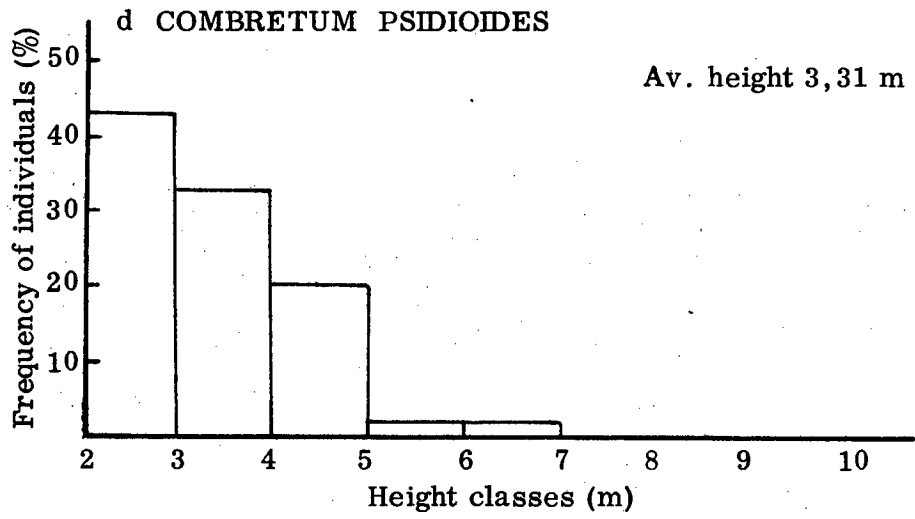
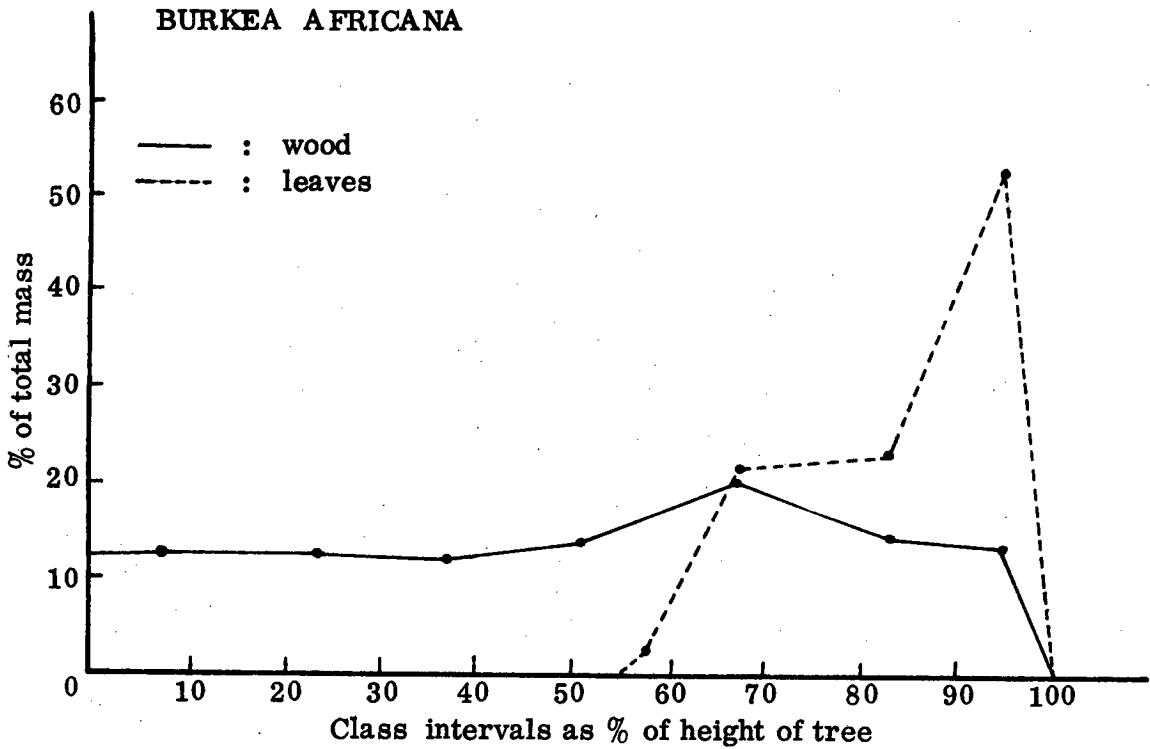
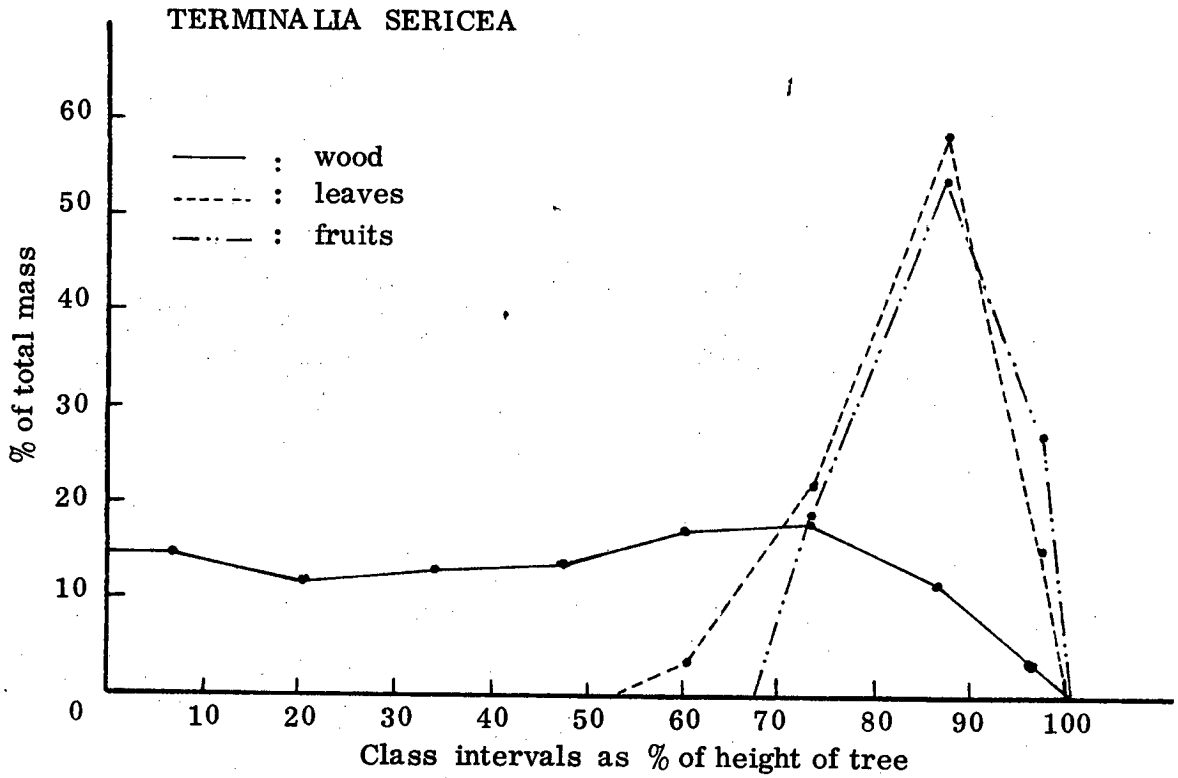


Fig. 4.11 (continued) Distribution of the frequency of tree individuals in height classes



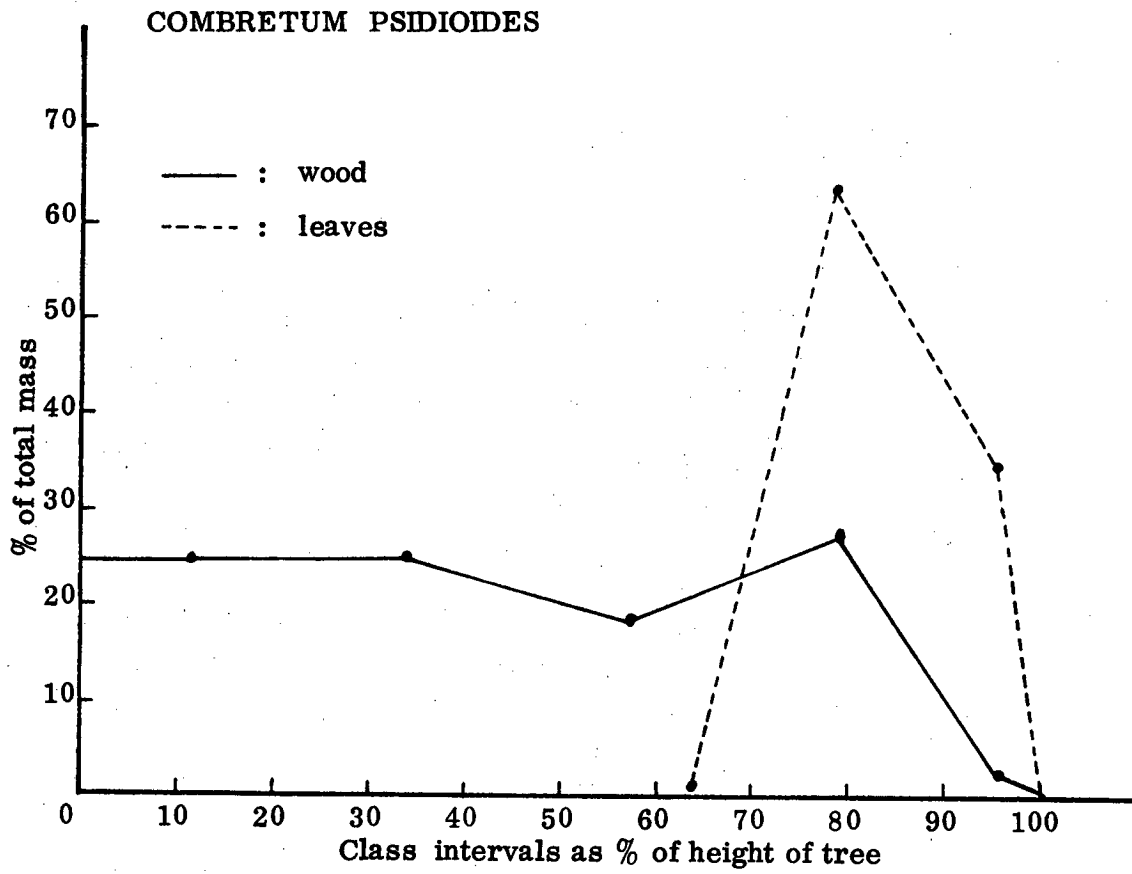
Height (m)	6,6
Total dry wood mass (kg)	243,5
Total dry leaf mass (kg)	10,7
Number of leaves	6 956
Leaf surface area (cm ² /leaf)	125,04
(cm ² /leaflet)	4,47
(m ² /individual)	86,98
Maximum canopy diameter (m)	6,3
Trunk diameter at 1 m (cm)	26,4

Fig. 4.12a Vertical distribution of materials in trees



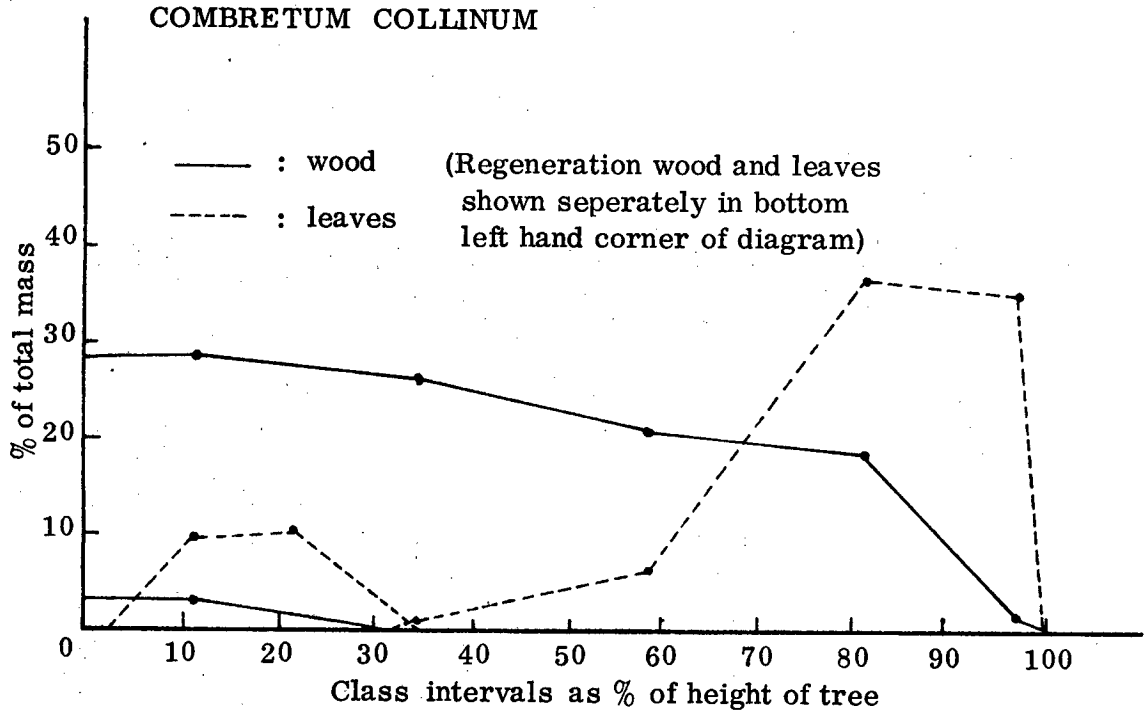
Height (m)	7,5
Total dry wood mass (kg)	170,2
Total dry leaf mass (kg)	3,2
Number of leaves	33 420
Number of fruits	254
Leaf surface area (cm ² /leaf)	4,70
(m ² /individual)	15,71
Maximum canopy diameter (m)	5,9
Trunk diameter at 1 m (cm)	23,8

Fig. 4.12b Vertical distribution of materials in trees



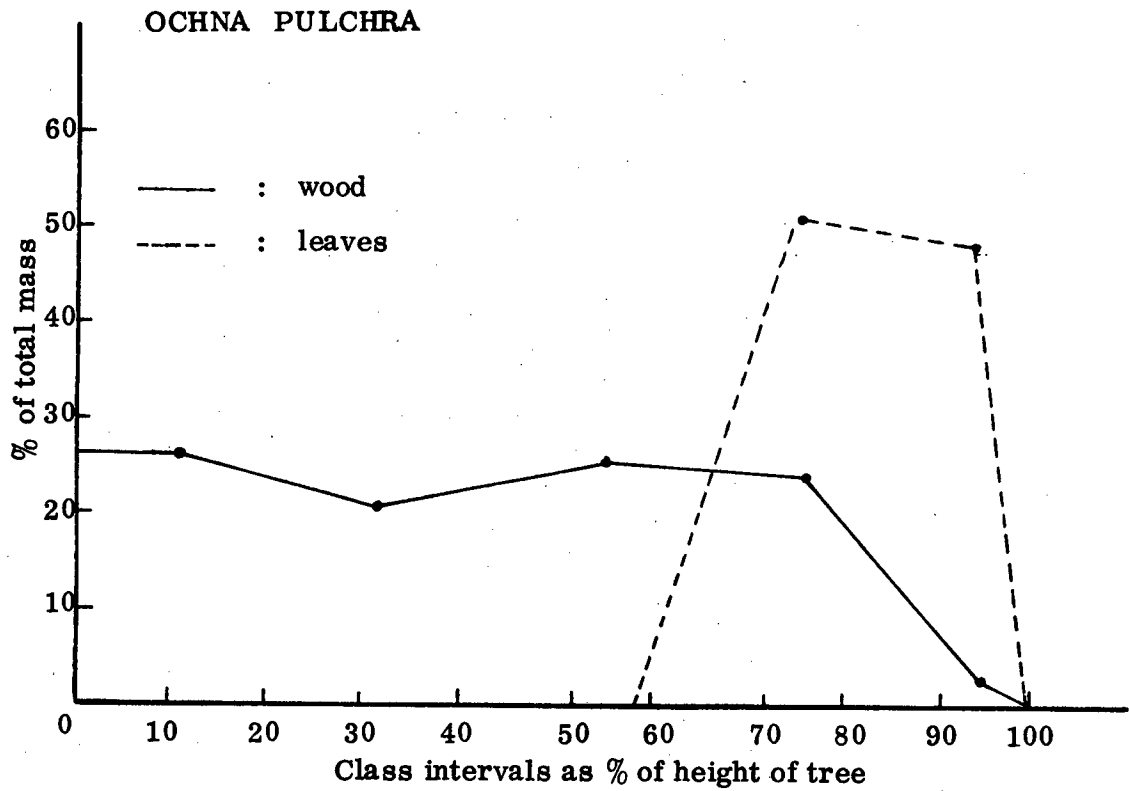
Height (m)	4,4
Total dry wood mass (kg)	36,6
Total dry leaf mass (kg)	2,5
Number of leaves	9 615
Leaf surface area (cm ² /leaf)	15,41
(m ² /individual)	14,82
Maximum canopy diameter (m)	3,8
Trunk diameter at 20 cm (cm)	13,0

Fig. 4.12c Vertical distribution of materials in trees



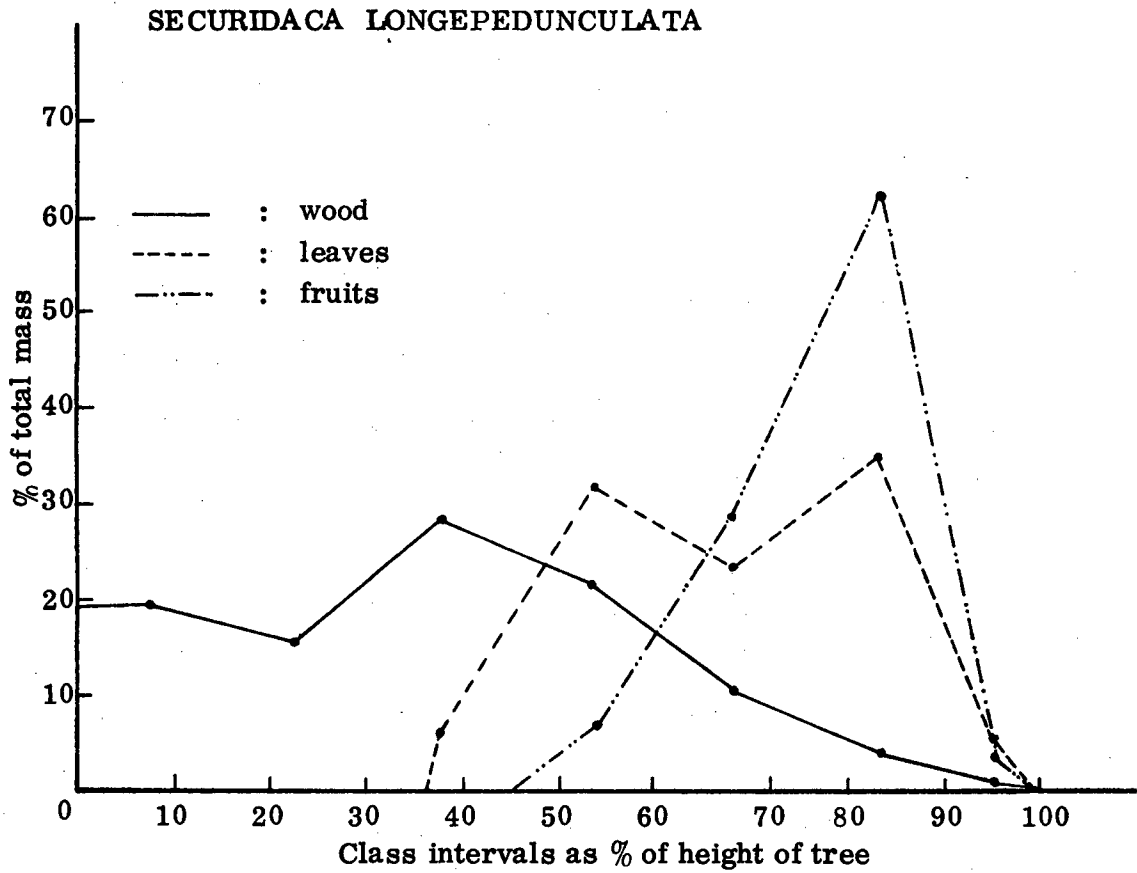
Height (m)	4,3
Total dry wood mass (kg)	13,6
Total dry leaf mass (kg)	0,8
Number of leaves	4 350
Leaf surface area (cm ² /leaf)	16,70
(m ² /individual)	7,26
Maximum canopy diameter (m)	1,3
Trunk diameter at 20 cm (cm)	9,2

Fig. 4.12d Vertical distribution of materials in trees



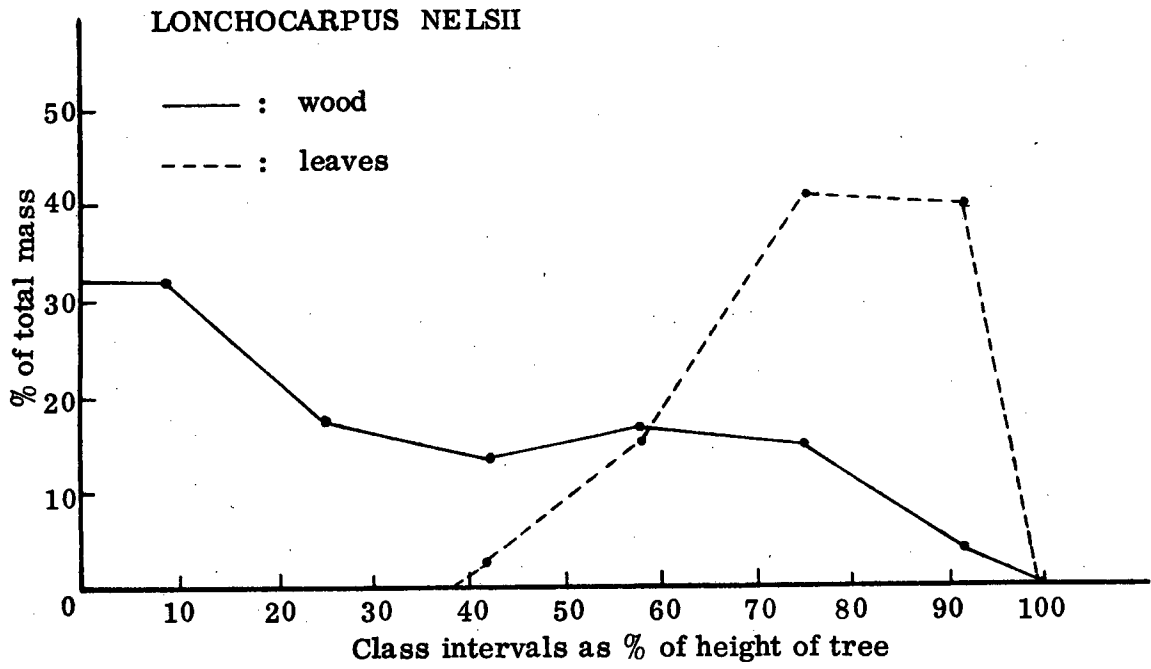
Height (m)	4,6
Total dry wood mass (kg)	33,6
Total dry leaf mass (kg)	1,3
Number of leaves	7 715
Leaf surface area (cm ² /leaf)	11,17
(m ² /individual)	8,62
Maximum canopy diameter (m)	2,7
Trunk diameter at 20 cm (cm)	14,4

Fig. 4.12e Vertical distribution of materials in trees



Height (m)	6,6
Total dry wood mass (kg)	71,9
Total dry leaf mass (kg)	2,0
Number of leaves	53 795
Number of fruits	292
Leaf surface area (cm ² /leaf)	1,66
(m ² /individual)	8,93
Maximum canopy diameter (m)	3,9
Trunk diameter at 1 m (cm)	19,4

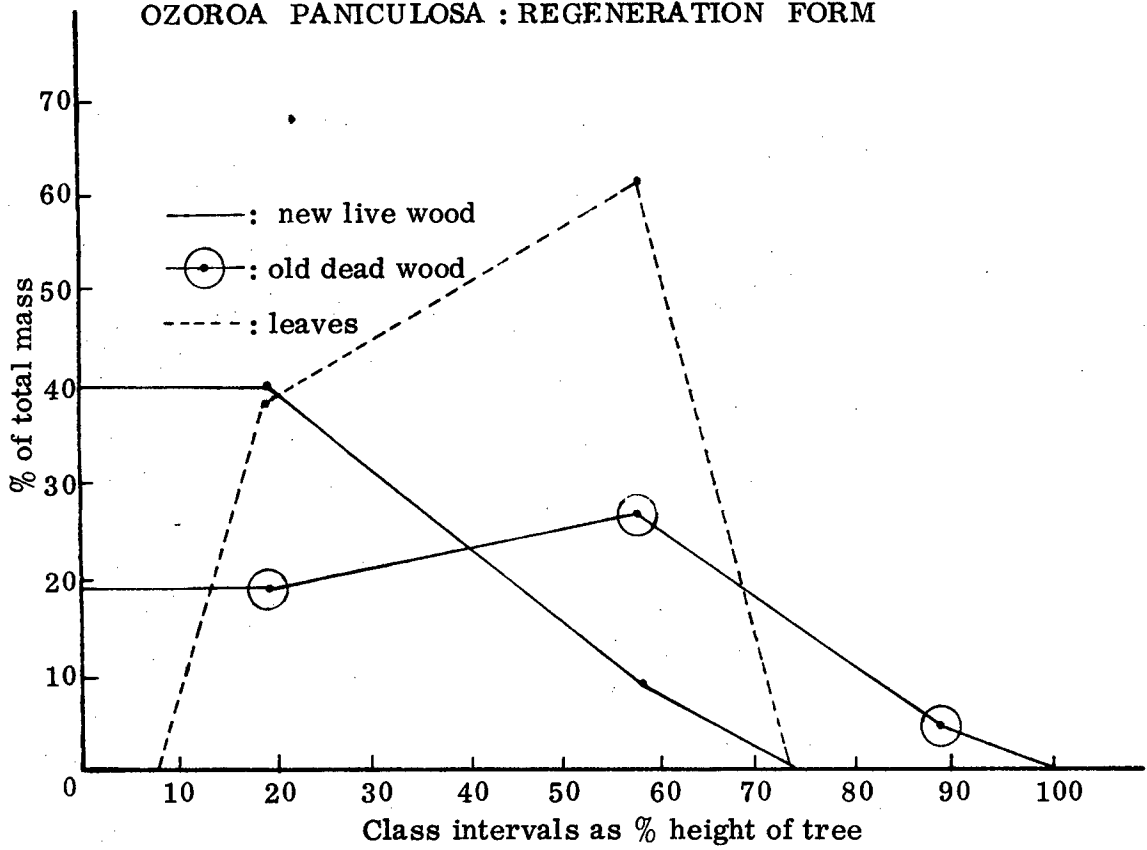
Fig. 4.12f Vertical distribution of materials in trees



Height (m)	6,0
Total dry wood mass (kg)	43,6
Total dry leaf mass (kg)	1,6
Number of leaves	4 630
Leaf surface area (cm ² /leaf)	30,19
(m ² /individual)	13,98
Maximum canopy diameter (m)	2,4
Trunk diameter at 1 m (cm)	20,6

Fig. 4.12g Vertical distribution of materials in trees

OZOROA PANICULOSA : REGENERATION FORM



Height (m) : Dead	2,58	
: Live	1,91	
Total dry wood mass (kg) : Dead	5,4	} 8,1
: Live	2,7	
Total dry leaf mass (kg)	1,2	
Number of leaves	9 270	
Leaf surface area (cm ² /leaf)	10,60	
(m ² /individual)	9,83	
Maximum canopy diameter (m)	2,0	
(3 sets of stems)		
Trunk diameter at base (cm) : Dead	2	
: Live	1	

Fig. 4.12h Vertical distribution of materials in trees

5 PRODUCTION

Leith (1972) has briefly sketched the main periods in the development of production studies and has indicated that these studies received a great impetus from about 1960 onwards, a period coinciding with the start of the International Biological Programme.

Petrusewicz (1967a) defines production as the amount of organic matter which is elaborated by a population in a defined period of time in a defined area, whether or not all of it survives to the end of the investigation. Production is divided into gross production and net production (Milner and Hughes, 1968). Gross production is the sum of energy accumulated in organisms, and energy used in the life process, chiefly by respiration (Medwecka-kornás, 1967). Net production is the energy accumulated in material and is the visible, realized or observable production (Medwecka-kornás, 1967 and Petrusewicz, 1967b).

Biomass is the quantity of organic matter present in an ecosystem at a stated time (Ovington, 1962). As pointed out earlier, it is a measure of the energy fixation within the community and can be used as a measure of importance of species. The terms "crop", "standing crop" and "yield" are scientifically imprecise (Westlake, 1963) and are avoided as they appear to often connote the maximum amount of material present or the peak of seasonal growth in an area. Ovington (1962) points out that the term "standing crop" does not apply well to all the different biotic components of an ecosystem. Petrusewicz (1967a) has stressed the importance of average biomass which is the averaged biomass for the study period and should be properly averaged to avoid serious error.

Biomass change is the difference between biomass at two arbitrary moments and ignores the variations in biomass in the time between these moments, merely giving final increase or decrease of biomass at the end of the intervening time interval (Petrusewicz, 1967a). Biomass change may be positive or negative in contrast to net

production which is often treated only as a positive quantity, similar to the term "growth".

Medwecka-kornás(1967) and Westlake (1963) use the term "productivity" to describe rates of production (including growth rates) also expressed as instantaneous production rates ($\frac{dP}{dt}$). Net productivity is, however, defined for the present study as the rate at which biomass changes, that is $\frac{dW}{dt}$. This rate may be positive or negative and is similar to Olson's (1964) 'Plant Accumulation Rate'. Except in species where previous season's biomass is stable, true productivity is taken as the rate of change of only new season's biomass. For comparisons of relative efficiency, a useful allometric concept is relative productivity, that is productivity per unit mass of organism.

Primary productivity is that associated with autotrophic photosynthetic and to a much lesser degree chemosynthetic organisms, whereas secondary productivity is associated with heterotrophic, holozoic and saprophytic types of nutrition and applies to all animals, fungi and many bacteria (Evans, 1967). The primary producers are in most cases clearly divided into aerial and subterranean parts so that aerial and subterranean productivities may be differentiated (Milner and Hughes, 1968).

The sections below are aimed at determining net primary aerial productivity of the more important herbaceous layer species as well as the average aerial biomass of each of the sampled species of the study area.

5.1 Productivity

Almost no work in tropical savannas has been done where rate of biomass change is seen as a function of both production and die-off and where there is separate treatment of species, previous and new season's material and generative and vegetative material (Bourlière and Hadley, 1970).

5.1.1 Field method

To follow the growth of the main components of the herbaceous layer over the year, only a method of destructive sampling or a harvesting technique was considered feasible. Harvesting could only be performed once a month to provide an even flow of work each month.

The random layout of quadrats for sampling vegetation each month has already been described in Section 3. With the labour available, the maximum sample size that could be taken each month was 100 m² so that the period of harvesting would not take more than about 5 days.

The harvesting of each set of pre-selected quadrats took place in the last week of every month. Only individuals or those parts of individuals that were rooted within the quadrat frame were harvested. However in 2 quadrats with tangled Pentarrhinum abyssinicum, harvesting took place without regard to rooting points. All herbage layer material was clipped with sheep shears at a constant distance of 5 cm (lateral and vertical) from the rooting points of the individuals. Difficulties in maintaining a constant clipping height were encountered; for example, in some elevated tufts of Brachiaria nigropedata, clipping at a 5 cm height was difficult owing to the hard, compact material of the tuft base. In some species, for example Cyperus margaritaceus and Tephrosia cephalantha, that have several individuals about 5 cm high, the clipping height was critical, but could not be lowered if a uniform clipping height was to be maintained for all the species of the herbaceous layer. All woody stems, with a diameter of greater than 1 cm at a height of 5 cm within the quadrat, were not harvested. This proved suitable since woody stems that were not harvested excluded only the majority of individuals of all tree species and the few large shrub species present. All lower shrub species, for example Grewia avellana, had stems of less than 1 cm in diameter at 5 cm height, and were included in the herbaceous layer.

All species harvested were clipped separately or sorted from one another during clipping. Where generative parts were present, they were separated from the vegetative parts in most species. Usually structures of the plant individual that

appeared exclusively for the generative propagation of the species were sorted as generative material, for example, in grass species, that portion of the culm above the node of the uppermost photosynthetic leaf was generative material. Vegetative and generative material of each species was placed in strong polyethylene bags that were suspended on a portable rack (Fig. 5.1) which provided 12 rows of 8 labelled pockets for the sorted components of each species. This rack greatly facilitated the sorting of species while clipping in the field. A plastic tarpaulin was kept in the vicinity to cover the rack and prevent the bags from filling with water, should it rain during harvesting.

Each day's harvested material was taken to a covered sorting site near the study area. In species where it was possible, the vegetative as well as generative new season's growth was handsorted from the previous season's material. This resulted in most species each being sorted into 2, 3 or 4 groups. With few exceptions, sorting was carried out on the day of harvesting, since a day after harvesting, most of the new season's material became wilted and shrivelled and more difficult to distinguish from the previous season's material. Sorting of the new season's material from the old was carried out until the height of the growth season in March. From April, a significant amount of new material had started to die off (probably accelerated by the relative drought in March) which rendered distinguishing of the new dead material from the previous season's material impracticable within the time available.

As the sorting was completed, the material was clipped into smaller pieces to facilitate packing in drying trays and to promote more rapid drying. Evans (1972) has emphasised the importance of the early stabilisation of harvested material's mass and points out that "when the material is once stable, it can be further dried at leisure". New season's material as well as any previous season's rain-damped material was loosely packed and placed in labelled perforated metal drying trays in an oven on the site (Fig. 5.2). Material was rapidly heated for 1 or 2 hours firstly to terminate respiration of live material and prevent breakdown by autolysis, and secondly to partially dry it to minimize loss of mass due to fungal growth while in temporary storage, awaiting completion of the remaining harvests

of the month. No means for the final accurate weighing of material was available at the site. The site oven was constructed large enough to require only 4 loadings to dry one day's harvest. It was relatively high with a chimney to promote a strong upward draught from the heating element which consisted of an evenly spread flame over the entire basal area of the oven. The fuel used was bottled gas. The lowest gauze shelf was placed at somewhat less than 1 m above the flame-level. A thermometer was used and the gas flow regulated for a temperature of between 80 to almost 100°C in the shelf area, with the oven doors shut. The period in which a tray remained in the oven depended upon the amount of moisture present in the material. The wettest material was placed on the lowest shelf, to dry this material more effectively. Two sets of trays were used for rapid changing of material in the oven.

So that the sorting and preliminary drying of material could be completed on the same day as harvesting, usually not more than a 20 m² to 30 m² sample area was harvested each day. At the height of the growth season, harvesting time (which included density counts of individuals and preliminary sorting) with one assistant, was 4 to 6 hours each day while the subsequent work of the day, with 2 or 3 assistants, took between 10 to 12 hours.

Immediately after the final harvest and sorting for a particular month, all the partially dried material was transported to Windhoek for accurate drying and weighing. The material was dried in batches in ventilated electric drying ovens for 24 hours at a constant temperature of 85°C, and weighed to the nearest 0,05 g. The least dry material was always included in the first batch. The period from the time of harvesting until final weighings were taken, rarely exceeded 8 days. Drying for a period of 24 hours at the above temperature was found to be more or less equivalent to drying to a constant weight, and the temperature was low enough to avoid spontaneous combustion or breakdown of some chemical compounds or loss of volatile substances. Each tray was usually weighed within one minute of removal from the warm oven. Warm air currents from the trays did not prevent accurate weighings to the nearest 0,05 g for trays with about 100 g of dry material, while small trays with less than 10 g of material could be stably weighed to the nearest 0,01 g.

Since weighing took place in a generally arid climate with exceptionally low humidity (Windhoek), it was found that the error incurred by the hygroscopic warm dry plant material absorbing water vapour within 1 minute of removal from the ovens, was usually much less than 0,4% above the true dry mass of the material. The marked masses of the drying trays had to be revised periodically as the season progressed, since many of the masses increased slightly with use.

5.1.2 Processing of results

a Limitation of regressions

The amount of material of each species that is sampled each month is determined at any single time by the variability in distribution of numbers of individuals that occur in the random samples and by the variability in, for example, size of the material itself. Although the selection of the study area was based upon consideration of maximum uniformity of vegetation, the phenomenon of aggregation of individuals of species, referred to earlier, created small-scale heterogeneity in the vegetation. If production is to be expressed per unit area, variation in number of individuals from one month's sample to another can not readily be eliminated. The individuals harvested each month can also not be selected initially for increased uniformity of, for example, size, leaf area, and potential rate of growth, without the sample becoming seriously unrepresentative of the population of the species.

Because of variability, sampling different numbers and types of individuals of a species each month cannot easily be avoided. Each month's sample of harvested material, viewed separately, thus has a decided but expected error, that is especially pronounced in the less common species where sampling error often completely masks the pattern of productivity of the species. None of the different species studied had consistently error-free monthly harvests since the sudden variation of some of the month's harvests relative to the others did not always correspond with concurrent phenology and climatic data. Since the value of a particular month on a monthly productivity graph of a particular species is subject to decided error, all the points on the graph should be viewed as a whole and not

individually. To this end, regressions were fitted between the plotted points by the method of least squares to reduce the error of individual points. Since the increase or decrease of plant biomass is a continuous process, curvilinear regressions were fitted to the data points and the appropriate equations computed.

Radford (1967) recommends curve fitting to plant growth data on condition that relation of mass to time can be resolved and formulised. He points out that this relatively new approach to growth analysis eliminates any further assumptions in the more detailed analysis of the growth pattern, and that there is no need for arbitrary pairing off of data for the calculation of growth rates. This technique also utilises information from all available harvests in determining values at any point in time. It appears, however, that in the process of relating mass to time, small but real irregularities are often smoothed over and any smaller real variations in growth are often masked by this technique. In cases where each plotted point is considered reliable, these minor but real irregularities in the course of growth can be taken into account without recourse to regressions.

In the present study, only total amounts of harvested material each month were large enough to be considered reliable for analysis of real irregularities in biomass change without the use of regressions. The analysis of mean growth rates by use of differences between successive values, is referred to by Radford (1967) as the "traditional practice" of growth analysis.

b Clarity of growth trends

From inspection of plotted points of mass against time for total biomass, new material or old material, it became clear that only the 10 species with a density of greater than 3 000 individuals per ha or alternatively a frequency of greater than 19%, could provide adequate values for a clear growth trend per unit area. These included the 6 herbaceous layer species with the greatest average biomass, viz. Digitaria polevansii, Brachiaria nigropedata, Grewia avellana, Andropogon gayanus, Andropogon schirensis and Aristida stipitata as well as the two less important species Tephrosia cephalantha and Cyperus margaritaceus. The material of the remaining 2 species in this group, however, appeared too variable to provide adequate values

for a clear growth trend. In Aristida meridionalis this was probably due to the presence of an abnormally large number of dead individuals, while Rhynchelytrum species was a mixture of perennial and annual species (see species list).

A test was carried out to determine whether the discernment of the growth trend of the above species and some other common species would be improved by expressing biomass change per individual harvested, in contrast to biomass change per unit area. The density of individuals clipped and those not clipped were recorded separately. In some species, expression of the biomass change per individual improved the clarity of the trend slightly, for example in Cyperus margaritaceus. In most other species, however, there was no clearly apparent improvement in clarity by expressing biomass per individual (Fig. 5.10c). It appeared that in most cases there was little difference between the variability in mass of the individuals of a species and the variability in their distribution. For uniformity of expression (of biomass and productivity) and to agree with the usage of other workers (for example, Westlake, 1963), biomass and productivities of all species and components were expressed per unit area rather than per individual.

The monthly or seasonal trends of generative material were found to be very variable, since, apart from the mentioned sources of variability, the ability of each individual to produce generative parts varied greatly and, in the sorting of generative from vegetative parts, difficulties in maintaining a standard criterion of separation were experienced. Of the 8 species which provided adequate growth trends, only Grewia avellana did not produce generative parts in the samples. Of the 5 grass species of this group, only the dominant Digitaria polevansii (Fig. 5.10a) provided a clear trend of new and previous season's generative material through the year. Some of the other grass species produced clear growth trends of previous season's generative material only. The expression of generative material as a percentage of the total biomass at the same time of the year, was too strongly affected by the change in the total biomass to be of use in illustrating the progression of the generative material through the year. Cyperus margaritaceus and Tephrosia cephalantha provided clear growth trends of total generative material and are presented with Digitaria polevansii as examples of the change of generative material

per unit area through the year in a grass species (Fig. 5.10a) a sedge species (Fig. 5.10b) and another herbaceous species (Fig. 5.10c).

There were many species which were less abundant than 3 000 individuals per ha or with a frequency of less than 19%, that still showed a meaningful seasonal tendency of total biomass change if samples were grouped into 4 seasons (Sept. - Nov.; Dec. - Feb.; March - May; June - Aug.), each season's biomass value being the average of three 100 m² samples. It was found from inspection that, apart from the abovementioned 8 species which provided adequate growth trends, the 15 herbaceous layer species (including Ochna) with a density of more than 250 individuals per ha and a frequency of greater than 2% could show reasonable seasonal changes in total biomass. Of these, 6 species provided clear changes in biomass in seasonal groupings and were, in descending order of frequency, Commelina africana, Ancylanthos bainesii, Aristida congesta, Mariscus laxiflorus, Turbina oblongata and Rhynchosia venulosa. For special reasons, the remaining 9 species, however, proved unsuitable for indicating seasonal growth trends:

- (i) The 3 species of this group that had the lowest height above ground, namely Blepharis maderaspatensis, Cassia biensis and especially Fimbristylis exilis, showed erratic seasonal biomass since the height of clipping was critical.
- (ii) The 3 species of this group which has the greatest average mass per individual, that is Dicliptera eonii (14,56 g/individual), Stipagrostis uniplumis (11,06 g/individual) and Triraphis schinzii (10,26 g/individual) had relatively erratic seasonal biomass since the addition or loss of only 2 or 3 of these individuals, created a large sampling error.
- (iii) Due to probable dependence upon burned back stumps of varying ages, the regenerative shoots of those Ochna pulchra of the herbaceous layer did not provide clear seasonal growth trends.
- (iv) The same reasons for unsuitability of Aristida meridionalis and Rhynchelytrum species for clear biomass change trends per month appeared still to apply in seasons.

c Mathematical description of biomass changes

It has been emphasized that, except in the case of total productivity of the herbaceous layer, mathematical curves must be fitted to plotted points of biomass against time for individual species to smooth out differences which are clearly due to sampling errors. Once the correct curve has been fitted, the calculation of rates of change of biomass at any instant in time can be done accurately by differentiation of the equation of the curve. A systematic programme was followed to determine which types of mathematical functions best described each set of data for the 8 species concerned. Yarranton (1971) has discussed the distinction between mathematical models and mathematical representation or description of a phenomenon. That which follows, is strictly a mathematical description of changes in biomass and growth through the year. Yarranton (1971) states that "the purpose of a first mathematical representation is to provide an intelligible description of observational data".

i Total biomass changes over the year

From inspection of data of total biomass of each of the 8 species each month, it was clear that there was in most cases a tendency toward a decrease in biomass with the first few rains of the season and an increase as the major rains of the season occurred. Thereafter a maximum was attained, followed by a gradual decrease into the winter months. The latter decrease of biomass after the attainment of maximum biomass has also been found for example by Wiegert and Evans (1964) in grassland vegetation in Michigan (U.S.A.). A polynomial was selected for description because the form of the relation was uncertain. A description of this form requires at least one point of inflection which is found in third degree polynomials. However, to provide for a possible point of inflection at the beginning of the graph so that the graph may run smoothly from that of the previous season, and to provide a point of inflection toward the end of the graph to allow for decreasing rates of fall in biomass with time, a fifth degree polynomial appeared best suited to the data. To test the suitability of a fifth degree polynomial regression, polynomials from the third to seventh degree were fitted for most of the species by the method of least squares. In all cases, except one, a fifth degree polynomial appeared to provide the best description of the data in the form of:

$$W = b(0) + b(1)t + b(2)t^2 + b(3)t^3 + b(4)t^4 + b(5)t^5$$

where W = biomass, t = time and b = coefficients. The misleading data for the last 2 months of the study period in Digitaria polevansii resulted in the curve for the 3 winter months being ignored for this species.

ii Decrease of previous season's material

Previous season's material was sorted only for the first 7 months of the study year in the 5 most important grass species (Fig. 4.1) and Cyperus margaritaceus. Exponential forms ($W = pe^{qt}$), power forms ($W = at^u$) and linear forms ($W = a(0) + a(1)t$) were fitted to the data of the first 7 months. It was found that the function $W = at^b$ appeared to provide the best description of the data since it allowed for a relatively smooth follow on from the previous season's decreasing dead material. It also reflected the expected more rapid loss of easily removable material at first, and less rapid loss later when most of this material had been removed. The form of this curve also explained the decrease in total biomass in the beginning of the growth season when the rate of loss of previous season's material at first exceeds the new growth. A most important characteristic of this decreasing $W = at^b$ curve is that it appeared to be extrapolatable after the 7th month until the end of the study year, and from other concurrent data of phenology and climate, there appeared to be no reason for a further sudden decrease in the remaining previous season's material.

iii Increase and decrease of new growth

The new material of the growth season is the most important constituent for growth analysis since it is only new growth which reflects the true productivity of the species, and not only the change in total biomass since this is affected by varying amounts of dead previous season's material present (Porter, 1967). Wiegert and Evans (1964) have pointed out that even the use of new material data does not describe the true growth of a species, since it does not account for mortality of new plants before the peak biomass is attained, nor measure growth which may occur during the decline of biomass. This is not of critical importance since, in the study area, individuals of the same species tended to be relatively well synchronised in growth and in mortality. No analysis of new material of Andropogon schirensis was attempted

since it appeared to have too variable data.

The basic and most important problem in the determination of change in new material throughout the year was that it was only possible to separate new material from previous season's material until the height of the growing season in March. An approach to this problem was made by using the extrapolatability of the previous season's material curve, and the fitted curve of the total biomass. By subtracting the former curve from the latter for the last 5 months of the study year, an estimate was obtained of change in new season's material in this period. Using actual new material biomass values for the first 7 months of the study year and estimated values for the last 5 months an attempt was made to fit a single exponential and negative exponential function to describe the change of the new material through the whole study year. This function, however, underestimated the maximum biomass of the new material. Using Brachiaria nigropedata as an example, a logistic growth function of the type $W = \frac{A}{1 + be^{-kt}}$ (Richards, 1969) was fitted by the method described by Ricklefs (1967) to the new material biomass values of the first 7 months, together with the estimated value of the maximum new material's biomass, derived from the curve of the decrease of previous season's material subtracted from the curve of the total biomass. This logistic curve (Fig. 5.6b) was found to provide a good description of the start of new growth but, as in other growth curves (Gompertz and Von Bertalanffy), it only provided for an asymptote at the end of the growth range. In the change in new material of each species in seasonal vegetation, an asymptote would appear to be non-existent. In Brachiaria nigropedata, the asymptote given by the logistic equation approached the maximum biomass of the new material too gradually, about 2 months after the maximum should have been reached (Fig. 5.6b). The traditional growth functions appeared therefore, not to provide adequate description of the maximum biomass of new material. This is possibly not unexpected as Pielou (1969) has pointed out the highly simplified assumptions that underlie the application of the logistic equation to the growth data.

It was decided that some form of graph segment should be used to describe the change in new material throughout the year. Williams (1964) has discussed some of the difficulties in fitting single functions to describe growth patterns through the year, and has shown the usefulness of graph segments for describing each section of

growth by different functions. He, however, warns against the splitting up of the graph into too many segments as some segments become precariously dependent upon a few points of the data, thus defeating the object of the curve fitting. Description of the growth and decrease of the new material was split into only 2 segments, so that only one point of discontinuity was present in the curve.

The function fitted to the new material biomass values of the first 7 months was taken up to the point where it intersected the curve of the fifth degree polynomial function of the total biomass minus the fitted and extrapolated function of the decrease of previous season's material. The intersection of the 2 curves usually took place at a point roughly half way through the study year. Although the first part of the logistic equation might describe the first part of the new material's growth effectively, the following functions were found to be almost as effective and to be less laborious to apply. The function $W = ct^d$ was used for *Digitaria polevansii* and *Brachiaria nigropedata*, and $W = pe^{qt}$ for *Andropogon gayanus* and *Aristida stipitata*, while the function for the latter half of the study year was in all 4 species:

$$W = [b(0) + b(1)t + b(2)t^2 + b(3)t^3 + b(4)t^4 + b(5)t^5] - [at^b]$$

Absolute growth rates each month were calculated for some species by differentiation of the above equations. Where relative growth rates were calculated, these were done by dividing the actual mass at a particular time into the rate of growth at that time. In *Digitaria polevansii* where the 2 curve segments intersect at a relatively large angle (Fig. 5.6a), the rate of growth nearest this point of intersection was taken as the average of the 2 functions at the point concerned, that is the relative rate of growth of *Digitaria polevansii* in the middle of February (a point in time which lies near the point of intersection) was calculated by:

$$\text{RGR} = \frac{\frac{d}{dt}(\text{Polynomial} - at^b)}{2} + \frac{\frac{d}{dt}(ct^d)}{ct^d}$$

where Polynomial = $b(0) + b(1)t + b(2)t^2 + b(3)t^3 + b(4)t^4 + b(5)t^5$

Rates and relative rates of change in the total biomass of the herbaceous layer were worked out from the actual monthly biomass values, resulting in mean rates for a

particular month. The mean growth rate is given by

$$GR = \frac{W_2 - W_1}{t_2 - t_1}$$

and the mean relative growth rate is given by

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad \text{Radford (1967),}$$

where W_1 = mass at t_1 and W_2 = mass at t_2

iv Increase and decrease of generative material

Increases and decreases in generative material of species were expressed as actual differences in biomass values, and no mathematical relation between mass and time was attempted as the exact expectation of changes in generative biomass through the year was uncertain.

5.1.3 Results

5.1.3.1 Changes in total biomass

Change in total aerial biomass through the year may be divided into 4 phases. The last 3 of these phases correspond closely to the familiar growth and decrease of new material through the year. The 4 phases are, (a) decrease in biomass early in the growth season, (b) period of rapid increase, (c) attainment of maximum biomass and (d) decrease of biomass after the maximum. Andropogon schirensis started with a relatively high biomass early in the season (Fig. 5.4d) and is the only species that appeared to have a net decrease over the study year, due probably to low vitality of its individuals. Tephrosia cephalantha was almost absent in the beginning of the study year but increased greatly later in the season. The total biomass at any point in the year was thus roughly equal to its new growth material (Fig. 5.4h). Analysis of the abovementioned 4 phases in changes of total biomass gave the following results:

a Decrease in biomass early in the growth season

The herbage layer's first real increase in biomass started in October and increased

to a mean rate of $2,55 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in November, but then fell with a rate of $-1,50 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in December (Fig. 5.3). In each of the 5 grass species (Digitaria polevansii (Fig. 5.4a), Brachiaria nigropedata (Fig. 5.4b), Andropogon gayanus (Fig. 5.4c), Andropogon schirensis (Fig. 5.4d) and Aristida stipitata (Fig. 5.4e)), there was a slight decrease in total biomass in November or December after the new growth had started. The decrease of previous season's material appeared to occur more rapidly than the growth of new material in the period of the first rains, resulting in a net decrease of biomass at first. This disagrees with the statement of Bourlière and Hadley (1970) that a feature of "tropical" herbaceous vegetation is the very rapid rate of biomass increase at the start of the growth season. Although there was no net decrease early in the growth season in Cyperus margaritaceus, there was a tendency for the biomass to remain more or less constant in October and November after growth had started (Fig. 5.4f). No early decrease in biomass of Grewia avellana was apparent (Fig. 5.4g), since this shrub had already shed its leaves by the start of the growing season and soon acquired a new flush of leaves.

b Period of rapid increase

The herbaceous layer's biomass increased rapidly in January and attained a maximum mean rate of $15,90 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in February (Fig. 5.7). This falls within the reported range of 10 to 40 kg/ha daily dry mass increase in the growth season for most savanna communities (Bourlière and Hadley, 1970). The rate was also similar to the maximum average rate of increase of $16,4 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in a month for the living material of a protected cropland in Oklahoma (Penfound, 1964). Rapid increase in the total biomass of Cyperus margaritaceus started earlier, namely in December (Fig. 5.4f), while Grewia avellana had its period of maximum rate of increase in December ($1,22 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in the middle of December) and January ($1,10 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ in the middle of January) (Fig. 5.8c). Total biomass of both Digitaria polevansii and Brachiaria nigropedata increased most rapidly in January and February (Fig. 5.4a, b). The period of rapid increase extended into March for Andropogon gayanus (Fig. 5.4c) and Aristida stipitata (Fig. 5.4e) and into April for Tephrosia cephalantha (Figs. 5.4h and 5.8d) (and less reliably for Andropogon

schirensis (Fig. 5.4d).

c Attainment of maximum biomass

The maximum biomass of the herbaceous layer's material was reached in April (1 420 kg/ha) (Fig. 5.3). Ovington, Heitkamp and Lawrence (1963) found the maximum living biomass of the herbaceous layer of a savanna vegetation in central Minnesota was 1 916 kg/ha. Grewia avellana attained its maximum biomass (151 kg/ha) earlier, namely in March (Fig. 5.4g) while Brachiaria nigropedata and Cyperus margaritaceus attained maximum biomass (196 kg/ha and 14 kg/ha respectively) (Fig. 5.4b, f) in April. Those species which attained maximum biomass about May were Digitaria polevansii (669 kg/ha in the beginning of May) (Fig. 5.4a), Andropogon gayanus (100 kg/ha) (Fig. 5.4c) and Aristida stipitata (53 kg/ha) (Fig. 5.4e). A maximum biomass (19 kg/ha) was only reached in June in the case of Tephrosia cephalantha (Fig. 5.4h). The maximum biomass of Andropogon schirensis appears to be unreliable since it occurs too late in the season (Fig. 5.4d).

d Decrease of biomass after the maximum

The herbaceous layer's biomass started to decrease rapidly in May and attained its most rapid mean rate of decrease ($-5,54 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$) in June becoming progressively less rapid in July and August (Fig. 5.7) from the maximum until September, the mass dropped by about 33% which is somewhat greater than the 25% decrease after the maximum in Nigerian savanna (Hopkins, 1968). In all 8 species it is clear that the total biomass was never stabilised near its maximum point since all decreased relatively rapidly soon after the maximum biomass had been attained.

The annual net increase in the total biomass of the herbaceous layer can be estimated by extrapolating the graph of the herbaceous layer material (Fig. 5.3) by one month into September, 1971 giving a biomass value in the region of 950 kg/ha. When the biomass in September, 1970 is subtracted from this value, an annual net increase of about 500 kg/ha is obtained. The calculation of net annual increase for this particular period appears suitable since in September the biomass was stable relative to the biomass values for most of the other months of the year. In the course

of the study year, the second season after fire, the aerial biomass of the herbaceous layer thus more than doubled. The range of biomass within one year (often referred to as annual production by for example, Westlake (1963)) appears greatly to exceed the net increase of biomass in that year. Thus, although the total biomass of the herbaceous layer increased by about 500 kg/ha from the beginning to the end of the study year, the range from the minimum to the maximum biomass in this year was about 900 kg/ha. This value is similar to "annual production" (995 kg/ha) on the Springbok Flats of the Transvaal (Louw, 1968). Minimum biomass expressed as a percentage of maximum biomass was 23,5% for the total and was 25,1% for Digitaria polevansii, 24,8% for Brachiaria nigropedata, 31,0% for Andropogon gayanus, 41,5% for Aristida stipitata, about 13,9% for Grewia avellana, 1,6% for Tephrosia cephalantha and 18,2% for Cyperus margaritaceus. These usually low percentages indicate the large amount that biomass of important constituent species of a community can vary throughout the year. Only Andropogon schirensis had the relatively high percentage of 72,0%, due probably to the poor vitality of its population.

The 6 less-important species which gave meaningful seasonal biomass changes are shown with these changes in Fig. 5.5a - f. The months September to November constitute Spring; December to February, Summer; March to May, Autumn; and June to August, Winter. Two of the six species had a maximum biomass in summer and a decrease in autumn. These were Mariscus laxiflorus with a summer maximum of 1,3 kg/ha (Fig. 5.5a) and Turbina oblongata with a maximum of 3,0 kg/ha (Fig. 5.5b). Commelina africana, had a maximum biomass in autumn (6,4 kg/ha) which slightly exceeded that of summer (Fig. 5.5c). The 3 remaining species increased in summer relative to spring, but only attained maximum biomass in autumn which corresponded well with the dominant species. Autumn maxima were 2,1 kg/ha for Aristida congesta (Fig. 5.5d), 2,9 kg/ha for Rhynchosia venulosa (Fig. 5.5e) and 12,0 kg/ha for Ancylanthos bainesii (Fig. 5.5f).

5.1.3.2 Decrease of previous season's material

As pointed out earlier, a negative power curve of the form $W = at^b$ appeared to

provide the best description (all $P < 0,02$) of decrease of previous season's material per species (for the 5 grass species concerned, the correlation coefficients are 0,97; 0,97; 0,92; 0,79 and 0,76). Wiegert and Evans (1964) also found that rate of disappearance of dead material in a grassland vegetation was highest during the early part of the growth season, and decreased as the season progressed. Not all the 5 grass species had previous season's material decreasing to the same level, for example, material had decreased in the 4 months from start of the rains in October to height of rains in February by 22,7% in Digitaria polevansii (Fig. 5.4a), 34,2% in Brachiaria nigropedata (Fig. 5.4b), 53,7% in Andropogon gayanus (Fig. 5.4c), 51,5% in Andropogon schirensis (Fig. 5.4d) and 46,6% in Aristida stipitata (Fig. 5.4e). The rate of disappearance of previous season's material was thus, for example, higher in Andropogon gayanus than in Digitaria polevansii.

By April or May, at the height of the growing season, the ratio of previous season's material to the maximum total biomass, expressed as a percentage, was approximately 16,4% for Digitaria polevansii (Fig. 5.4a), 11,7% for Brachiaria nigropedata (Fig. 5.4b), 11,0% for Andropogon gayanus (Fig. 5.4c) and 20,7% for Aristida stipitata (Fig. 5.4e). Since the new material of each species decreased rapidly after the maximum was attained, the ratio of previous season's material to total biomass increased appreciably toward winter. The ratio is also dependent on the success of growth in the previous season and would probably have been higher had there been more than one previous season of growth. Only one previous season's herbaceous layer growth existed due to a fire at the beginning of that season.

5.1.3.3 Growth and decrease of new material

Analysis of new material's growth and decrease was only fully undertaken for the 4 grass species, Digitaria polevansii, Brachiaria nigropedata, Andropogon gayanus and Aristida stipitata, as well as for Tephrosia cephalantha. The last species' new growth at any point in the year, was roughly equal to its total biomass (Fig. 5.4h). The growth of new material in Cyperus margaritaceus (Fig. 5.4f) was somewhat masked in the beginning by the previous season's material present. New material

could not be sorted from previous season's material in the shrub species Grewia avellana (Fig. 5.4g). The data for Andropogon schirensis was not considered reliable for detailed analysis of new growth as was that for the estimation of new material for Digitaria polevansii in the winter months.

All 4 grass species started growth in October and new material increased most rapidly about February. The rate of increase at the middle of February was $6,70 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ for Digitaria polevansii (Fig. 5.8a) and $1,26 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$ for Brachiaria nigropedata (Fig. 5.8b). For Andropogon gayanus the corresponding value was $0,81 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$. Tephrosia cephalantha increased most rapidly in April ($0,14 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$) (Fig. 5.8d). The relative growth rates at the mid points of these months of maximum growth were for Digitaria polevansii $0,018 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ (Fig. 5.9a), for Brachiaria nigropedata $0,017 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$, for Andropogon gayanus $0,024 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$, and for Tephrosia cephalantha $0,012 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ (Fig. 5.9c). Andropogon gayanus appeared thus to be a relatively efficient producer of new material in the period of maximum rate of growth. This species had the greatest average mass per individual (21,51 g) of the herbaceous species.

New material accumulation reached a maximum at the beginning of May for Digitaria polevansii (estimated at 558 kg/ha) (Fig. 5.6a), in late May for Brachiaria nigropedata (174 kg/ha) (Fig. 5.6b) and Andropogon gayanus (89 kg/ha) (Fig. 5.6c), and in June in the case of Aristida stipitata (42 kg/ha) (Fig. 5.6d) and Tephrosia cephalantha (19 kg/ha) (Fig. 5.4h). The maximum biomass of new material of the herbaceous layer could not be estimated, since the sorting of previous season's material from new growth in some species, for example Grewia avellana, could not be carried out. Considering the maximum new material in the dominant grass species, however, it appeared that the maximum new material of the whole herbaceous layer, probably somewhat exceeded the peak green standing crop of 944 kg/ha of a prairie herbaceous layer in central Minnesota, but did not reach the maximum of 1 916 kg/ha of the herbaceous layer of an adjacent savanna (Ovington, et al., 1963). Soon after the maximum was attained in the above species, there was a definite decrease in new material following the end of effective rains in early May. The rate of decrease

appeared greater in Andropogon gayanus than, for instance, in Brachiaria nigropedata.

Relative growth rates through the year are given for new material of a grass species (Digitaria polevansii) (Fig. 5.9a), for the total biomass of a woody species (Grewia avellana) (Fig. 5.9b) and for the material of a small herbaceous species (Tephrosia cephalantha) (Fig. 5.9c). In each species there was progressive decrease in relative growth rate as the total biomass of the populations increased. In both the grass species and the woody species, the maximum relative growth rate occurred in the first month of growth, that is $0,113 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ in October (Fig. 5.9a) and $0,024 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ in November respectively (Fig. 5.9b). In Tephrosia cephalantha, due to the presence of some unstable previous season's material at the beginning of the season, the relative growth rate was slightly irregular, but nevertheless high, in the beginning of the growth season (Fig. 5.9c). About the middle of December the relative growth rate was $0,045 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Digitaria polevansii (Fig. 5.9a), $0,019 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Tephrosia cephalantha (Fig. 5.9c) and $0,017 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Grewia avellana (Fig. 5.9b). Four months later, in the middle of April, the relative growth rates were $0,002 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Digitaria polevansii (Fig. 5.9a), $0,012 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Tephrosia cephalantha (Fig. 5.9c), and $-0,003 \text{ kg} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ for Grewia avellana (Fig. 5.9b). The rate of fall in the relative growth rate thus varied not only according to the time of the year, but also between species. The woody species, Grewia avellana, had a lower relative growth rate than Digitaria polevansii throughout the year, owing to the retention of much dead material in woody species.

Although relative growth rates are useful to compare efficiency of growth of species, it nevertheless appeared that the absolute growth rate of a species indicated the success of growth of the species in the community.

5.1.3.4 Changes in generative material

As pointed out earlier, only Digitaria polevansii, Cyperus margaritaceus and Tephrosia cephalantha generative material was considered suitable for showing

changes over the year. Monthly changes in previous season's and present seasons generative material are presented for Digitaria polevansii and Cyperus margaritaceus in Fig. 5.10a, b. The previous season's generative material of these 2 species decreased steadily, so that by December the amount of material was less than 15% of that in September, and had vanished after February. In both species, the new season's generative material exceeded that of the previous season's from January. New season's generative material appeared in November in Cyperus margaritaceus (Fig. 5.10b), January in Digitaria polevansii (Fig. 5.10a), and February in Tephrosia cephalantha (Fig. 5.10c). In all 3 these species, the generative material reached maximum around March with the approximate maximum values of 18,5 kg/ha for Digitaria polevansii, 9,0 kg/ha for Cyperus margaritaceus and 1,6 kg/ha for Tephrosia cephalantha.

5.1.3.5 Relation of biomass increase to climate changes

Watson (1963) has pointed out that the dependence of "yield" on climatic factors is usually far too complex to be described adequately by linear regressions on a few gross measures of climatic variation except perhaps where a factor such as rainfall dominates over all other factors. Expectedly, the average monthly relative humidity and temperature were found to be not directly correlated with changes in biomass of the herbaceous layer, or the changes in biomass of different species. In the nonhumid tropics, the biological year is, however, dominated by water, and species phenology and production are closely linked to the alternation of wet and dry seasons (Bourlière and Hadley, 1970). Some relation of biomass change to rainfall was found to exist. Several trials were made to determine possible relations between growth of total herbaceous layer and rainfall. The period of October to April was taken since this was the active growing season in which a close correlation between rainfall and growth could be expected.

A linear test of correlation between the rainfall of each month of the study year and the herbaceous biomass of the month following (for biomass from October to April) was found to be not significant ($r = 0,58$). A correlation between the actual mean monthly

rate of change of herbaceous layer biomass and the deviation of actual rainfall from average rainfall for the same month was also found to be not significant ($r = 0,57$). This deviation was obtained by taking the difference between the actual measured monthly rainfall on the study site and the monthly average record at the Waterberg Rainfall Station.

The only anomalous significant relation resulted from linear correlation between the average annual monthly rainfall data of the Waterberg Rainfall Station and the biomass of the following month which gave a high correlation coefficient of $r = 0,913$ ($P \leq 0,001$). A correlation of the average monthly rainfall of the Waterberg Station with the standing biomass of the herbaceous layer for the same month was found to be not significant ($r = 0,344$).

5.2 Biomass

Determinations of the biomass of crops and to a lesser extent of forests have often been carried out (e.g. Ovington, 1962; Westlake, 1963; Rodin and Bazilevich, 1967; Whittaker and Woodwell, 1969; Leith, 1972). It appears, however, that determinations of biomass of savanna vegetation have rarely been carried out or have been restricted to the ground layer vegetation (e.g. Walter, 1939).

5.2.1 Herbaceous layer biomass

Changes in biomass over the year have already been given for the herbaceous layer and its main constituent species (Section 5.1). The oven-dry biomass of this layer and its constituent species is taken as the average of the samples throughout the year (Table 4.1).

Ovington, Heitkamp and Lawrence (1963) also took biomass as the average of the observations over the entire sample period. Any single biomass determination only reflects one part of the seasonal variation in biomass through the year. Petrusiewicz

(1967a) has drawn attention to the importance of the proper weighting of the mean to reflect the correct average biomass for the study period. The average biomass of the herbaceous layer for the study year was 912,85 kg/ha which is equivalent to 91,285 g/m². This average value is very much lower than the biomass values of many crops but is higher than the 770 kg/ha of the herbaceous layer of the savanna vegetation in Michigan (Ovington et al., 1963). Walter's (1939) ground layer values for South West Africa (re-cited in Walter and Volk, 1954; Odum, 1959; Walter, 1962 and Rodin and Bazilevich, 1967) appear excessively high; the 5 533 kg/ha for the Waterberg area was obtained using a non-standardized method and was based on a very small and highly biased sample. Walter's (1939) reasons for the unexpectedly high values include the admission that maximal values were sought.

Biomass differs according to different species composition. Average biomass in Aristida congesta quadrats differs from that of Dicliptera eonii quadrats of the flats. The biomass of these areas was calculated using average masses of species individuals and known density of individuals of the species in these quadrats. The biomass of the herbaceous layer in the Aristida congesta quadrats was 71,79 g/m² (= 717,9 kg/ha) while that in the Dicliptera eonii quadrats was 123,03 g/m² (= 1 230,3 kg/ha). The biomass of the Aristida congesta areas was thus below the herbaceous layer average of 91,285 g/m² while that of the Dicliptera eonii areas of the flats was above this average.

The 2 species of the herbaceous layer with the greatest average biomass were Digitaria polevansii (42,2 g/m²) and Brachiaria nigropedata (11,9 g/m²) which together made up 59,4% of the biomass of the herbaceous layer. The species with the third highest biomass (8,9 g/m²) was Grewia avellana, followed by the grass species Andropogon gayanus (5,9 g/m²). Andropogon schirensis (4,2 g/m²) and Aristida stipitata (3,6 g/m²). These 6 most important herbaceous layer species constituted 84,3% of the herbaceous layer's biomass. The only other reasonably important shrub species of the herbaceous layer was Ancylanthos bainesii with a biomass of 0,63 g/m². The smaller basal shoots of tree species and large shrub species together only made up 0,86% of the herbaceous layer's biomass. The grass species with a biomass greater than 3 g/m² were 74,57% of the total biomass while

grass species with less than $3,0 \text{ g/m}^2$ and more than $0,5 \text{ g/m}^2$ were 9,41% of the total. The grasses with biomass less than $0,5 \text{ g/m}^2$ were 0,92% of the total while other herbaceous species were 3,74% of the total biomass. The woody species of the herbaceous layer constituted 11,33% of the total and unidentified species only 0,01%.

Although biomass of a species is usually expressed as mass of material per unit area, it may also be expressed as the average biomass per species individual. A distribution of individuals (irrespective of species) into classes of average masses of species individuals is given in Fig. 5.11. Since each mass concerned was the average mass for the individuals of each species, all individuals of a particular species could only fall in one class. The vast majority of species individuals fell between 0 and 12 g. Within this range, most species individuals occurred in the class 8 to 12 g. Species individuals with average mass from 12 to 20 g were infrequent but those in the class 20 to 24 g were relatively more frequent. Sporadic occurrences of individuals with greater average mass per individual such as Sphedamnopus puriens (29 g), Eragrostis pallens (48 g), Cenchrus ciliaris (91 g) and Grewia deserticola (177 g) occurred.

Species with a density greater than 0,1 individuals per m^2 are distributed in the following average individual mass classes. Cyperus margaritaceus, Tephrosia cephalantha and Cassia biensis fell below 2 g and Aristida meridionalis, Ancylanthos bainesii and Commelina africana between 2 and 4 g. Andropogon schirensis, Aristida stipitata and Rhynchelytrum species fell between 4 and 6 g and Grewia avellana between 6 and 8 g. Digitaria polevansii fell between 8 and 10 g and Brachiaria nigropedata and Triraphis schinzii between 10 and 12 g. Andropogon gayanus fell between 20 and 22 g.

5.2.2 Tree biomass

Since biomass of large individuals (e.g. trees) with a low relative growth rate, does

not vary much relative to the total mass within a one-year study period, biomass of these individuals determined at any one time in the study year were taken as more or less equal to the average biomass for the study year.

5.2.2.1 Method

The measurement of biomass of ecosystems containing trees is difficult. According to Newbould (1967) usually only relatively low confidence limits can be given for estimates of forest production and using short-cut approaches for biomass determinations, errors of up to 50% are not unexpected.

The density of tree species showed that Burkea africana, Terminalia sericea, Combretum psidioides as well as Ochna pulchra overwhelmingly dominated the tree layer. The biomass of the rarer tree species could thus be less accurately estimated than these 4 species without affecting greatly the estimate of total tree layer's biomass. To estimate the aerial biomass of each of the 3 dominant tree species and Ochna pulchra, an attempt was made to draw up a correlation between an easily measurable characteristic or property of the tree individual and the biomass of that individual. In this way, by harvesting only the relatively few individuals required for the above relation, the biomass of the entire population could be estimated without recourse to large scale, time-consuming and unwanted destruction of the population.

Some problems, encountered in determining the relationship between various properties of a tree individual and its biomass, have been given by Jordan (1971). Usually, some property of tree trunk circumference (Holland, 1969) or diameter (diameter at breast height - DBH) (Jordan, 1971, Peterken and Newbould, 1966), or some property of the tree trunk combined with the height of the individual (Post, 1970) is used for correlating with the biomass of the individual. In the present study, the only reasonable correlation between height of tree individual and biomass was found in Terminalia sericea, but in other tree species very poor correlations resulted.

A method similar to that followed by Jordan (1971), was used to correlate wet

diameter, at a set height above ground, with dry biomass. Tape was used to measure circumference and the resulting value divided by π to obtain the diameter of the trunk. Newbould (1967) indicates that measuring trunk diameter by tape is preferable to measuring by calipers. Although in most woodland ecosystems diameter at breast height (DBH) is in general use, in the low savanna vegetation of the study area, DBH could not be used since, in many individuals, especially in species such as Combretum psidioides, individuals had already branched at breast height. To avoid complications caused by branching, diameter was measured below the first major branch of most individuals, that is one metre above ground in Burkea africana and Terminalia sericea and 20 cm in Combretum psidioides and Ochna pulchra. Although writers such as Holland (1969) and Jordan (1971) have used measurement of tree trunks at ground level, it was felt that diameter at ground level was too dependent on other factors such as varying degrees of burning back in individuals after past fires.

Heights and stem diameters of trees were used to select individuals for correlation of trunk diameter and biomass. By taking individuals ranging on both sides of the average height of each tree species, a relation of trunk diameter to biomass was obtained which applied to almost all individuals of the species. Individuals for sampling numbered at least 15 per species and were mostly selected in the fourth subdivision of the study area (Fig. 3.1).

Measured circumference (diameter) of tree trunks was not easily related to dry biomass. The relation appeared curvilinear, similar to that found by Jordan (1971), Peterken and Newbould (1966) and Holland (1969). Polynomials of the second order did not describe the relation of stem diameter to biomass of small individuals well (also evidenced by Jordan, 1971). Only in Terminalia sericea did the second degree polynomial provide a good regression for the entire mass range of those individuals present. Holland (1969) found this function to apply to Eucalyptus species. A power function, although generally a good fit (correlation coefficients of $r = 0,98$ for Burkea africana, $r = 0,95$ for Combretum psidioides, and $r = 0,93$ for Ochna pulchra), did not adequately describe the upper range of mass in each of the species.

Thus, in Burkea africana, Combretum psidioides and Ochna pulchra two graph segments were used; the lower range of mass was described by a power curve while the upper range by a second degree polynomial. The 2 functions intersected at 115,2 kg(dry) for Burkea africana (Fig. 5.12a), 9,4 kg for Combretum psidioides (Fig. 5.12c) and 1,8 kg for Ochna pulchra (Fig. 5.12d). Only the second degree polynomial was used for Terminalia sericea (Fig. 5.12b).

The circumference of each individual of the 4 species was measured at the above stated heights of 1 m or 20 cm in an area of 6 000 m² (2 strips of 300 x 10 m). Each diameter value was substituted in the appropriate regression equations to give the dry biomass of each individual which was then used to give the biomass of the species per hectare.

By weighing a few individuals of mean postulated mass of the rarer tree species, and using density of individuals of these species, a rough estimate was made of their biomass.

Dry mass of trees was determined by sampling stems and branches including leaves of several individuals of each species and sealing the samples very well in plastic bags. The samples were dried later for conversion to dry mass. The mass of the wet samples was found to decrease to differing dry mass; the average dry mass as a percentage of the wet mass was 55% for Burkea africana, 74% for Terminalia sericea, 67% for Combretum psidioides and 54% for Ochna pulchra, 66% for Combretum collinum, 57% for Securidaca longependunculata, 60% for Lonchocarpus nelsii, 52% for Ozoroa paniculosa, 62% for Dombeya rotundifolia and 66% for Combretum apiculatum. These percentages were determined by drying the wet samples at 85^oC. It took about 5 to 6 days to dry a half kilogram (on a dry mass basis) tree trunk.

In the estimates of tree biomass per unit area, no correction for wet leaf mass was made.

A rough estimate of the total biomass of tree leaves was made by estimating the leaf mass of each of the 3 dominant tree species. This estimate would be only a slight

underestimate of the total biomass of tree leaves. A few individuals of mean height and mean stem diameter and with a average degree of insect grazing damage were selected and each analysed for leaf mass by counting and mass determination (dry).

5.2.2.2 Results

The total biomass of the tree layer was estimated at 22 290 kg/ha (without the 8 kg/ha of individuals of tree species found in the herbaceous layer). This is approximately two-thirds of the biomass found by Ovington et al. (1963) for the Michigan savanna vegetation. The total biomass of the plant aerial system was about 23 203 kg/ha or 23,20 metric tons/ha (Table 4.1). It is thus much lower than the biomass of most woodland ecosystems (Rodin and Bazilevich, 1965). The total biomass was made up of 3,93% herbaceous layer and 96,07% tree layer.

Burkea africana had an estimated biomass of 11 801 kg/ha or 52,9% of the tree layer biomass (Table 4.1). Terminalia sericea had a biomass of about 6 153 kg/ha and Combretum psidioides 3 405 kg/ha. These 3 species alone made up about 95,8% of the tree layer biomass or 92,0% of the entire community. Ochna pulchra had an estimated biomass of about 226 kg/ha, Combretum collinum 195 kg/ha and Securidaca longepedunculata 160 kg/ha. The biomass of the other rarer tree species was estimated at 350 kg/ha.

The individuals of each of 4 tree species in mass classes, have a higher frequency in the lowest mass class and progressively lower frequencies in higher mass classes (Fig. 5.13). The distribution is discontinuous in the higher mass classes, especially in Ochna pulchra where there are 2 distinct sets of individuals.

Burkea africana had more than half (54,4%) of its individuals weighing less than 50 kg, Terminalia sericea more than half(57,3%) weighing less than 40 kg, Ochna pulchra more than half(53,8%) of its "tree" individuals weighing less than 1 kg and Combretum psidioides more than half (52,3%) weighing less than 10 kg (Fig. 5.13).

Rounding the total estimate off to the nearest 100 kg/ha, an estimate of 1 000 kg/ha

was obtained for the leaves of the 3 dominant deciduous tree species. The mass of tree leaves was thus roughly of the same order as the average biomass of the herbaceous layer. Since loss of material of the herbaceous layer amounted to about 400 kg/ha after the maximum biomass was recorded (Section 5.1.3.1), the litter added each year from trees to the soil surface would appear to be more than twice that from the herbaceous layer. It should also be remembered that the herbaceous layer does not lose mass by break-away or litter alone, but also by translocation of material to roots. However, Bray and Gorham are quoted (Hopkins, 1966) as stating that for most tree species, the dry mass of a leaf just before abscission was very close to a mean value of 81% of the normal dry mass.

Ovington (1962) has mentioned the importance which insect damage can have on the biomass of tree leaves. In the study area, the total biomass of leaves produced in some tree species may be increased as a result of insect damage, for example in some Burkea africana where eating of the flush of leaves by the caterpillar Crina forda was followed by a second flush of leaves.

5.2.3 Energy

To be able to relate biomass more directly to the function of the ecosystem and more particularly to energy flow through the system, initial determinations of the energy values (heats of combustion) of the leaves of the 12 more important herbaceous layer species and of the leaves of the 6 more important tree species (Table 4.1), were made for various times of the year. Two Gallenkamp adiabatic bomb calorimeters were used following the procedure set out in the maker's manual. Due to lack of time, only sufficient determinations were made for obtaining reliable overall values.

The average energy value of the herbaceous species was in the order of 17 600 J/g, whereas the tree leaves were in the order of 20 550 J/g that is, energy values were about 17% greater for tree leaves and although all values were uncorrected for ash, determination of ash in the more important species (Appendix 3) indicate the percentage of ash content in tree leaves is only in the order of 2% less than that of the herbaceous material. There appeared to be no marked variation in energy value through the year in either the herbaceous species or tree species. The average values correspond

to those of, for example, Golley (1961), Kucera, Dahlman and Koelling (1967) and Hughes (1971). The latter, for example, found calorific values in an English deciduous woodland of 17 397 to 18 899 J/g for the ground layer vegetation and 19 380 to 23 577 J/g for canopy leaves.

5.3 Chemical analysis of plant material

Chemical determinations were carried out by the Institute of Soils and Irrigation (Pretoria) on plant material of the more important herbaceous layer and tree species of the study area (Appendix 3). Phosphorus and calcium were the main determinations. Other additional determinations relating to immediate agricultural utilization (protein, fibre, fat and ash) are mentioned in Section 8. Material from most months of the year was analysed in the most important herbaceous species (Brachiaria nigropedata, Digitaria polevansii and Andropogon gayanus) while in the more important tree and shrub species and other important herbaceous species (Burkea africana, Terminalia sericea, Combretum psidioides, Ochna pulchra, Combretum collinum, Grewia avellana, Andropogon schirensis and Aristida stipitata) attention was given to analysis of material from January to March and June to August. In addition, some other species material was also analysed for isolated parts of the year (Cenchrus ciliaris, Commelina africana, Triraphis schinzii, Rhynchelytrum species, Eragrostis pallens and Securidaca longepedunculata). Main types of material analysed were new vegetative material from October to March and total vegetative material from April to August. The value for September 1970 is that of total vegetative material. Some samples were taken for analysis of previous seasons material (before April) and of generative material at various times of the year.

Phosphorus and calcium content were determined in ashed samples. The calcium content was determined by precipitation using the ammonium oxalate and phosphorus permanganate method and the phosphorus content was determined using the ammonium molybdate and ammonium vanadate method. The other determinations made were those of: protein content, which was determined by the Kjeldahl method; fibre content, which was determined using the sodium hydroxide and sulphuric acid method; fat content was determined by the standard Soxhlet petroleum ether extraction method; and ash content which was determined by ashing at 450°C.

Results

(1) Phosphorus

There was a general trend for the new material to contain, in October or November,

the highest concentration of phosphorus; this was followed by a steady decrease as the season progressed for example in Brachiaria nigropedata (Fig. 5.14a). This general decline in phosphorus over the growth season is commonly reported (for example Boyd, 1970). The average phosphorus content in January, February and March was, in the species sampled, higher than the average content for the winter period (June, July and August). For the first mentioned period, the average phosphorus content of the 5 most important grass species (Digitaria polevansii, Brachiaria nigropedata, Andropogon gayanus, Andropogon schirensis and Aristida stipitata) was 0,076%, with species averages ranging from 0,053 to 0,091%, while for the winter period the average was 0,024% ranging from 0,023 to 0,025%. The common shrub species, Grewia avellana, had an average phosphorus content of 0,108% for January to March and 0,051% for June to August. The average phosphorus content of leaves of the 5 most important tree species (Burkea africana, Terminalia sericea, Combretum psidioides, Ochna pulchra and Combretum collinum) was 0,102% (with species averages ranging from 0,091 to 0,112%) for January to March, and was 0,060% (ranging from 0,045 to 0,080%) for June to August. The phosphorus content of leaves of the woody species was thus higher than that of the vegetative material of the grass species. This also applied to other grass and woody species that were analysed, namely, Cenchrus ciliaris and Securidaca longepedunculata.

The phosphorus content of previous season's dead material (sorted until March) was lower than that of corresponding new material. The phosphorus content of previous season's material of Digitaria polevansii was about two-thirds of that of the new material in February, and the phosphorus content of previous season's material of Andropogon schirensis was about one-third that of the new material in January. The phosphorus content of generative material appeared very variable. In some cases, it was less than the content of the new vegetative material, that is, about 30% less for Digitaria polevansii and about 5% less for Andropogon gayanus in March. In the same month, however, the phosphorus content of generative material was more than twice that of the new vegetative material in Triraphis schinzii and Eragrostis pallens. The phosphorus content of generative and vegetative materials appeared to be equal during the winter months, that is, in June for Rhynchelytrum species, and in August for Aristida stipitata.

(2) Calcium

In the most species analysed, there was a general trend for calcium content to

increase as the season progressed, but this pattern was irregular. In most of the more important grass species, the calcium content was distinctly lower for the new material of October to December, than for the rest of the year (see for example Brachiaria nigropedata Fig. 5.14b). The average calcium content for the 5 most important grass species during January to March was 2,8% (with species averages ranging from 1,40 to 3,55%), while for June to August it was 2,94% (ranging from 0,80 to 4,21%). The leaves of the 5 most important tree species had an average calcium content of 7,78% (with species averages ranging from 3,46 to 11,50%) for January to March and 9,92% (ranging from 3,80 to 14,00%) for June to August. The ranges show the variability of content within each group. Aristida stipitata had the lowest calcium content of the 5 grass species and Burkea africana the lowest content of the 5 tree species. Combretum collinum had the highest content in the latter group. The calcium content of leaves of the woody species analysed, appeared to be mostly greater than that of the herbaceous species. There were, however, a few clear exceptions to this, for example, in the herbaceous species, Commelina africana, the calcium content for January to March was 11,60%, while the woody species, Securidaca longepedunculata, had an average of only 2,52% for this period.

Using the August content of calcium in the abscising leaves of Burkea africana, Terminalia sericea and Combretum psidioides and the previously estimated 1 000 kg/ha of their leaves, the annual addition of calcium from trees to the litter layer was estimated to be in the order of 10 g/m^2 or 100 kg/ha. Using corresponding data for the herbaceous layer and other published figures, annual addition of calcium from the herbaceous layer and from rainfall was probably much less than a quarter of this value (Carlisle, Brown and White, 1966; Likens et al., 1967).

Combretum collinum, with the highest leaf calcium content, has been shown to be significantly associated with mounds, which have more soil calcium than the flats, especially at lower depths where Combretum collinum roots are also found. That Combretum collinum may be an essential part of the calcium cycle of the mounds, might partly account for the development of the mounds and for maintenance of their specifically associated species, since a rapid cycle of calcium, for example, raises the pH of the soil and maintains it at a relatively high level.

Fig. 5.1 (on following page) The portable rack used for suspending labeled bags for sorting of species during harvesting.

Fig. 5.2 (on following page) The field drying oven on the site that was used for sorting the clipped vegetation near the study area.



Fig. 5.2



Fig. 5.1

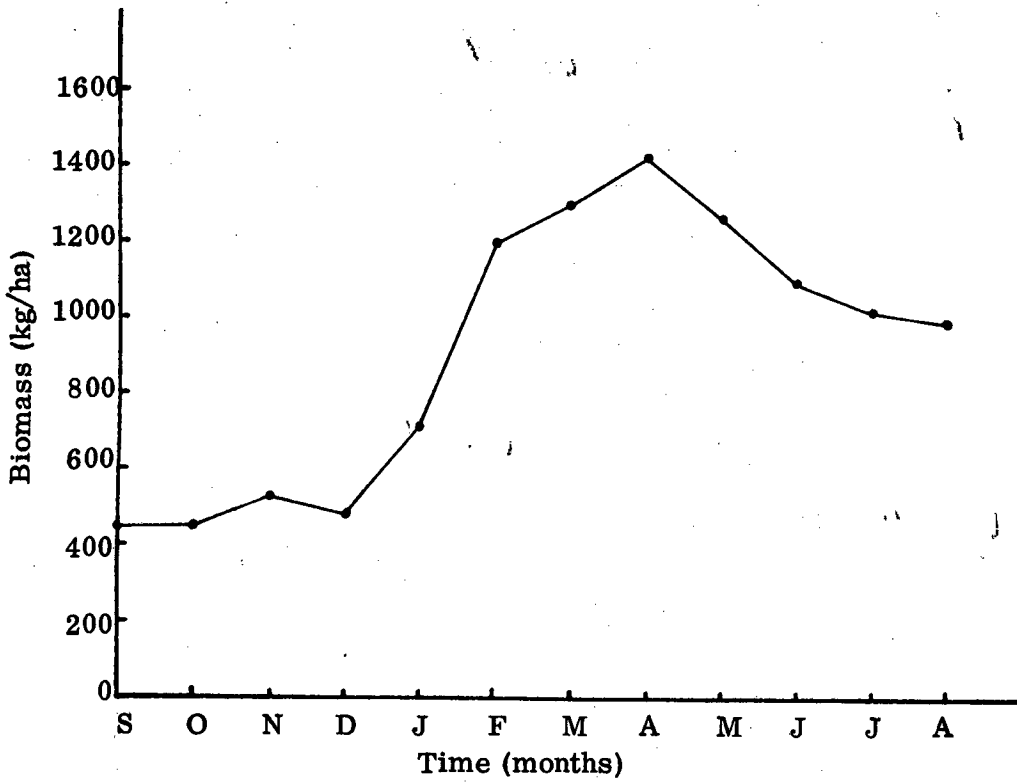
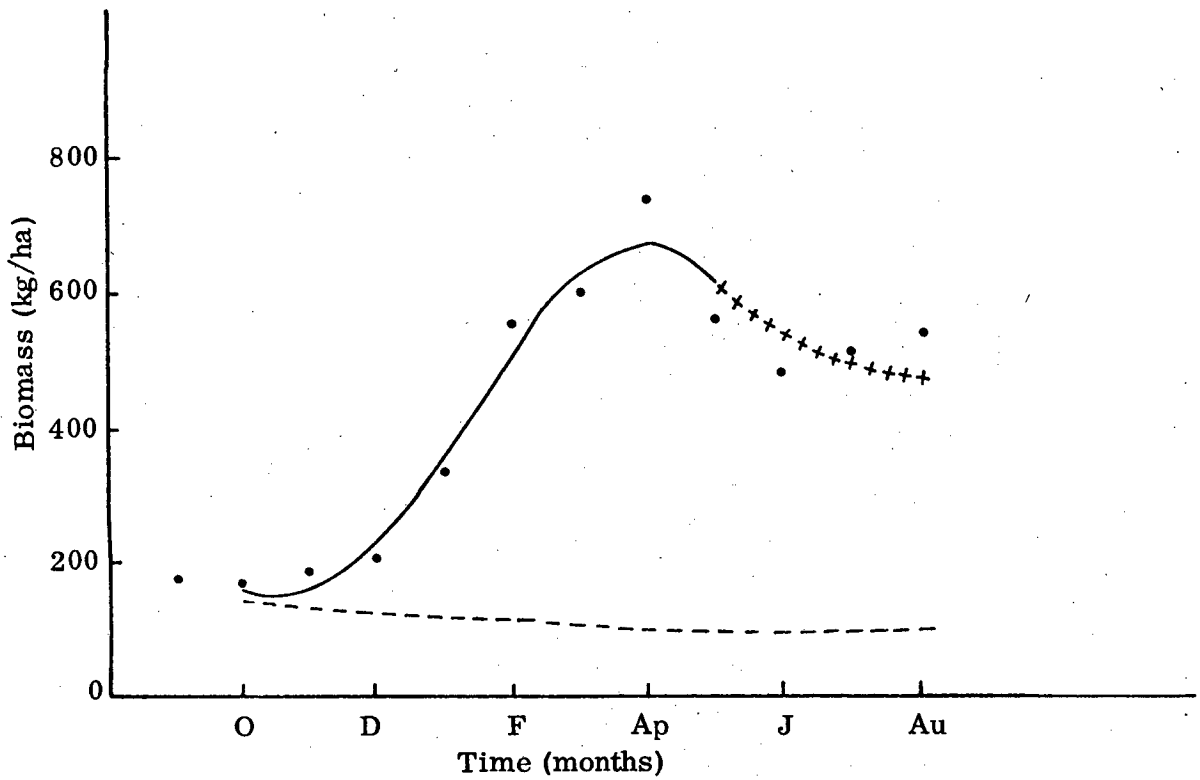


Fig. 5.3 Relationship between biomass and time for the herbaceous layer vegetation



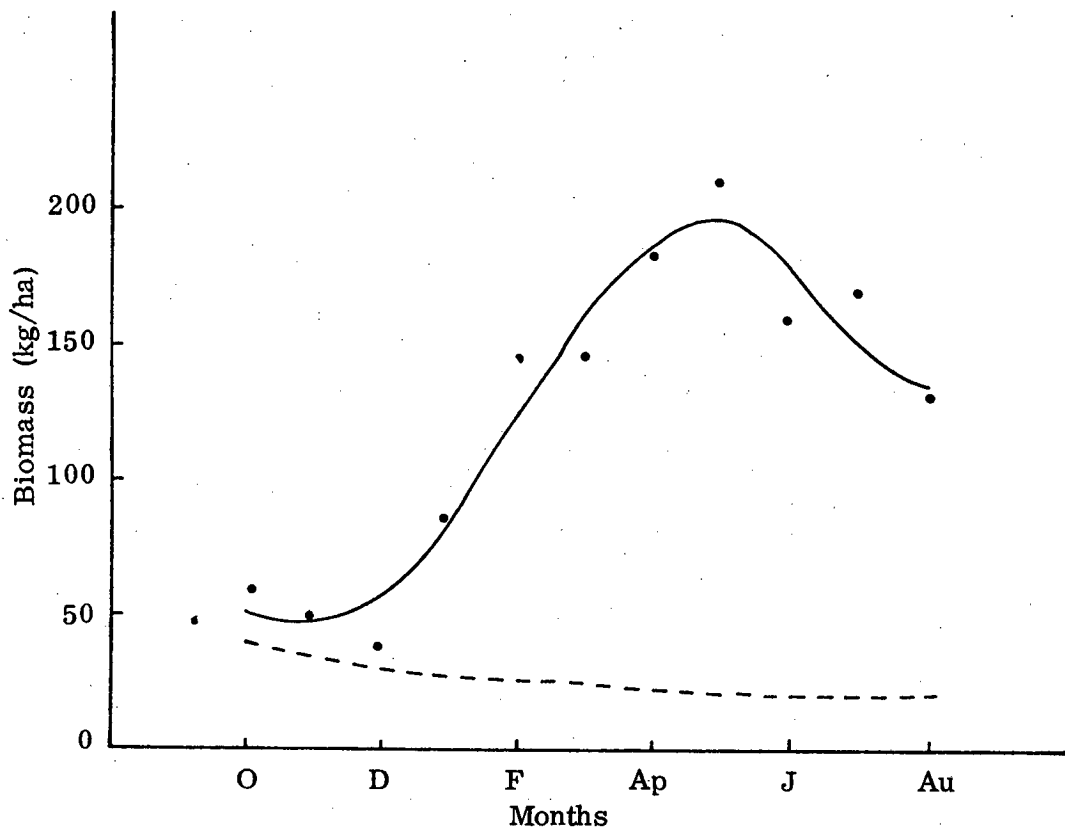
— Total biomass:

$$W = (1514,69536 + 1093,79042 t - 1111,68025 t^2 + 360,05839 t^3 - 40,09372 t^4 + 1,44812 t^5) 10^{-1}$$

--- Previous season's material: $W = (1792,33573 t^{-0,23327}) 10^{-1}$

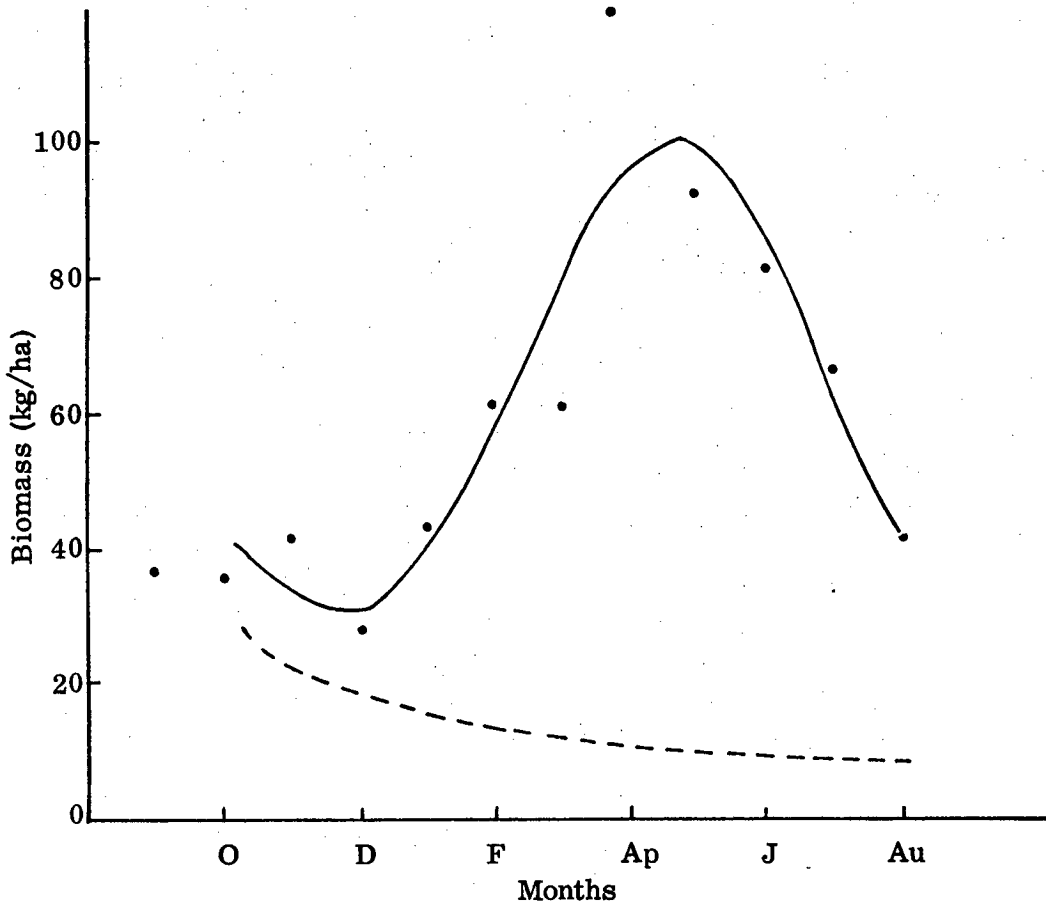
+ Total biomass - free drawn

Fig. 5.4a Digitaria polevansii: Relation of total biomass and previous season's material with time



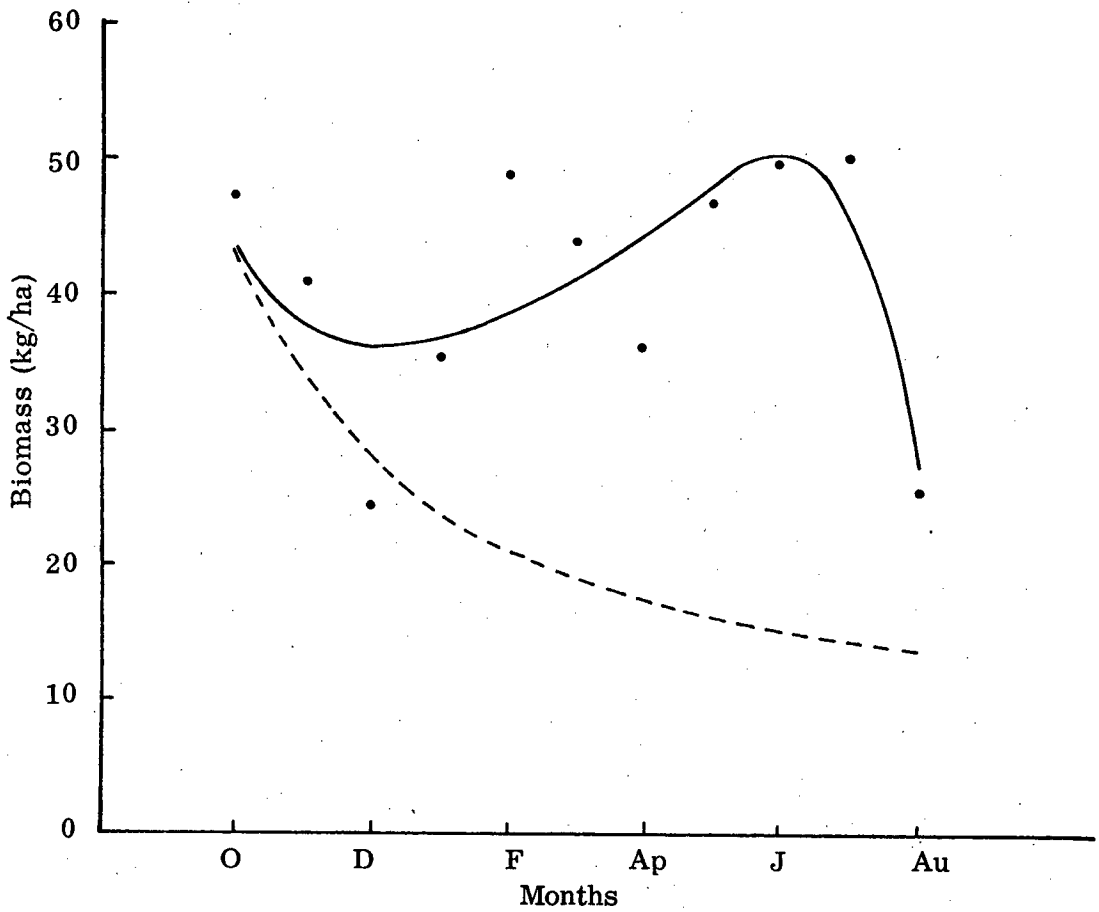
— Total biomass:
 $W = (74,68565 + 813,86042 t - 486,93657 t^2 + 116,86969 t^3 - 10,91269 t^4 + 0,34558 t^5) 10^{-1}$
 --- Previous season's material: $W = (528,30819 t^{-0,38236}) 10^{-1}$

Fig. 5.4b Brachiara nigropedata: Relation of total biomass and previous season's material with time



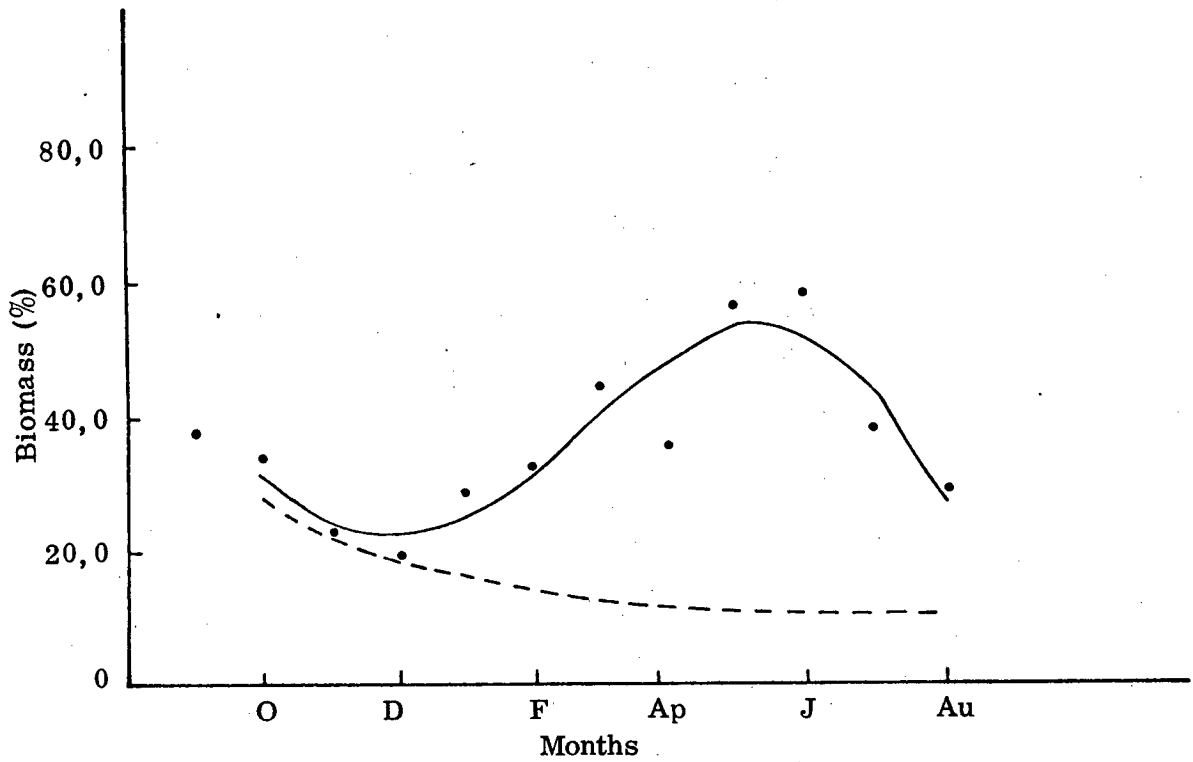
— Total biomass: $W = (-187,17872 + 917,44928 t - 477,87812 t^2 + 100,86061 t^3 - 8,78020 t^4 + 0,26609 t^5) 10^{-1}$
 --- Previous season's material: $W = (504,5829 t^{-0,70298}) 10^{-1}$

Fig. 5.4c Andropogon gayanus: Relation of total biomass and previous season's material with time



— Total biomass:
 $W = (1035,36263 - 582,92048 t + 196,46108 t^2 - 32,52222 t^3 + 2,67276 t^4 - 0,08552 t^5) 10^{-1}$
 --- Previous season's material: $W = (672,81539 t^{-0,63929}) 10^{-1}$

Fig. 5.4d Andropogon schirensis: Relation of total biomass and previous season's material with time

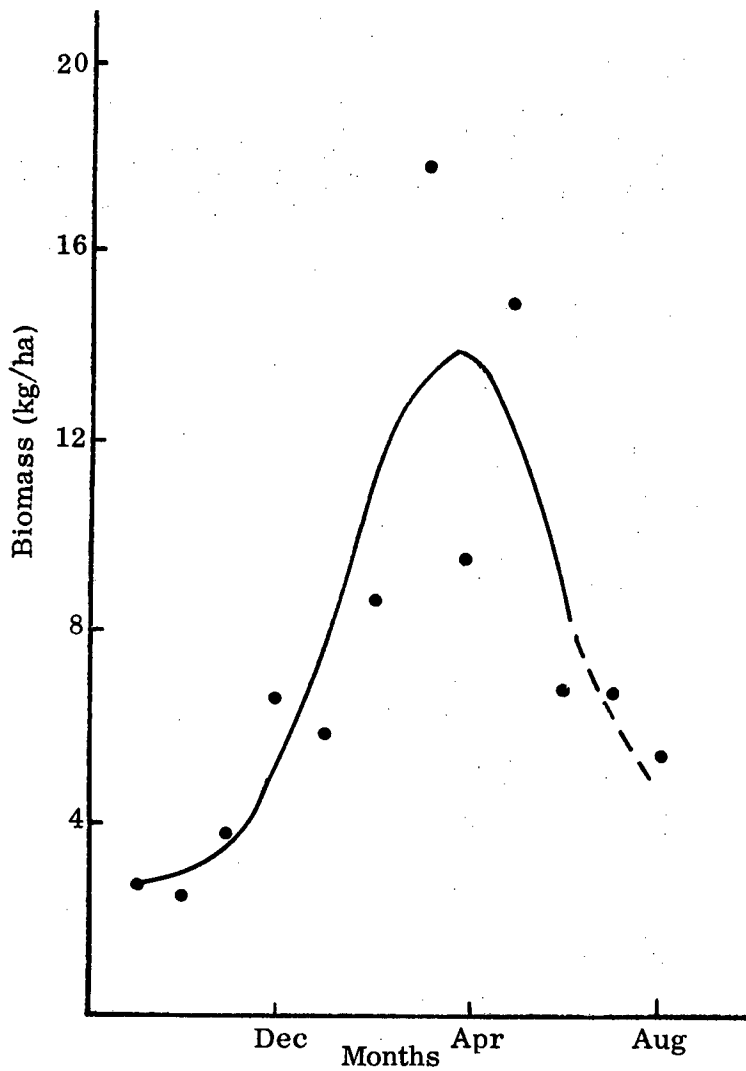


— Total biomass:

$$W = (399,9550 + 26,33587 t - 64,40754 t^2 + 16,87094 t^3 - 1,44704 t^4 + 0,03894 t^5) 10^{-1}$$

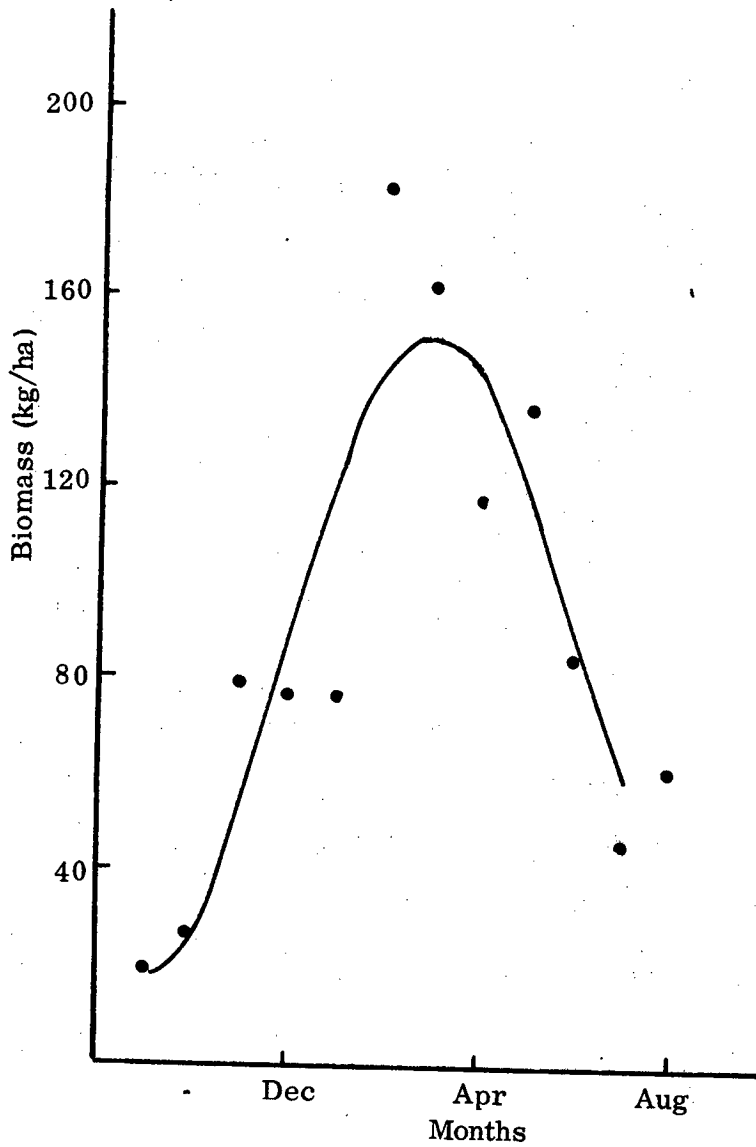
--- Previous season's material: $W = (409,2209 t^{-0,5709}) 10^{-1}$

Fig. 5.4e Aristida stipitata: Relation of total biomass and previous season's material with time



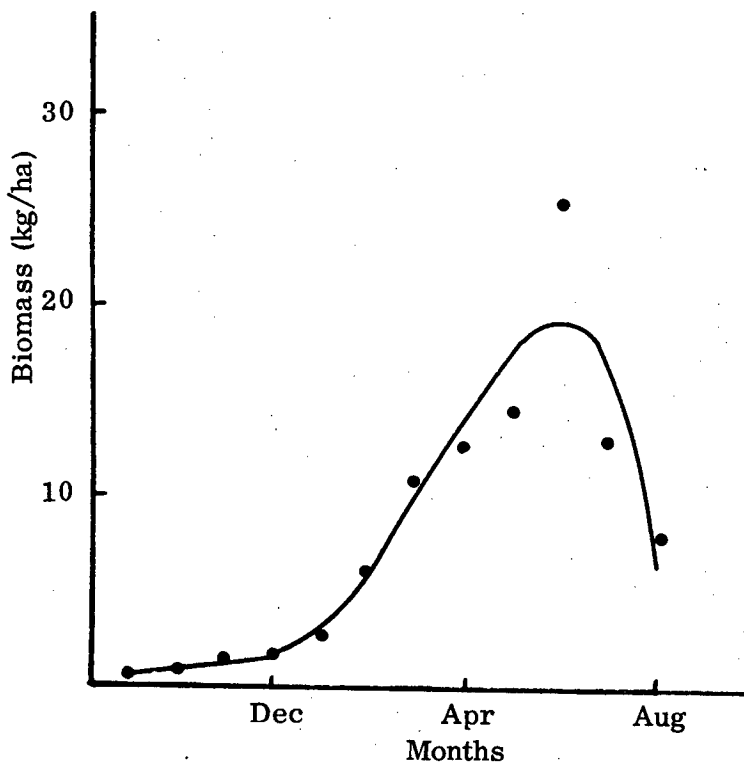
$$W = (-9,45419 + 64,35260 t - 38,67682 t^2 + 10,15209 t^3 - 1,04065 t^4 + 0,03577 t^5) 10^{-1}$$

Fig. 5.4f Cyperus margaritaceus: Relation between total biomass and time



$$W = (704,43429 - 764,43483 t + 350,93534 t^2 - 43,57656 t^3 + 1,62893 t^4) 10^{-1}$$

Fig. 5.4g Grewia avellana : Relation between total biomass and time



$$W = (-8,40910 + 17,79880 t - 7,09699 t^2 + 0,94444 t^3 + 0,05306 t^4 - 0,00741 t^5) 10^{-1}$$

Fig. 5.4h Tephrosia cephalantha: Relation between total biomass and time

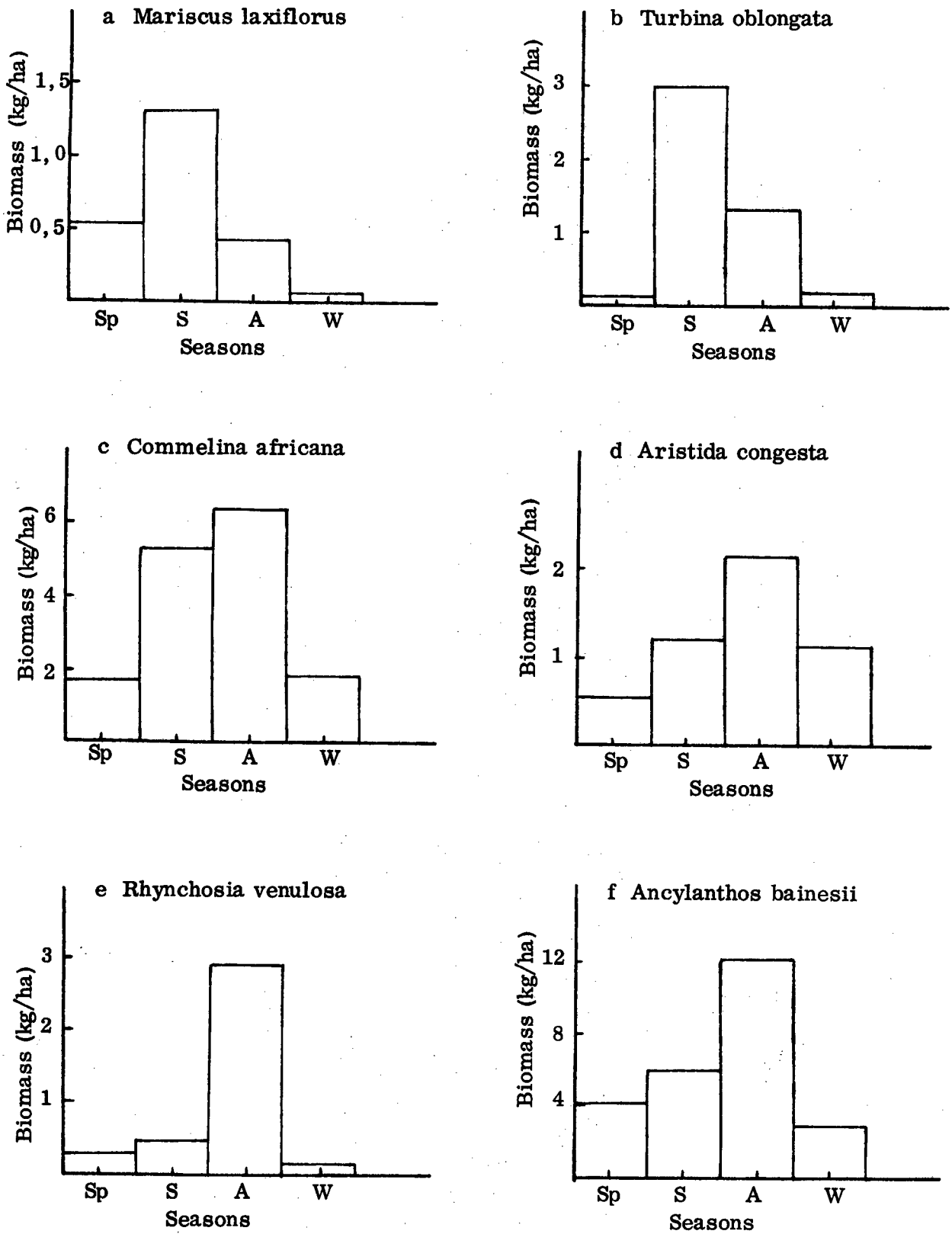
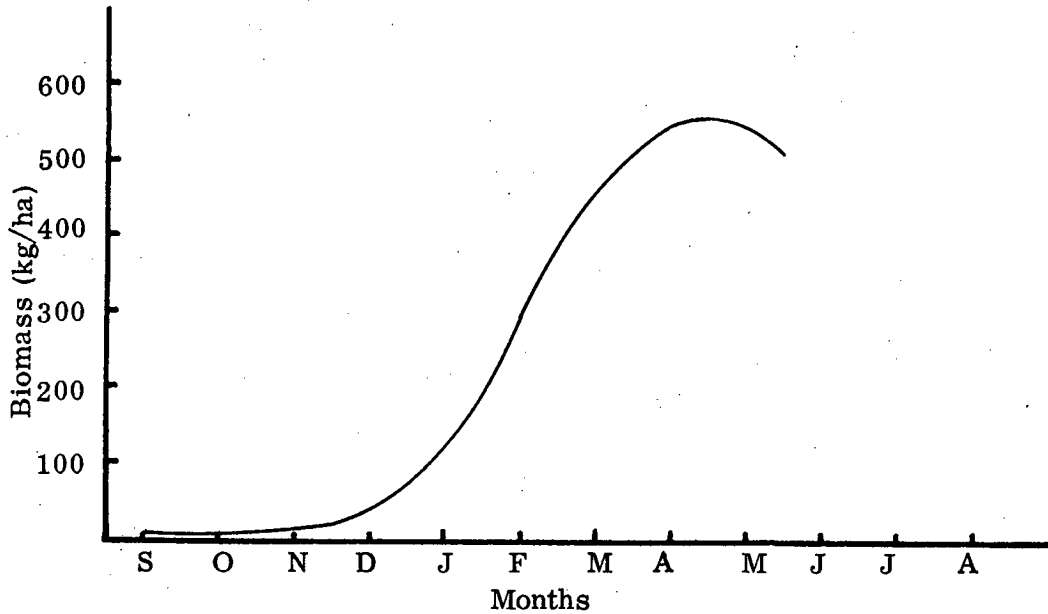


Fig. 5.5 Distribution of biomass in seasons

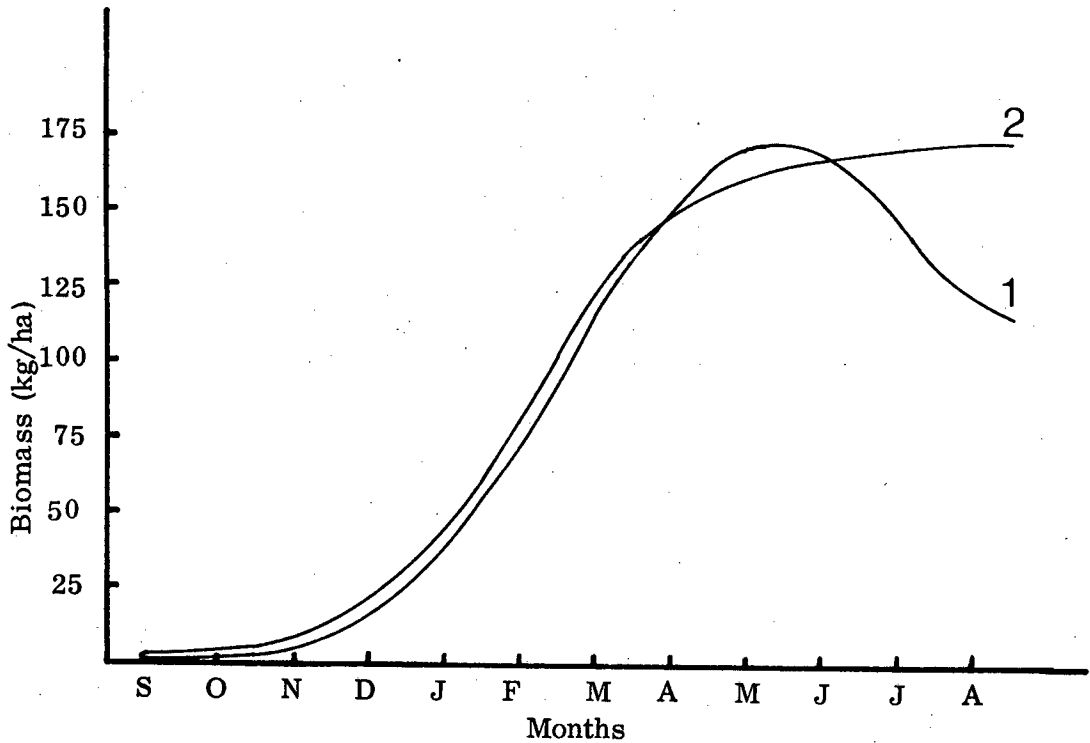


$$t = 1 \rightarrow 5,7 \quad W = (1,36726 t^{4,50815}) 10^{-1}$$

$$t = 5,7 \rightarrow 9 \quad W = (1514,69535 + 1093,79042 t - 1111,68024 t^2 + 360,05838 t^3 - 40,09372 t^4 + 1,44811 t^5 - 1792,33572 t^{-0,23326}) 10^{-1}$$

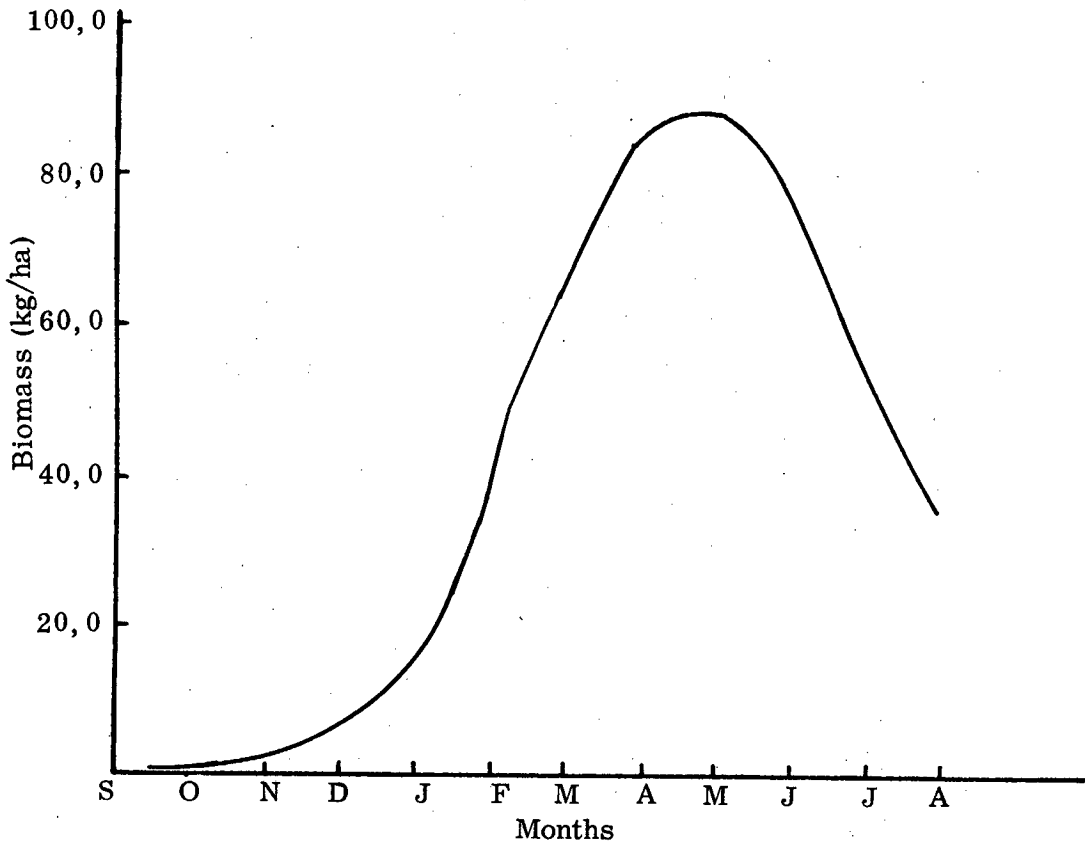
t = 9 → 12 W uncertain

Fig. 5.6a Digitaria pulevansii: Relation between biomass of new material and time



$$\begin{aligned}
 &1 \left\{ \begin{aligned} t = 1 \rightarrow 5 & W = (1,99882 t^{3,49164}) 10^{-1} \\ t = 5 \rightarrow 12 & W = (74,68564 + 813,86041 t - 486,93656 t^2 + 116,86969 t^3 - 10,91268 t^4 \\ & + 0,34557 t^5 - 528,30819 t^{-0,38235}) 10^{-1} \end{aligned} \right. \\
 &2 \left\{ t = 1 \rightarrow 12 \quad W = \left(\frac{1735}{1 + e^{-0,9612(t - 5,646)}} \right) 10^{-1} \right.
 \end{aligned}$$

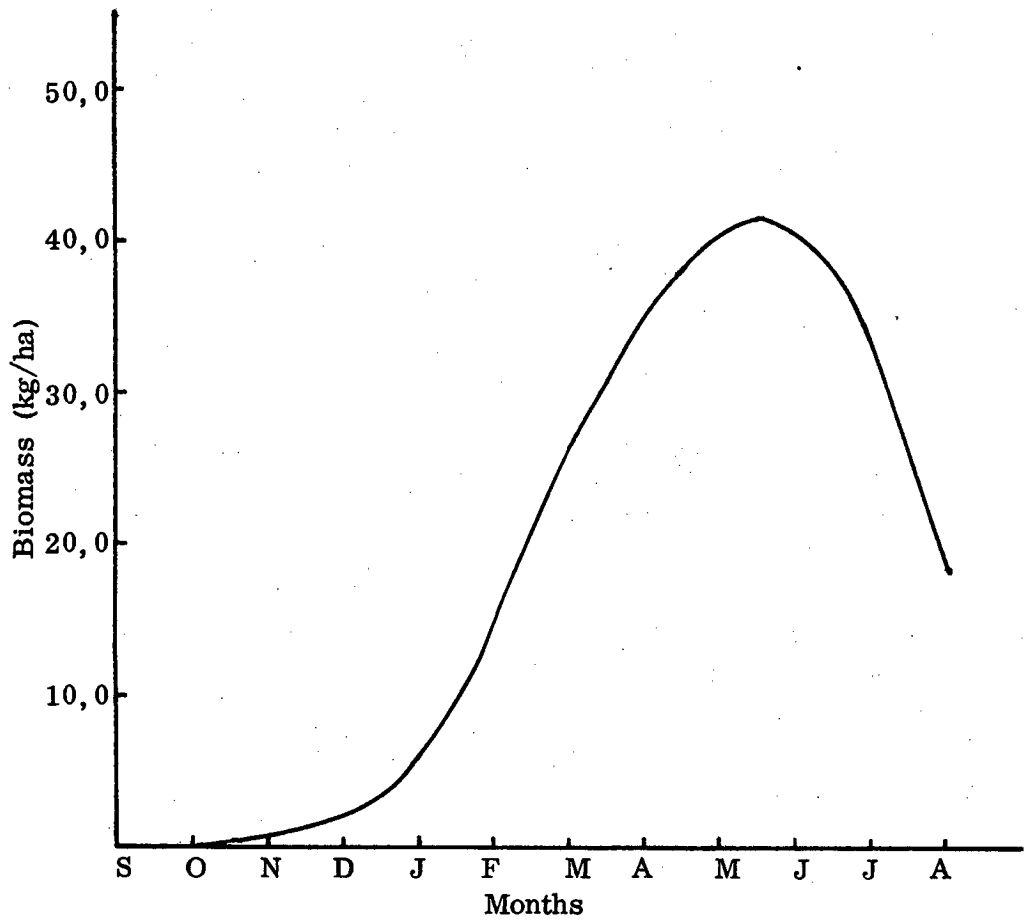
Fig. 5.6b Brachiaria nigropedata: Relation between biomass of new material and time



$$t = 1 \rightarrow 6,3 \quad W = (1,36416 e^{0,94324 t}) 10^{-1}$$

$$t = 6,3 \rightarrow 12,0 \quad W = (-187,17872 + 917,44927 t - 477,87811 t^2 + 100,86060 t^3 - 8,78019 t^4 + 0,26609 t^5 - 504,58295 t^{-0,70297}) 10^{-1}$$

Fig. 5.6c Andropogon gayanus : Relation between biomass of new material and time



$$t = 1 \rightarrow 6 \quad W = (0,26369 e^{1,08357 t}) 10^{-1}$$

$$t = 6 \rightarrow 12 \quad W = (399,955 + 26,33587 t - 64,40754 t^2 + 16,87094 t^3 - 1,44704 t^4 + 0,03894 t^5 - 409,2209 t^{-0,5709}) 10^{-1}$$

Fig. 5.6d Aristida stipitata: Relation between biomass of new material and time

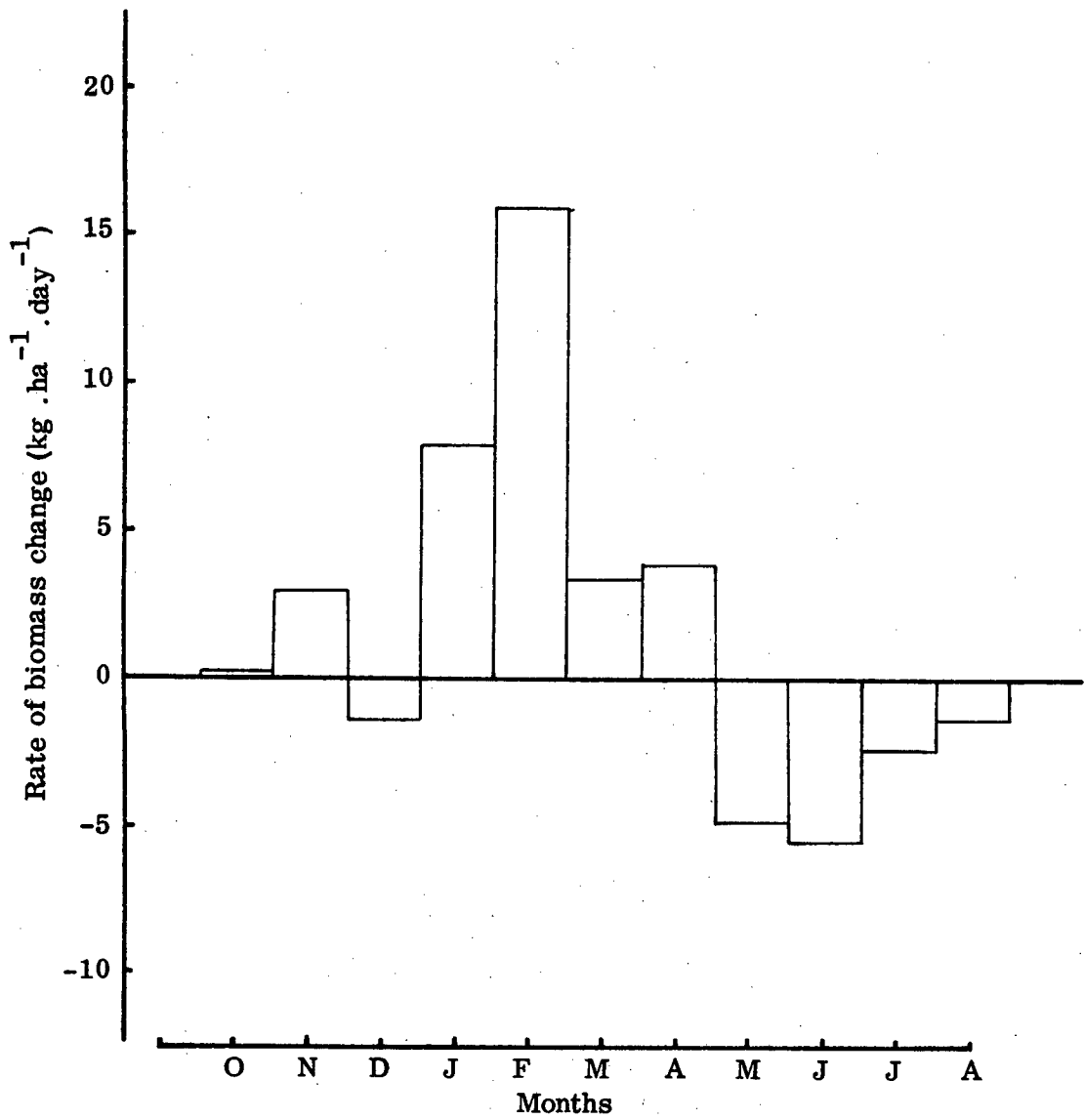


Fig. 5.7 Mean rates of biomass change in months for herbaceous layer vegetation

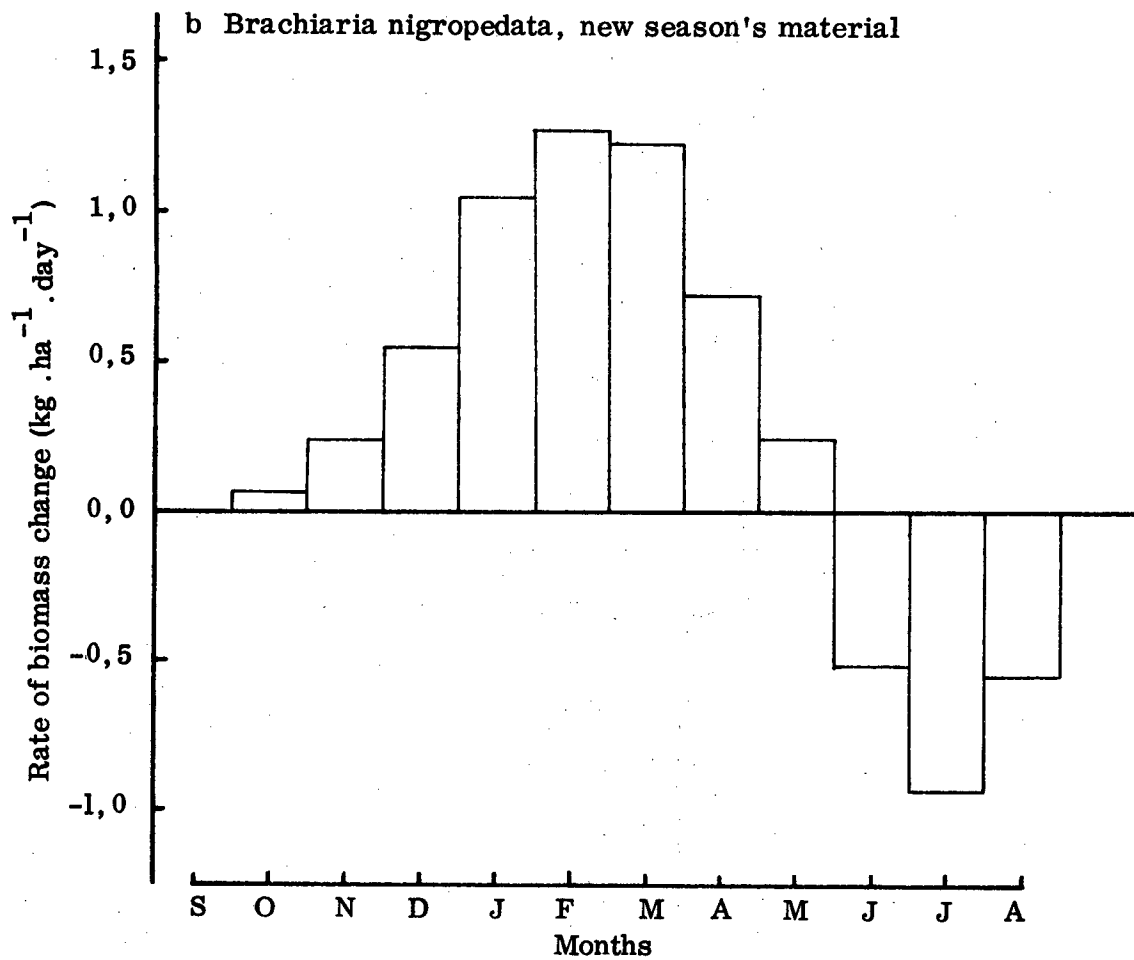
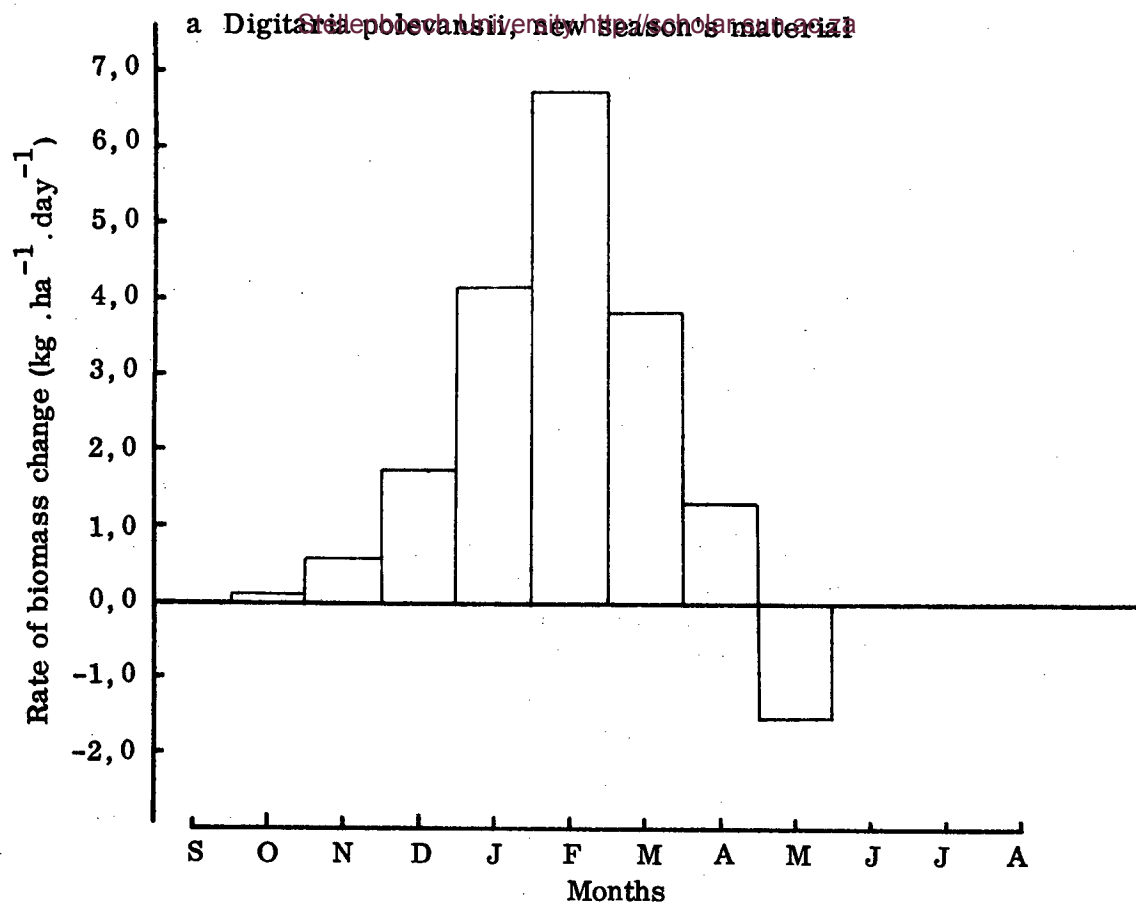


Fig. 5.8 Rate of biomass change at the midpoint of each month

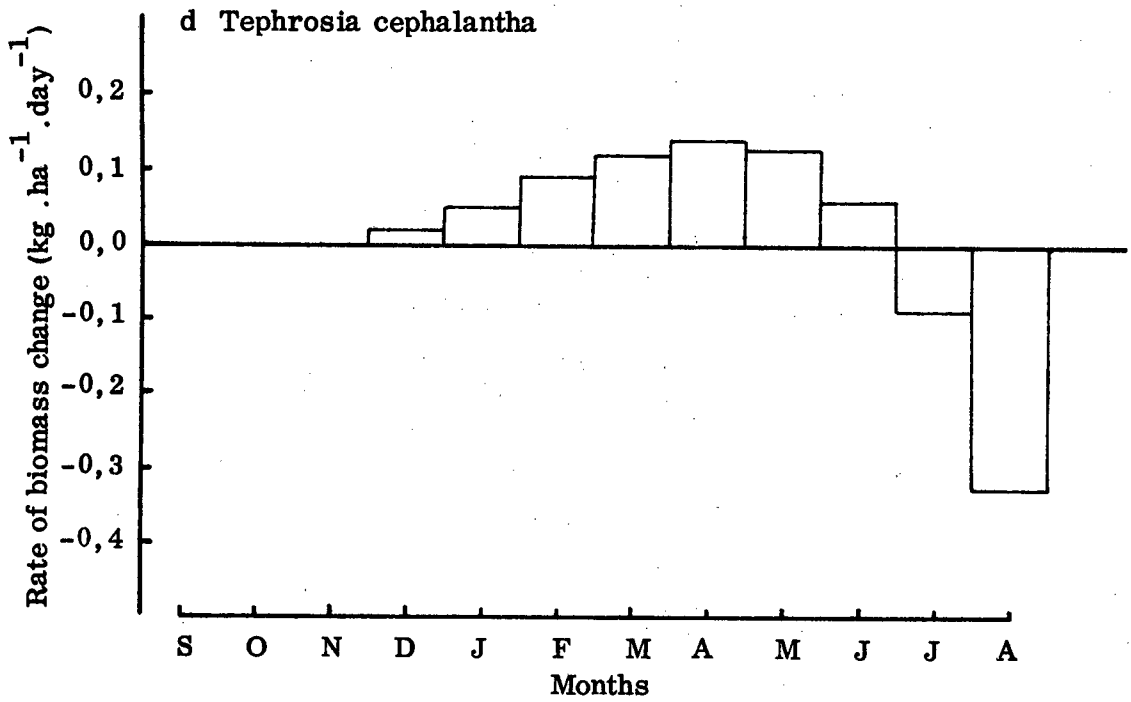
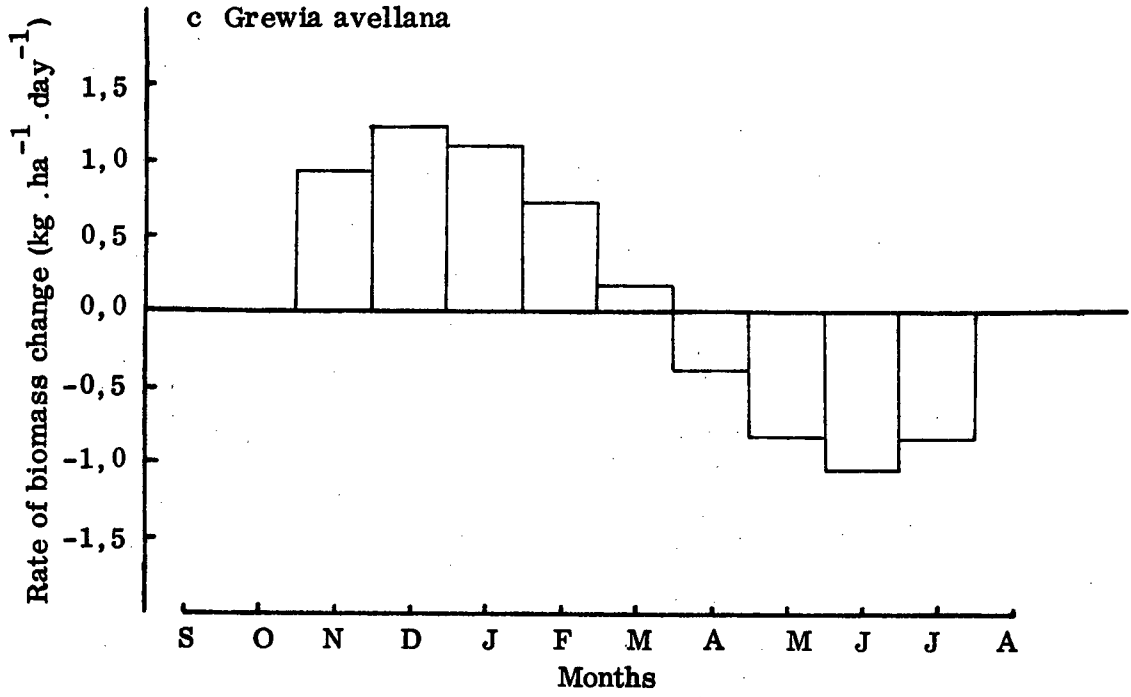


Fig. 5.8 (continued) Rate of biomass change at the midpoint of each month

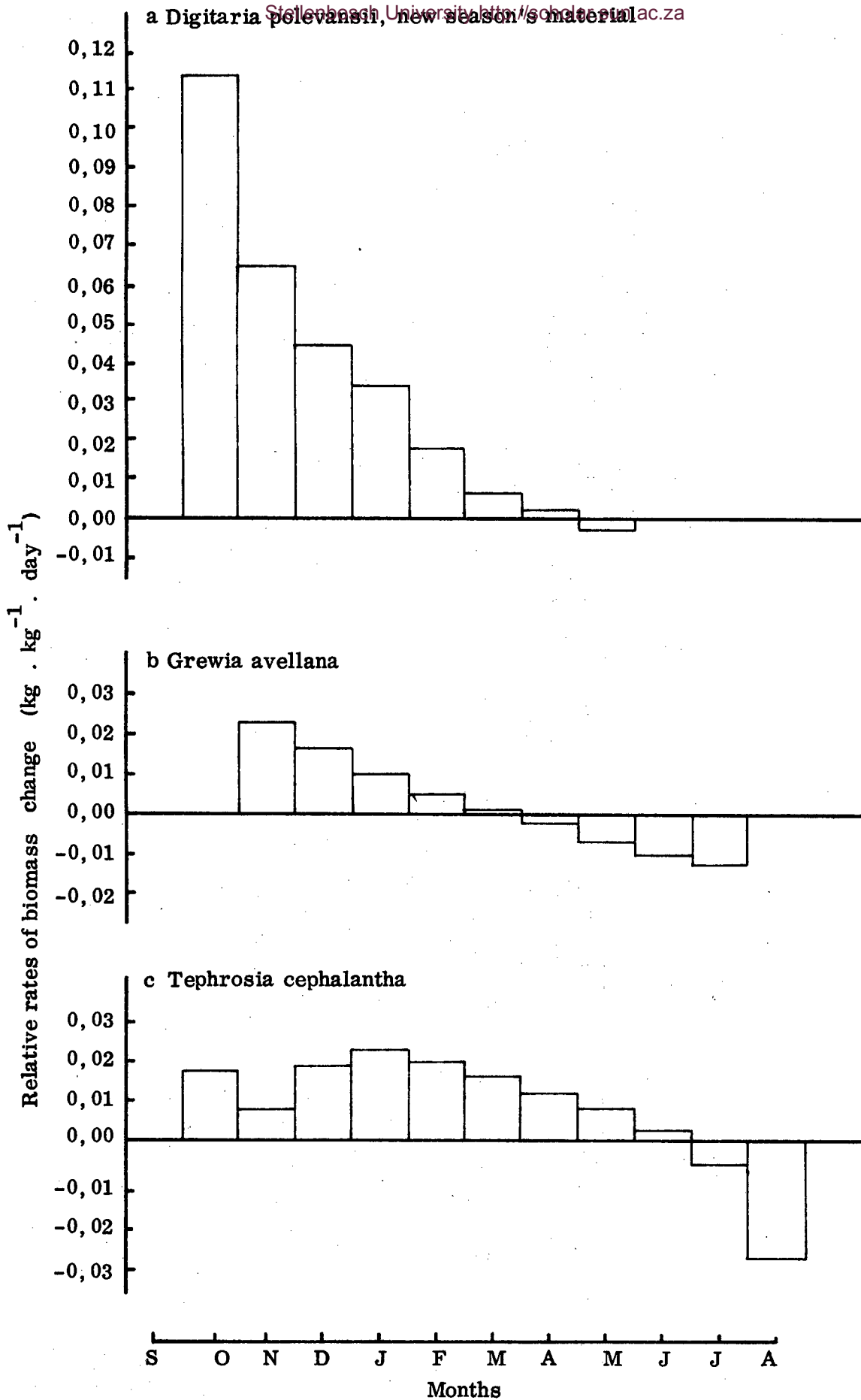


Fig. 5.9 Relative rate of biomass change at the midpoint of each month

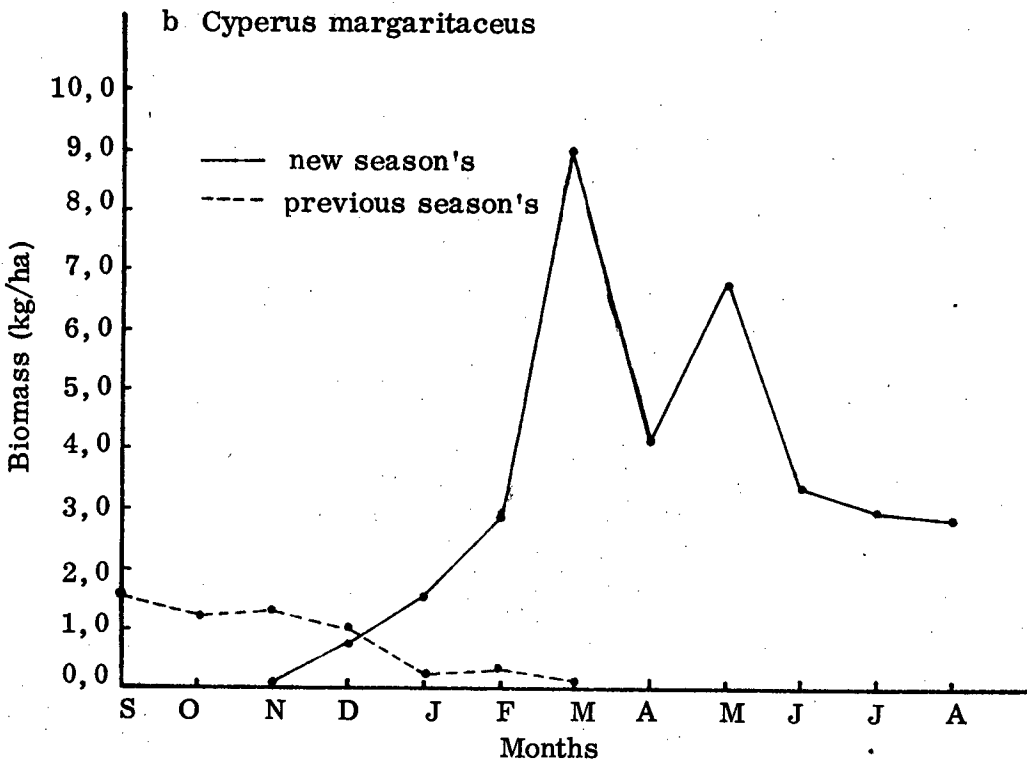
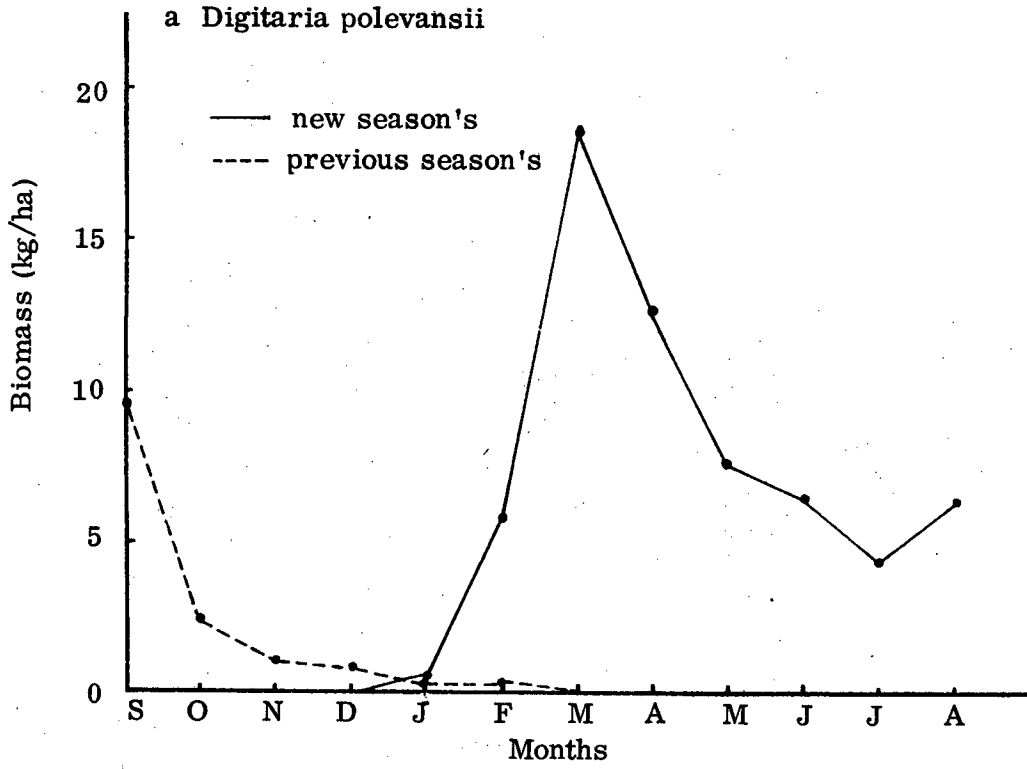


Fig. 5.10 Relationship between biomass of generative material and time (months)

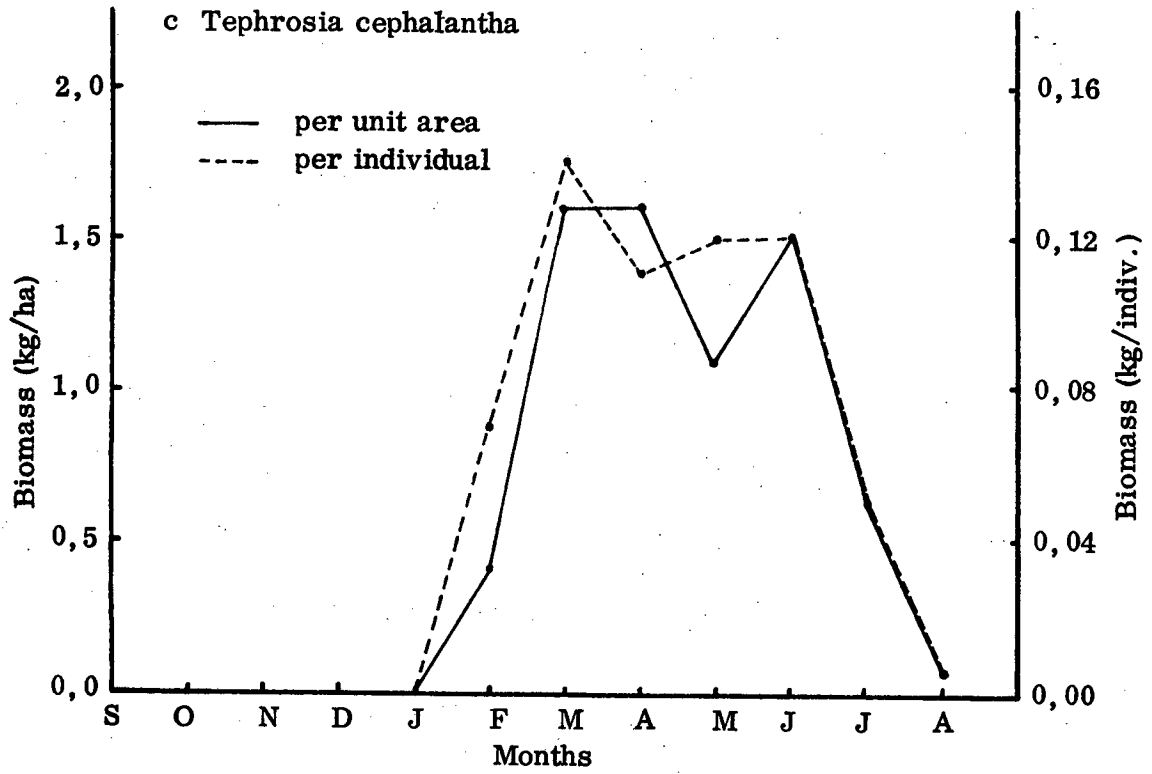


Fig. 5.10 (continued) Relationship between biomass of generative material and time (months)

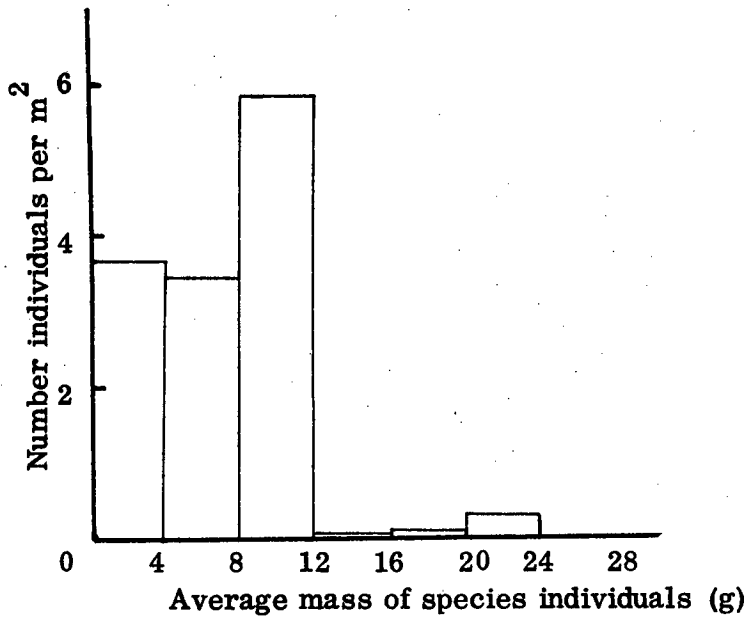
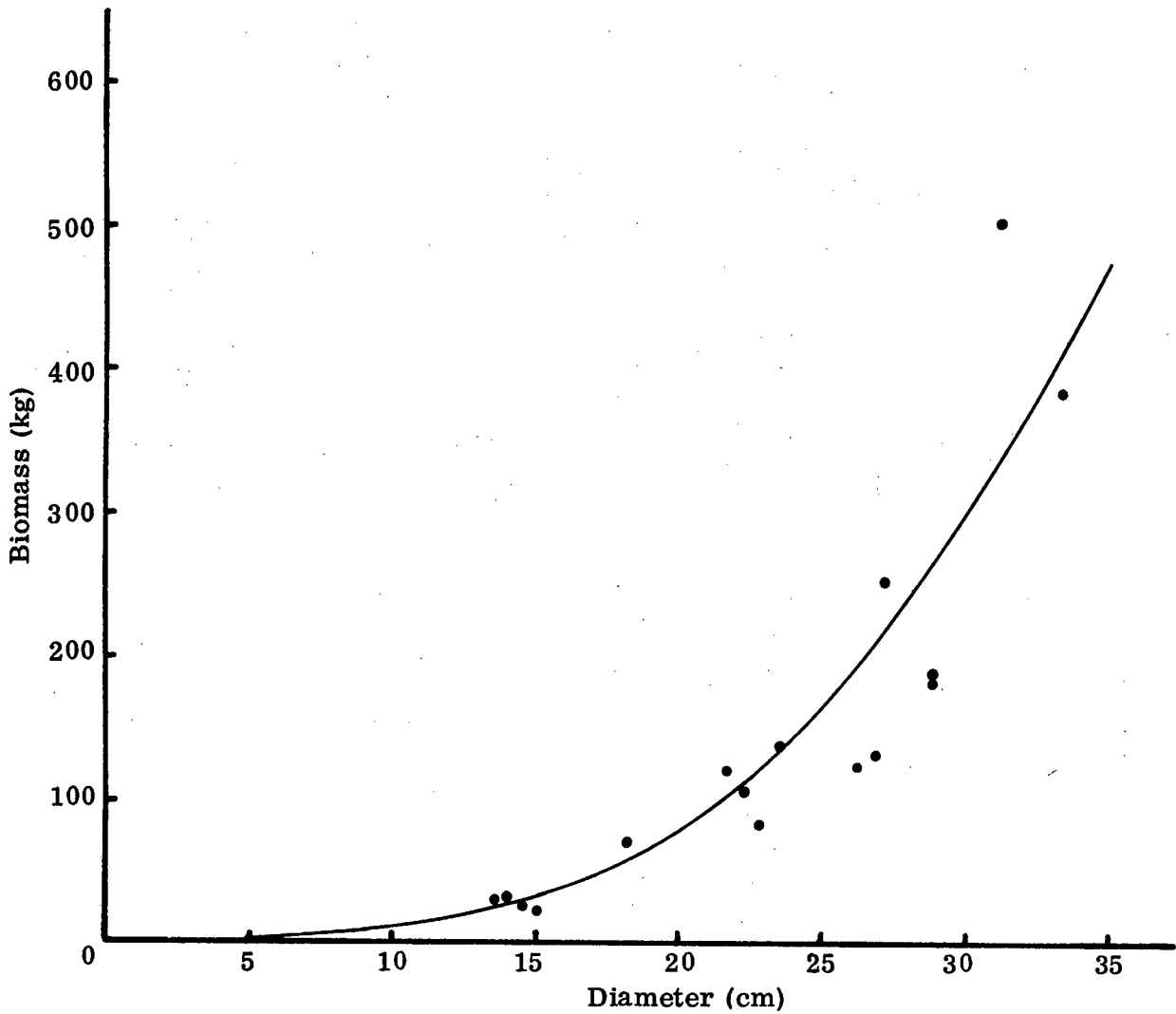


Fig. 5.11 Distribution of number of individuals in classes of species individual mass (herbaceous layer)



$$x = 5 \rightarrow 22,7 \quad W = 0,01146 x^{2,95614}$$

$$x = 22,7 \rightarrow 35 \quad W = 103,21737 - 17,78338 x + 0,81034 x^2$$

Fig. 5.12a Burkea africana: Relation between diameter and dry biomass

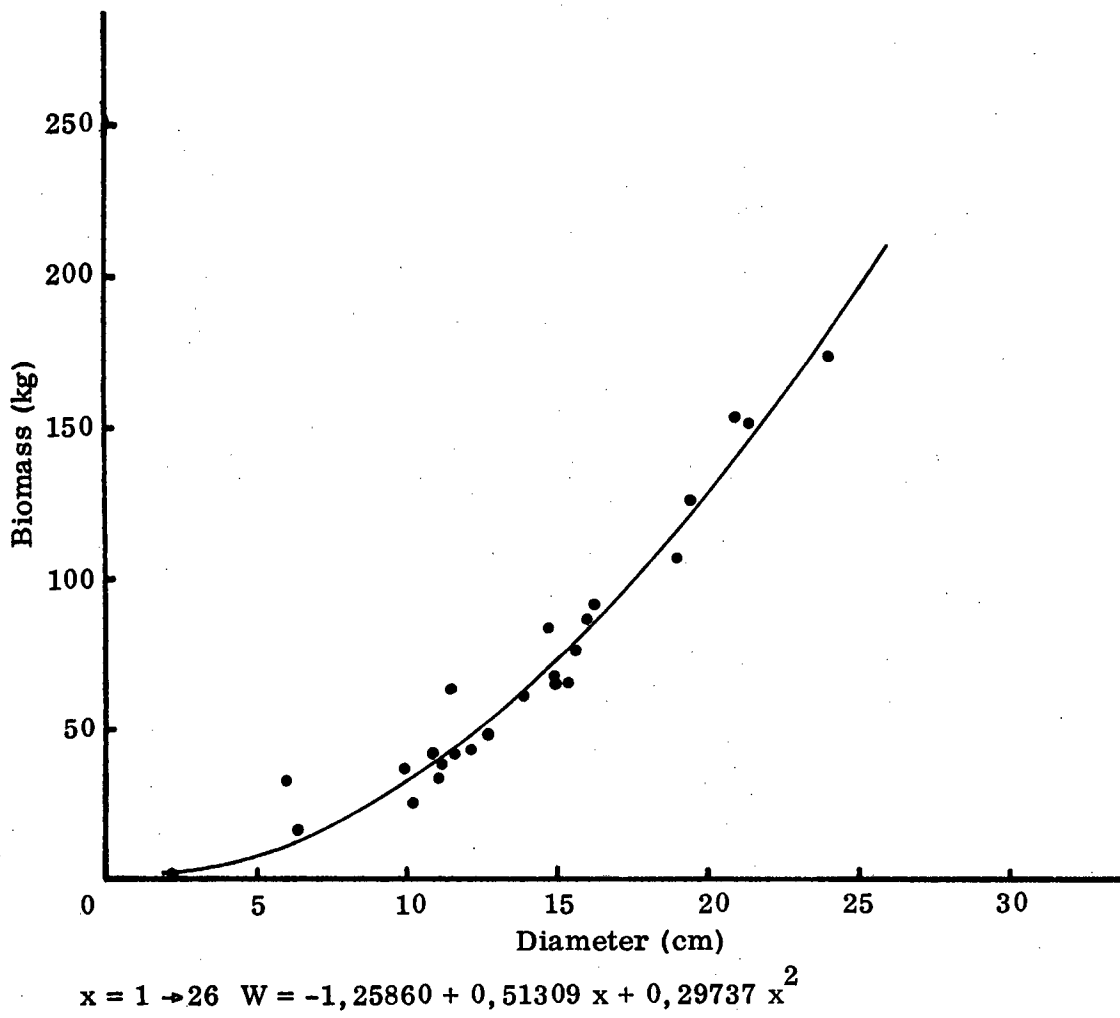
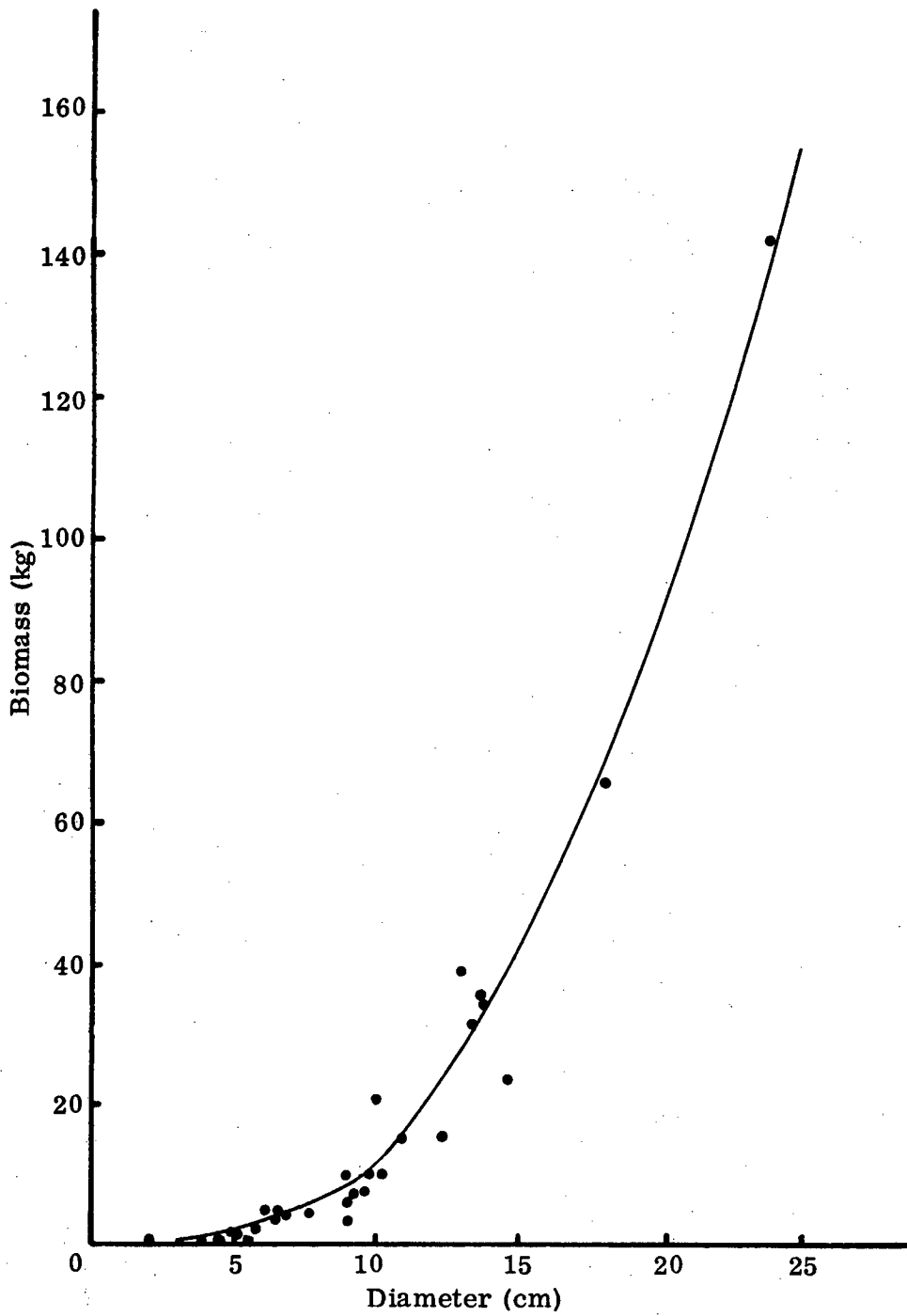


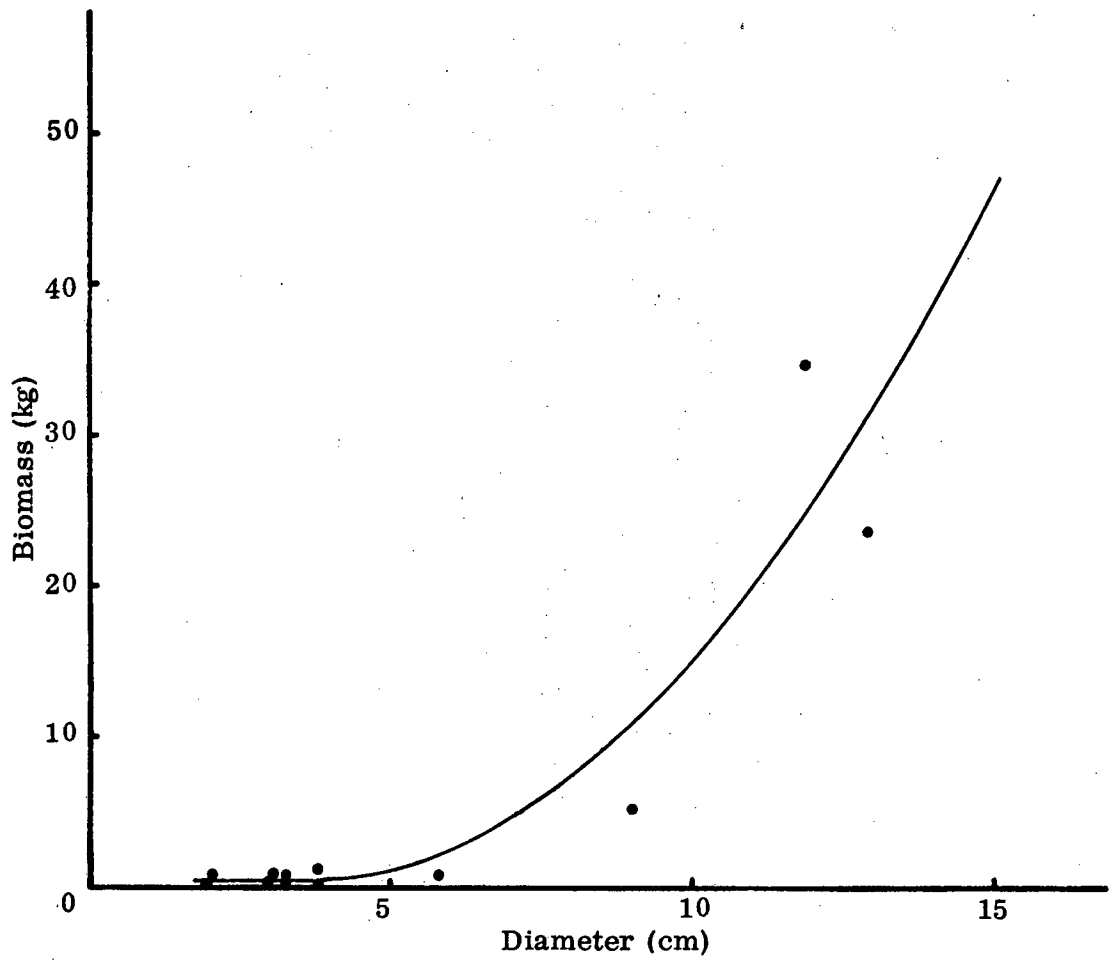
Fig. 5.12b Terminalia sericea: Relation between diameter and dry biomass



$$x = 1 \rightarrow 9,3 \quad W = 0,03701 \cdot x^{2,48634}$$

$$x = 9,3 \rightarrow 25 \quad W = 6,93043 - 3,07345 x + 0,35995 x^2$$

Fig. 5.12c Combretum psidioides: Relation between diameter and dry biomass



$$x = 1 \rightarrow 5,6 \quad W = 0,01250 x^{2,88710}$$

$$x = 5,6 \rightarrow 15 \quad W = 3,73180 - 2,23858 x + 0,33974 x^2$$

Fig. 5.12d Ochna pulchra: Relation between diameter and dry biomass

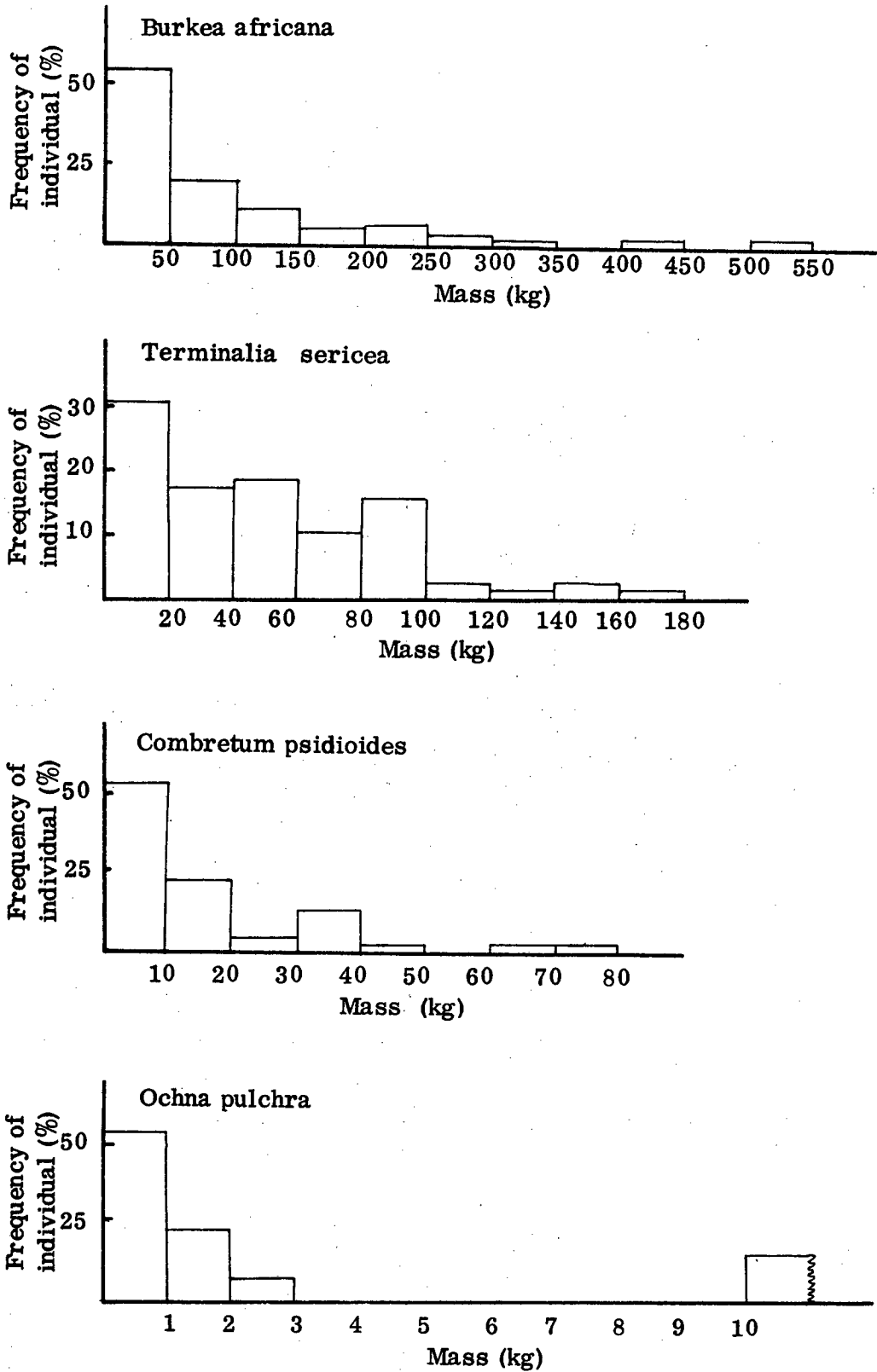


Fig. 5.13 Distribution of tree individuals (stem-individuals) in mass classes

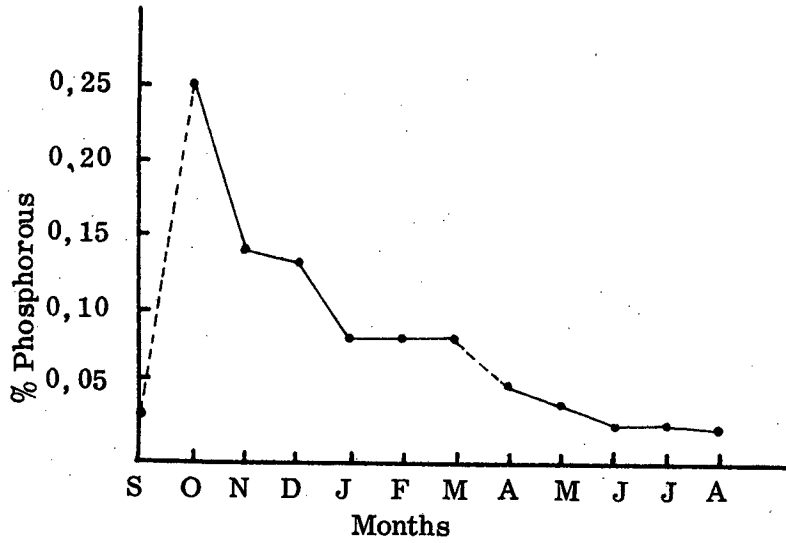


Fig. 5.14a Changes in phosphorous (expressed as % of the dry material) over the year in *Brachiaria nigropedata*. Dotted lines signify discontinuities owing to changes in the type of material analysed (see Appendix 3).

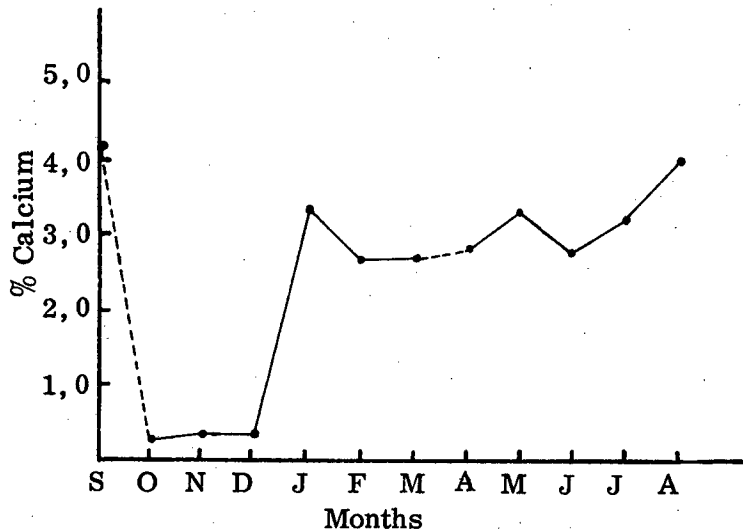


Fig. 5.14b Changes in calcium (expressed as a % of the dry material) over the year in *Brachiaria nigropedata*. Dotted lines signify discontinuities owing to changes in the type of material analysed (see Appendix 3).

6 PHENOLOGY

6.1 Introduction

Presence, timing and duration of each phenological phase of individuals of each species is an important framework within which the quantitative data, such as production, can be viewed. The field of phenology appears to be traditionally restricted to more obvious averaged annual changes in a population of plants. This includes the recognition and comparison of periodic phases and the relation to environmental periodicity. Usually noted are macroscopic and above ground characteristics, although Schnelle (1955) has pointed out the validity of the study of microscopic phenological changes and changes below ground. However, seasonal changes in the system have not been frequently emphasized. Seasonal characteristics, not usually noted under phenology, include changes in parts of plants which have become separated from the standing plant (for example leaf litter) and irregular yet annual changes to plants brought about by seasonal insect damage.

Phenological phases

The phases that were suited to provide an adequate description of the vegetation of the study area were:

- A Initiation of vegetative growth. This was taken as the time when buds began to expand or new leaves unfurl. Only the first few months were recorded.
- B Adult green leaf phase. This was the period in which adult green leaves were present on individuals. Where all the leaves were partly dead, this phase had ended.
- C Initiation of die-off of leaves. This phase usually corresponded closely to the end of the adult green leaf phase but it often overlapped that phase, since, this phase commenced whenever any leaves started to die-off. Since it was difficult to define the end of the die-off period, only the first 3 months of die-off were recorded.
- C₁ Period of dead leaves on plant. This phase was closely related to the period in which leaves abscised from the individual. In some species the drop of leaves was sudden in the beginning while in others the loss of leaves occurred over an

extended period. The phase was applied to tree species and shrub species, and was not recorded for most grass species, since the loss of dead leaves here was only due to sporadic breakaway, and did not occur at any clearly predetermined morphological abscission point.

D Flowering phase. This phase covered all stages of flowering from development of flower buds to wilting away of the flowers.

E Fruit phase. This phase extended from appearance of young green fruits until the fruits were ripe. If fruit was clearly unviable, it was nevertheless recorded.

F Initiation of fruit drop. Where it was possible, the month in which first separation of fruit or seed from the individual occurred, was recorded.

Difficulties in interpretation of phenological phases

In the course of phenological observations, various types of difficulty of interpretation of the above phases were encountered. These difficulties and complications are briefly mentioned under each phase.

A Initiation of vegetative growth

The presence of green leaves from the previous season sometimes reduced the effect of the appearance of new leaves, for example, in Dombeya rotundifolia, Combretum collinum, Blepharis maderaspatensis, Dicliptera eonii, Dicoma gerrardii, Dicoma schinzii, Felicia muricata and Nidorella resedifolia. In some species, there was more than one flush of leaves, for example, in some Burkea africana individuals, where the leaves were almost completely eaten in summer by the caterpillar Crina forda, a new flush of leaves on most of these individuals resulted in the following month. Also in the severely insect-eaten Ochna pulchra individuals, a new flush of leaves occurred just before winter. The above-average rains of April, following upon the below-average rains of March during the study year, appeared to result in a new flush of growth in some individuals of, for example, Grewia avellana, Blepharis maderaspatensis, Tephrosia cephalantha, Polygala kalaxariensis, Aristida stipitata and Aristida meridionalis, while the most clear reaction to these late April rains occurred in Digitaria polevansii.

In some species, new growth commenced unseen, for example, where it started below ground level so that only by disturbing excavation could initiation of this new growth be observed, for example in Hermannia tomentosa, Dicliptera eonii and to a lesser degree in Commelina africana. In some grass species, new growth was not only observed from the base as expected, but also from the higher nodes, for example in Cenchrus ciliaris.

B Adult green leaf phase

This phase was usually fairly easy to recognise, although difficulties in defining die-off of green leaves clearly affected recognition of the ending of this phase. In some grass species, during the relative drought of December (1970), some adult leaves underwent involution making it difficult to distinguish juvenile from adult leaves in, for example, Eragrostis pallens and Triraphis schinzii. In Tephrosia cephalantha, toward the end of winter, the leaves bent and closed the upper surface but still remained green even though only the blue-green underside was visible.

C Initiation of die-off of leaves

In some species this phase was difficult to recognise, for example in species where the leaves were apparently semi-dead and desiccated, although still green and living, as in some leaves of Tephrosia cephalantha, Dicoma gerrardii, Ximena americana, Boscia albitrunca, Tarchonanthus camphoratus, Lonchocarpus nelsii and, especially, Dicoma schinzii. In some species severe insect damage to leaves caused necrotic areas on the leaves which could be confused with initiation of die-off of the whole leaves, for example in Ochna pulchra, and to a lesser degree in Securidaca longepedunculata. The scorching of some leaftips in December or March (relatively dry months of the study year) could also be confused with the general initiation of final die-off, especially in March. In December, scorching was evident in several individuals of Panicum kalahareense, Mariscus laxiflorus, Cyperus margaritaceus and Cenchrus ciliaris. In March, scorching of leaftips was seen in some individuals of Mariscus laxiflorus and Triraphis schinzii.

An unusual pattern of die-off created some difficulty in some species where the stem

leaves died off, but basal leaves persisted, for example in Nidorella resedifolia. In Cenchrus ciliaris die-off started from the lower levels of the plant. The leaf sheath remained green for a time although leaf blade as well as culm had died, for example, in some individuals of Andropogon gayanus and Andropogon schirensis.

C₁ Period of dead leaves on plants (associated with leaf fall)

Although leaf fall is more applicable to woody species, some grass species, such as Eragrostis pallens, did lose leaf blades. In some other herbaceous species, the leaves disappeared by being borne down by splashed-up sand and then covered by sand, for example, the previous season's leaves of Cyperus margaritaceus and the dead leaves of Rhynchelytrum species. In some annual species, for example, Bidens biternata and Kyphocarpa angustifolia, that lost their leaves early, leaf drop occurred soon after formation, so that within one month, that is, between two inspections, the adult green leaves might have been formed, died and been dropped.

In some species, for example, Tephrosia cephalantha, Pavonia clathrata and Ozoroa paniculosa, leaves were dropped unexpectedly while still semi-green in colour. In other species, such as Sphedamnocarpus pruriens, dead, yet still greenish leaves were present on the individual. Species that dropped some totally green-coloured leaves were Combretum collinum, Ochna pulchra, Dombeya rotundifolia and Tapinanthus oleifolius.

D Flowering phase

This phase was difficult to recognise at an early stage since flower buds and vegetative buds were not easily differentiated. The flowering phase was also sometimes difficult to distinguish from the fruit phase in species such as Dicoma garrardii and Dicoma schinzii without disturbing the plant. In some species, flowers from earlier months remained shrivelled on the plants and could be mistaken for newly shrivelled flowers, for example in Polygala kalaxariensis and in Grewia deserticola in March (1971).

A new and often minor flush of flowering occurred in some species, probably as a result of the good April rains following the below-average rains of March (1971), for example, in some individuals of Aristida stipitata, Aristida meridionalis,

Triraphis schinzii, Indigofera daleoides, Nidorella resedifolia, Polygala kalaxariensis and Limeum fenestratum. The last mentioned species had a flush of flowers in May but these shrivelled in June. Irregular flowering flush also created difficulty in the recording of flowering of the Cenchrus ciliaris population.

E Fruit phase

Hopkins (1968) found the fruit phase difficult to recognize consistently in tropical vegetation. The recognition of this phase was complicated in some species that retained fruit from the previous season, such as, Ozoroa paniculosa or in species that retained fruit for a long time, for example, Dicoma gerrardii and Dicoma schinzii. In some species it was difficult to see if fruit had been formed without disturbing the plant. No rough handling of the individuals set aside for phenological inspection each month could be allowed as this would affect the outcome of the next month's observation of the same individuals. These species included many grass species with enclosing glumes, for example, Andropogon gayanus, Andropogon schirensis, Brachiaria nigropedata, Digitaria polevansii, Eragrostis species, Pogonathria squarrosa and especially the Cyperaceae species, Cyperus margaritaceus and Fimbristylis exilis. In some species, for example, many grass species and Anthospermum ericoideum, the fruits were small and were not easily seen. In other species, the fruit was often empty and barely recognisable as fruit, for example in Digitaria polevansii. In many species, the total abortion of flowers resulted in no fruit being produced, for example in Ochna pulchra as well as Turbina oblongata and Gloriosa virescens. In other species, insect damage apparently stopped all fruit formation, for example in Pentamenes zambesiacus. In one species, Limeum fenestratum, the fruit was morphologically anomalous and lacked the expected wing.

F Initiation of fruit drop

This phase was only easy to define where fruits dropped over a short period. In species that store fruits for a long time, for example, Dicoma species, Nidorella resedifolia and Ozoroa paniculosa, fruit drop was difficult to recognise. As pointed out earlier, it was difficult to see whether fruits were present without disturbing the plant; fruit drop in these species therefore, could not be determined. For these reasons fruit drop was only recorded for a few species.

6.2 Methods

To obtain a quantitative indication of the variation of phenology within each population (species), it was decided to make use of permanently tagged individuals which were randomly selected. Using this sample, some indication could be obtained of the frequency of a particular phase at a particular time within a population, and of the average intensity of a phase in a population.

In winter, prior to the start of the study, ten individuals of each species (except the very rare species) were randomly selected over the whole study area. About 50 species could be identified in the study area in this season. Fifty phenological marker poles were randomly distributed over the 8 ha main study area, avoiding, by a minimum of 3 m, quadrats to be clipped. The 50 species were divided into 5 equal groups from an alphabetically arranged list. A representative of each species of a group was sought in the vicinity of a marker-pole. The nearest individual to the pole was taken in preference to an individual of the same species farther away. No selection, however, was permitted in the immediate vicinity of quadrats to be clipped. To avoid congestion of selected plants around the marker-pole, no plant was selected closer than half a metre from it. Each consecutive group of species was sought around the next marker-pole. Thus each group of species was sought around 10 widely-separated marker-poles. If, after an intensive search of the area up to 30 m from the marker-pole, an individual of a required species could not be found, the search was carried over to the next pole. This occurred frequently in the case of rarer species.

This method of random selection of individuals for tagging was arduous and time-consuming, since individuals in winter were dormant, so that ready identifications were difficult. Also one could not differentiate clearly between dead and dormant individuals. Much time was taken in seeking out less common species individuals and it was sometimes difficult to decide readily which was the nearest individual of a particular species to the pole.

Each randomly-selected individual was marked by planting a wire peg, with

identification tag, between 20 to 25 cm from the base of the individual. Care was taken that the peg marked one specific individual. In the case of larger shrubs and tree species, a tag was fastened to a branch facing in a different direction and at a different height to that on the previously tagged individual of the same species. When new species were noticed in the course of the study, tags, kept in reserve, were used for 10 individuals. A rough map of the position of each tagged individual was found essential to locate each individual each month, especially at the height of the growing season when many tags were obscured by vegetation. Even with the use of this map, the random distribution of tagged individuals made location of these a lengthy task.

Selection of the individuals for intensive phenological observation in the winter resulted in only perennial individuals or dead annuals being initially selected. If it afterwards became clear that the selected individual was dead, the nearest live individual of the same species was tagged. In some species, therefore, the phenological sample in the beginning was reduced to less than 10 individuals, but increased to again 10 individuals later. The selection of individuals as above did, however, serve admirably to indicate the degree of mortality of the individuals of each species after one season's growth following a fire.

Usually all tagged individuals were visited during the second half of each month. At each inspection, notes were made following non-destructive and non-disturbing observation which, as mentioned earlier, sometimes presented difficulties in determining the presence of certain phases. To partially overcome this problem and to serve as a control of whether the 10 selected individuals were representative of the population as a whole, some non-tagged individuals of each population were also observed.

In addition to standard recordings of the various phenological phases, notes were made on any other clearly visible phenomena such as litter layer thickness, insect damage to various plant organs, presence of seedlings, re-greening of old material, pollination agents, method of seed dispersal, persistence of generative structures and colour changes.

The tagged individuals were also used for indications of mortality and the average dimensions of the individuals of each herbaceous species.

6.3 Results

6.3.1 General aspects

a Seedlings

The majority of species in the study area had no seedlings clearly recognisable. Although many grass seedlings were seen, identification was difficult since the mortality was high. Seedlings of Aristida stipitata, Aristida congesta, Aristida meridionalis, Rhynchelytrum species and some rare seedlings of Andropogon gayanus and Stipagrostis uniplumis were identified. Firm identifications were made of seedlings of Tephrosia cephalantha, Polygala kalaxariensis, Cassia biensis and Blepharis maderaspatensis as well as a few very rare seedlings of Pavonia clathrata and Dicliptera eonii. The only seedlings of a tree species that was firmly identified were those of Burkea africana.

b Re-greening of old material

The phenomenon of apparent re-greening of old material was difficult to study over only one year since the history of each individual was not fully known for the previous year. The description re-greening of old material is used when part of the plant individual concerned apparently died off completely in the previous season, but became green again in the early part of the study season. Plants where this occurred thus had some live above-ground parts present in the dormant season that did not, however, stay green and sappy. In some individuals of Polygala kalaxariensis and Dicliptera eonii and to a lesser degree in Blepharis maderaspatensis, partial re-greening of some of the twigs occurred. In old apparently dead individuals of Rhynchosia venulosa the parts up to 10 cm above ground had re-greened by the end of November. Re-greening in grass species was usually restricted to the culms of the hardy grasses. For example, in October, the bottom quarter of old culms of

some individuals of Eragrostis jeffreysii had re-greened. The lower half of old culms of most individuals of Eragrostis pallens had started to re-green by November, that is before the new culms had appeared. In most individuals of Aristida stipitata the bottom quarter to a third of the old culms had re-greened by December. Almost all individuals of Stipagrostis uniplumis had the lower half of their old culms green by November or December. No re-greening of old culms was seen in the related species of Aristida congesta and Aristida meridionalis.

Rapid die-off of flowers or young seeds (including glumes) in some individuals of Cyperus margaritaceus by February created a false impression that the culm had re-greened.

c Pollination

The most important pollination agent for most species in the study area would appear to be wind. Pollination by insects appeared to be of possible importance in some species. An insect of the family Lycidae (Coleoptera) was found in swarms on the flowers of Pentarrhinum abyssinicum in February and March while swarms of insects of the family Lygaeidae (Hemiptera) were found on the flowers of Ozoroa paniculosa in January. The swarming of these insects on flowers of these particular species in the study year might have been partially due to the poor flower production of other species in the study area and immediate surroundings.

d Dispersal

The majority of species of the study area had little effective and specialised means for dispersal of their disseminules, although many had weak adaptations for telechorous dispersal by means of wind. A few species, however, did have special modifications of their disseminules that appeared highly effective for telechorous wind dispersal. These were the plumed disseminules of Clematis brachiata, Clematopsis scabiosifolia, Raphionacme burkei and Pentarrhinum abyssinicum, as well as the elongated winged fruits of Securidaca longepedunculata and Sphedamnocarpus puriens. A few species produced drupaceous fruits which might be dispersed by birds, for example, Ozoroa paniculosa, Grewia species and

Ziziphus mucronata. One species had a myxospermous seed which promotes telechorous dispersal by birds. This species was the parasite Tapinanthus oleifolius which was found only on the higher branches of Burkea africana and Combretum psidioides individuals. Although the extremely rare species, Croton gratissimus, ejaculates seeds forcibly from its fruits, no fruits were formed in the study area.

There were a few species which had disseminules suitable for dispersal on the exterior parts of animal bodies. These included the Aristida species (especially Aristida stipitata), Kyphocarpa angustifolia, Blepharis maderaspatensis and Bidens biternata. The amount of animal life in the study area was however relatively small compared with that in other parts, such as the slopes and cliff zone of the mountain. The only common animal life consisted of insects. The cliffs surrounding the plateau provided an effective barrier against intrusion by larger mammals such as kudu (Tragelaphus strepciseros) and cattle, although smaller buck easily surmounted the cliffs but did not appear to traverse the study area often. Several troops of baboons (Papio ursinus) traversed the study area only very occasionally and smaller mammals (for example, Mongooses and mice), birds (for example, grey hornbills and francolins) and reptiles (for example, leguans but no snakes) were rarely seen. Since there were few reptiles, birds and mammals present, adaptations for dispersal through animal agents were probably relatively ineffective.

e Persistence of generative structures

The persistence of generative structures on the plant differed from species to species and formed part of the seasonal change in species. It is often important to know how long the generative structure of a species persists, since, after generative structures have disappeared, the identification of species is often difficult. Only after experience in the study area, could identifications be made from vegetative structures alone.

Most of the woody species did not have any persisting generative structure other than the fruits themselves, and those that do normally have an associated generative structure, did not produce generative parts in the study year. Many of the herbaceous

species have persistent generative structures in addition to the fruits themselves. The degree of persistence of these structures can vary greatly.

Grass species, especially, have persistent structures such as glumes and culms. The glumes of the previous season often lasted until the beginning of the study season in September to November (1970) in Panicum kalaharensis, Cenchrus ciliaris and Andropogon schirensis. Some species such as Digitaria polevansii, Rhynchelytrum species and Brachiaria nigropedata already had lost all glume structures by this time. Some previous season's glumes persisted until December to February, such as in some individuals of Mariscus laxiflorus, Cyperus margaritaceus, Eragrostis jeffreysii and Schmidtia pappophoroides. Some of the previous season's glumes persisted until almost the end of the study season in 1971, for example in Aristida stipitata and Triraphis schinzii. New culms disappeared as early as March (1971) in Eustachys paspaloides or in May and June in the case of Mariscus laxiflorus, Panicum kalaharensis and Cenchrus ciliaris. The following species culms persisted until the end of the study season in some individuals: Eragrostis jeffreysii, Eragrostis pallens, Aristida stipitata, Aristida congesta, Aristida meridionalis, Stipagrostis uniplumis and Pogonarthria squarrosa. Thus virtually all the hardy grass species' culms persisted well, whereas the softer grass species lost their generative material more quickly.

Non-grass herbaceous species which lost the previous season's generative parts (for example pods and capitula) relatively early were Rhynchosia venulosa, Pentamenes zambesiacus, Indigofera daleoides in November to December (1970), Nidorella resedifolia in March (1971) and Cassia biensis in April. New material persisted until August (1971) in some Tephrosia cephalantha, Nidorella resedifolia, Dicoma schinzii, Blepharis maderaspatensis, Rhynchosia venulosa, Pentarrhinum abyssinicum and Pavonia clathrata, the latter of which also had some associated generative material persisting from the previous season.

f Colour changes

With the exception of a few rarer species with striking red flowers (for example,

Pentamenes zambesiacus and Gloriosa virescens) in summer, the flowers (most commonly yellow to white) of the species of the area were not such that they could provide a conspicuous colour aspect in the community. The most conspicuous colour aspects were the light green colour of leaves in spring, the darker green colour of leaves in summer, the autumnal colours (in late winter) of Burkea africana, and the typical winter aspect (late winter and early spring) of leafless trees and dry grass (Fig. 6.1).

6.3.2 Expression of results

In the study of the phenology of a plant population it at once becomes apparent how difficult it is to express quantitatively a phenological phase in such a way that it reliably reflects the condition. When a phenological phase, for example the flowering phase, is investigated, it is often found that the phase is not fully developed compared with the average maximum possible under more appropriate circumstances. It is possible that (1) the intensity of the phase per individual is very low, for example, only 1% of the average maximum number of flowers per individual plant is present and that (2) the frequency of the phase in the population is very low, for example, only 1% of the individuals of the population are in the phase.

To express the intensity of a phenological phase in an individual, a subjective scale of integers from 0 to 10 was used, where 10 represented the near maximum expected intensity of the phase that could normally be achieved and 0 where the phase was only just present on a small part of the individual. This scale was difficult to apply accurately, since, (1) it was difficult to estimate the maximum potential development of each phase before it had occurred and (2) differences in the upper part of the scale could not be assessed as accurately as in the lower part.

To provide a semi-quantitative expression of each phenological phase, the following groupings, each with an accompanying term, were used:

A. Average intensity of the phase more than an estimated 10% of the average possible maximum intensity per individual with the phase - distinct

- (1) In more than half the sample individuals of the population - frequently distinct.
- (2) In less than half the sample individuals of the population - locally distinct.

B Average intensity of the phase less than an estimated 10% of the average possible maximum intensity per individual with the phase - slight

- (1) In more than half the sample individuals of the population - frequently slight.
- (2) In less than half the sample individuals of the population - locally slight.

Figures 6.2 to 6.8 are graphic representations of the phenological phases of a number of plant species in terms of the above groupings. Since observations were usually made monthly, some degree of latitude in the interpretation of the figures is needed since a phase recorded as, for example, frequently distinct in one month, might have just been attained at time of inspection or been present for almost a full month. Although a total of 98 species was recorded (Rhynchelytrum repens and Rhynchelytrum villosum were treated as a single species), the phenological representations are only given for the 54 species which provided a reasonable amount of phenological information. There was little or no phenological information concerning the large group of rare species.

The 54 species were grouped according to their general growth form and taken, in most cases, according to their ecological importance, defined previously as average biomass. This served to group the phenology of the more important species within each growth form together. By keeping rare species separate, their phenological pattern was not necessarily imposed on that of the more important species. All the species were grouped as follows:

- (i) a group of 18 grass species subdivided into 3 sub-groups
 - (a) 5 dominant grass species with biomass greater than 30 kg/ha (Fig. 6.2),
 - (b) 6 common grass species with biomass greater than 5 kg/ha and less than 30 kg/ha (Fig. 6.3) and
 - (c) 7 minor grass species, with recorded biomass less than 5 kg/ha (Panicum maximum excepted) (Fig. 6.4);
- (ii) 21 herbaceous species, other than grass species, with a recorded biomass (Fig. 6.5);

- (iii) 6 more important shrub species (including Tapinanthus oleifolius) (Fig. 6.6);
- (iv) 9 more important tree species (Fig. 6.7);
- (v) 44 rarer species divided into 4 groups according to degree of phenological knowledge about them:
 - (a) 14 species with virtually no phenological information;
 - (b) 11 species with very incomplete phenological information;
 - (c) 9 species with relatively more phenological information, and
 - (d) 10 aspect species (including 8 annuals) with incomplete information for the early phases.

Four species found rarely on the central sand area of the plateau (Rutherford, 1972) were not found in the study area itself. These were Digitaria eriantha, Lotononis platycarpa, Phragmanthera glaucocarpa and Rhigosum brevispinosum.

6.3.3 Results in species groups

When the level of degree of development of a phase is not specified, the phase is frequently distinct. Since this level is the most important, descriptions are largely restricted to frequently distinct phases.

6.3.3.1 Grass species

The 18 grass species with a recorded biomass (excepting Panicum maximum) were divided into the 3 above-mentioned groups according to their biomass, defined earlier as a measure of their importance. The phenology of constituent species of the 3 groups is discussed for each phenological phase:

A Initiation of vegetative growth

This phase became frequently distinct in October in 8 of the 18 species and in November for the remainder. Of the 5 dominant grass species the phase started frequently distinct in October for Brachiaria nigropedata and Andropogon gayanus (Fig. 6.2b, c). These were also the 2 species of this group with the largest average

mass per individual (Table 4.1). The phase in the other 3 species started frequently distinct in November (Fig. 6.2a, d, e). Of the 6 common species, Triraphis schinzii and Cenchrus ciliaris started frequently distinct in October (Fig. 6.3a, c). Apart from Eragrostis pallens, these 2 species had the largest average biomass per individual in this group. The other 4 species of this group started at the same level in November (Fig. 6.3b, d, e, f). Of the 7 minor grass species, Panicum kalahareense, Eragrostis jeffreysii, Eustachys paspaloides and Pogonarthria squarrosa started frequently distinct in October (Fig. 6.4a, b, e, g). The first 3 mentioned were the species of this group with the largest average biomass per individual. Three species started at the same level in November (Fig. 6.4c, d, f). The earliest start to this phase, at any degree, in the grasses was in September for Eustachys paspaloides (frequently slight) and Andropogon gayanus (locally slight) (Figs. 6.4e; 6.2c).

There appears to be a rough positive relation, within each grass group, between the earliness of the initiation of vegetative growth and the average biomass of the individuals of the species.

B Adult green leaf phase

Eustachys paspaloides and Eragrostis jeffreysii were the only two species that reached this phase to a frequently distinct degree by October (Fig. 6.4b, e). Eleven of the remaining 16 species reached this phase to this degree in November, 4 of the other 5 species reached it in December while one species reached it by about January. The earliest month in which this frequently distinct phase ended, was April. Of the 5 dominant grass species, Digitaria plevansii, Andropogon gayanus and Aristida stipitata ended in April (Fig. 6.2a, c, e). The other 2 species, Brachiaria nigropedata and Andropogon schirensis ended in May (Fig. 6.2b, d). Of the common grass species, only Stipagrostis uniplumis and Eragrostis pallens ended in April (Fig. 6.3e, f). Ending in May were Triraphis schinzii and Rhynchelytrum species (Fig. 6.3a, b). Ending in June was Aristida meridionalis (Fig. 6.3d) and ending in July was Cenchrus ciliaris (Fig. 6.3c). Of the minor grass species only 2 species, Schmidtia pappophoroides and Eustachys paspaloides ended in April (Fig. 6.4d, e). Ending in May was Eragrostis jeffreysii (Fig. 6.4b). Ending in June were Eragrostis stapfii and Pogonarthria squarrosa (Fig. 6.4f, g). Ending in July was Panicum kalahareense and ending in August was Aristida congesta (Fig. 6.4a, c). From the above it is clear that the adult green leaf phase

started at roughly the same time in all 3 groups of grass species, but in the more important species the phase ended with the last rains whereas in the common grass species and to a greater degree in the minor grass species, the adult green leaf phase often continued until well into winter.

The duration of the frequently distinct adult green leaf phase was 6 months for each of the dominant grass species (Fig. 6.2). For the common species (Fig. 6.3), the duration was 5 months in Eragrostis pallens, 6 months in Stipagrostis uniplumis, 7 months for Triraphis schinzii, Rhynchelytrum species, 8 months in Aristida meridionalis, and 9 months for Cenchrus ciliaris. For the minor species (Fig. 6.4) the duration of this phase was 6 months for Schmidtia pappophoroides, 7 months in Eustachys paspaloides and Pogonarthria squarrosa, 8 months in Eragrostis jeffreysii, Aristida congesta, Eragrostis stapfii and 9 months for Panicum kalaharensis. The duration of this frequently distinct phase was thus short for the dominant grass species compared to the duration in the common and rarer grass species, indicating a rough negative relation between the duration of this phase and the biomass of the species per unit area. There appeared to be no relationship between the average biomass per individual of grass species and duration of adult green leaf phase of the species.

C Initiation of die-off of leaves

In February, only Brachiaria nigropedata had already started this phase to a locally slight degree (Fig. 6.2b). In March, all except Schmidtia pappophoroides (Fig. 6.4d) had started to a locally slight degree, while Andropogon gayanus (Fig. 6.2c) was frequently distinct at this time. Only after a period of one or two months of locally slight die-off did the frequently distinct phase start, usually in April or May. The early start (at a slight intensity) in most species in March was probably due to the relative drought in this month. In all 5 dominant grass species, frequently distinct die-off had commenced by April (Fig. 6.2).

D Flowering phase

Only Schmidtia pappophoroides already flowered to a frequently distinct degree in December (Fig. 6.4d). Seven species commenced frequently distinct flowering in January while 8 out of the remaining 10 commenced in February. The other 2 species

commenced frequently distinct flowering only in March.

The dominant grass species did not start frequently distinct flowering before February. Digitaria polevansii, Brachiaria nigropedata and Aristida stipitata commenced in February while the 2 Andropogon species commenced in March (Fig. 6.2). In the common grass species the phase commenced in January for Cenchrus ciliaris, Stipagrostis uniplumis and Eragrostis pallens, and in February for Triraphis schinzii and Rhynchelytrum species (Fig. 6.3). Frequently distinct flowering never occurred in Aristida meridionalis (Fig. 6.3d). In minor grass species, the phase commenced as early as December for Schmidtia pappophoroides, January for Eustachys paspaloides, Eragrostis stapfii and Pogonarthria squarrosa, and February for Panicum kalaharensis, Eragrostis jeffreysii and Aristida congesta (Fig. 6.4).

In the dominant grass species, the length of the period of frequently distinct flowering was usually short, that is one month in Digitaria polevansii, Brachiaria nigropedata and Andropogon gayanus, and 2 months in Andropogon schirensis and Aristida stipitata (Fig. 6.2). In the common grass species this phase lasted for 2 months in Triraphis schinzii and Rhynchelytrum species and 3 months in Cenchrus ciliaris, Stipagrostis uniplumis and Eragrostis pallens (Fig. 6.3). For the minor grass species there was only one species with one month of frequently distinct flowering, Panicum kalaharensis (Fig. 6.4a). Those species with a 2 months period of frequently distinct flowering were Eragrostis jeffreysii, Aristida congesta and Eustachys paspaloides (Fig. 6.4b, c, e). Eragrostis stapfii and Pogonarthria squarrosa had a flowering period of 3 months (Fig. 6.4f, g). In Schmidtia pappophoroides flowering was recorded over 4 months (Fig. 6.4d), but it is doubtful whether this is representative of the species. The longest period that a grass species flowered at a frequent level was the 6 months from November to April in the case of Cenchrus ciliaris (Fig. 6.3c).

E Fruit phase

The species which fruited earliest (in February) were Cenchrus ciliaris, Eustachys

The long persistence of green leaves in the small Tephrosia cephalantha individuals might be related to the presence of a long tap root to well below one metre depth. In other species, the end of the adult green leaf phase at a frequently distinct level occurred as early as March for Mariscus laxiflorus (Fig. 6.5i) and April in Commelina africana, Pentarrhinum abyssinicum, Turbina oblongata, Elephantorrhiza elephantina, Pentamenes zambesiacus and Indigofera daleoides (Fig. 6.5d, e, f, o, p, q). The period of frequently distinct adult green leaf phase was usually the shortest (about 6 months) for the species of the last mentioned group. The shortest period was in Pentamenes zambesiacus with only 4 months (Fig. 6.5p), and Mariscus laxiflorus and Indigofera daleoides with 5 months (Fig. 6.5i, q).

C Initiation of die-off of leaves

As stated previously, leaf die-off was particularly difficult to recognise in some species. In the most important species, die-off started usually after the rains had ended in about May. However, frequently or locally slight die-off of many herbaceous layer species was found in March, for example, in Cyperus margaritaceus, Dicliptera eonii, Commelina africana, Pentarrhinum abyssinicum and Blepharis maderaspatensis (Fig. 6.5b, c, d, e, m).

C₁ Period of dead leaves on plant

Dead leaves on the plant was not a well suited phase for this species group. Leaf-drop was practically absent since no abscission occurred in many species. Only in Tephrosia cephalantha, Dicliptera eonii, Pavonia clathrata, Cassia biensis, Elephantorrhiza elephantina and Indigofera daleoides was dropping of leaves or leaflets easily noted. The time of leafdrop corresponded roughly to the time of die-off of these organs, that is, about May.

D Flowering phase

Of the 21 species only one species - Elephantorrhiza elephantina - did not flower during the study year (Fig. 6.5o). This is in contrast to the tree species, where very few flowered. Several species only had local flowering, for example, Tephrosia cephalantha, Commelina africana, Cissampelos mucronata and Pentamenes zambesiacus (Fig. 6.3a, d, g, p). The earliest frequently distinct flowering occurred

in November in Nidorella resedifolia and Anthospermum ericoideum (Fig. 6.5r, t) and in December for Cyperus margaritaceus (Fig. 6.5b). Most species' frequently distinct flowering period was from January to March (Fig. 6.8d). Some species produced flowers through more than half the year, for example, Dicliptera eonii and Nidorella resedifolia; the latter species flowering almost all the months of the study year (Fig. 6.5c, r). In some species flowers were only locally distinct in a single month, for example, in Pentamenes zambesiacus (Fig. 6.5p) or in 2 months, for example, in Tephrosia cephalantha, Commelina africana and Cissampelos mucronata (Fig. 6.5a, d, g).

E Fruit phase

Fruit was not formed in some species even though flowering had occurred, for example, in Turbina oblongata, Cissampelos mucronata, Pentamenes zambesiacus and Indigofera daleoides (Fig. 6.5f, g, p, q), while some species produced extremely few fruits, for example, Dicliptera eonii and Commelina africana (Fig. 6.5c, d). Usually, when fruit was produced, it was retained for a long time in species such as Cyperus margaritaceus, Pentarrhinum abyssinicum and Pavonia clathrata (Fig. 6.5b, e, l), but only for a short time, for example, in Tephrosia cephalantha and Mariscus laxiflorus (Fig. 6.5a, i).

It is clear that some perennial species of this group completed their functions in a shorter time than the rest. Examples of these short cycle species were Commelina africana and Mariscus laxiflorus (Fig. 6.5d, i).

6.3.3.3 Shrub species

A Initiation of vegetative growth

In Bauhinia macrantha and Grewia avellana this phase started at a frequently distinct degree in October (Fig. 6.6b, c), while Ancylanthos bainesii and Grewia deserticola started in November (Fig. 6.6a, d). Rhus ciliata also appeared to commence at a frequently distinct level in November but still had old green leaves from the previous season present (Fig. 6.6e). New growth, at a locally distinct

level, commenced earlier in September, in Bauhinia macrantha and Grewia avellana (Fig. 6.6b, c), and in October in Ancylanthos bainesii (Fig. 6.6a). Rhus ciliata started at a locally slight level in September (Fig. 6.6e).

B Adult green leaf phase

This phase started in most of the species in November (Fig. 6.6a, b, c, d). Although Rhus ciliata was in this phase throughout the year (Fig. 6.6e), the frequently distinct phase ended around March for Grewia deserticola, April for Bauhinia macrantha and May for Ancylanthos bainesii and Grewia avellana (Fig. 6.6d, b, a, c). Ancylanthos bainesii and Grewia avellana had this phase enduring at a frequently distinct level for 7 months, Bauhinia macrantha for 6 months and Grewia deserticola for 5 months (Fig. 6.6a, c, b, d). The phase ended frequently distinct in Ancylanthos bainesii (Fig. 6.6a), whereas in species such as Bauhinia macrantha and Grewia deserticola the phase had a slight intensity into the first winter month (Fig. 6.6b, d).

C Initiation of die-off of leaves

In all the species (Fig. 6.6) frequently distinct initiation of die-off of leaves occurred in May except in Rhus ciliata, where this occurred in July (Fig. 6.6e). Bauhinia macrantha already started at a frequently slight level in March (Fig. 6.6b), while Ancylanthos bainesii and Grewia deserticola started at a local level in April (Fig. 6.6a, d).

C₁ Period of dead leaves on plant

This period is associated with leaf drop, but it was difficult to recognise the time of maximum separation and fall. Four of the shrub species started at a frequently distinct level in May, continuing until July for Bauhinia macrantha, Grewia avellana and Grewia deserticola (Fig. 6.6b, c, d). Ancylanthos bainesii continued until the end of the study period (August, 1971) and dead leaves remained from the previous year until September, 1970 (Fig. 6.6a). The length of period of dead leaves on the plant individual was about 3 months for Bauhinia macrantha, Grewia avellana and Grewia deserticola (Fig. 6.6b, c, d), 2 months for Rhus ciliata (Fig. 6.6e) and about 5 months for Ancylanthos bainesii (Fig. 6.6a).

D Flowering phase

Only 2 of the tagged shrub species flowered, that is Grewia deserticola and Rhus ciliata (Fig. 6.6d, e). A few sporadic rare occurrences of flowering in the population of Grewia avellana were, however, noted (Fig. 6.6c).

Rhus ciliata started flowering at a frequently distinct level in December, Grewia deserticola in January, while the first rare flowers of Grewia avellana were noted in November (Fig. 6.6e, d, c). Grewia deserticola only flowered for 2 months at a frequently distinct degree, ending in February (Fig. 6.6d), while Rhus ciliata flowered for 4 months ending in March (Fig. 6.6e). No flowers of Grewia avellana were noted after December (Fig. 6.6c).

E Fruit phase

No fruits of Rhus ciliata were seen (Fig. 6.6e). Some fruits of Grewia deserticola were noted in the population in March, April, May and August and one previous season's fruit in October, 1970 (Fig. 6.6d). Isolated, rare and damaged fruits of Grewia avellana were found in the population in March, April and June (Fig. 6.6c).

Due to the extreme scarcity of fruits no record of fruit fall can be given for the shrub species.

An anomalous shrub species, the parasite Tapinanthus oleifolius (Fig. 6.6f) has not been included in the above description of the phenology of shrub species. New growth occurred in this species at a frequently distinct level from October. The adult green leaf phase extended for most of the year at a frequently distinct level and only in September and August was it present at a frequently slight level. A slight degree of leaf die-off occurred in April and the following months. In May, a frequently distinct leaf fall took place but soon ceased. Frequently distinct flowering extended from November to January and was locally distinct in February and slight in March. The fruit phase extended at a locally distinct level from February to July, several fruits being dropped in June. However, relatively few mature fruits were produced.

6.3.3.4 Tree species

The tree species' phenology is discussed for, first, the vegetative phases and then for the generative phases.

a Vegetative phases

The initiation and ending of the vegetative phase in the 3 dominant tree species Burkea africana, Terminalia sericea and Combretum psidioides was the most important factor in the aspect change of the vegetation (Fig. 6.1).

Burkea africana was, in September, the first to start vegetative growth at a frequently distinct level (Fig. 6.7a), while Combretum psidioides was local in September but frequent in October (Fig. 6.7c). Terminalia sericea started locally in October and reached a frequent level in November (Fig. 6.7b). The adult green leaf phase of all 3 species at a frequently distinct level extended from November (Fig. 6.7a, b, c). This was after a poor rainy season which may have delayed new growth. The summer flushes of new growth in Burkea africana brought about by leaf damage by Crina forda has already been mentioned (Section 6.1). The frequently distinct adult green leaf phase lasted until May in Terminalia sericea (Fig. 6.7b), and until July in Combretum psidioides and Burkea africana (Fig. 6.7c, a), extending, in Burkea africana, into August at a frequently slight level. Terminalia sericea extended at a locally slight level into July. The ending of the adult green leaf phase in these species was probably extended by the good rainfall of the study season, and was possibly related to the longer period in which the species could recover from the previous season's fire. The period of frequently distinct adult green leaf phase was shortest in Terminalia sericea (7 months) while it extended to about 9 months for Combretum psidioides and Burkea africana (Fig. 6.7b, c, a).

The leaf phenology of Securidaca longepedunculata and Ozoroa paniculosa is similar to that of Burkea africana (Fig. 6.7f, h, a). Lonchocarpus nelsii, Combretum collinum and Dombeya rotundifolia were semi-deciduous in the study season but retained many green leaves throughout the study year (Fig. 6.7g, e, i). In Combretum collinum, judging by evidence of previous season's litter layer, retention of green

leaves was only temporary and possibly due to the good rains of the study season. Vegetative development of Lonchocarpus nelsii individuals was almost static throughout the study season. Ochna pulchra had an anomalous vegetative growth pattern (Fig. 6.7d). At the start of the season, from about September to November some new leaves appeared. In April and May, however, a very rapid death and drop of leaves occurred (at this time, these leaves were severely damaged, apparently by insects) and simultaneously a new flush of leaves appeared just before winter. In August a few new leaves appeared again on a few individuals. It appears not improbable that the effect of the fire and the severe insect damage to the leaves was responsible for this pattern of growth.

The major period of leaf drop in the tree species was in June and July for Terminalia sericea (Fig. 6.7b), in August for Combretum psidioides and Burkea africana (Fig. 6.7c, a), as well as for the less important species, Combretum collinum, Securidaca longepedunculata, Lonchocarpus nelsii, Ozoroa paniculosa and Dombeya rotundifolia (Fig. 6.7e, f, g, h, i). The relatively early drop of leaves of Ochna pulchra in May has been referred to above.

b Generative phases

Most tree species appeared to be affected by the previous season's fire and did not flower or did so only to a slight degree. The only species which appeared to have flowered and fruited in the season immediately following the fire (1969 - 70) was Ozoroa paniculosa (Fig. 6.7h). Some fruits, scorched by the fire, were retained on the tree throughout the study year in a few Burkea africana and Combretum psidioides individuals. The only 2 species that flowered frequently distinct in the study season were Ozoroa paniculosa and Dombeya rotundifolia (Fig. 6.7h, i). Ozoroa paniculosa flowered profusely in both tree and regenerative forms in December and January (Fig. 6.7h) while Dombeya rotundifolia flowered in April, climaxing in May (Fig. 6.7i). The flowering time of Dombeya rotundifolia, noted by Riley (1963) as heralding the spring in the east of Southern Africa, appears not to apply to South West Africa, since, in several areas not burnt on the Omuverume Plateau edge, Dombeya rotundifolia also flowered in April and May.

Only the large tree individuals of Securidaca longepedunculata flowered, mostly in November (Fig. 6.7f). Only a few tree individuals of Ochna pulchra flowered in September and October but produced no fruits (Fig. 6.7d). Some large tree individuals of Terminalia sericea flowered, but mostly at a slight intensity, in December (Fig. 6.7b). Combretum psidioides flowered in November but this was restricted to very few individuals (Fig. 6.7c). No individuals of Burkea africana, Combretum collinum and Lonchocarpus nelsii flowered in the study year (Fig. 6.7a, e, g), although these species flowered profusely around October in unburnt sand flats between rocks in the summit perimeter belt of the plateau. The other species, Securidaca longepedunculata, Combretum psidioides and Ochna pulchra, that only flowered slightly in the study area, also flowered profusely in the unburned perimeter areas. At the beginning of the following season (1971 - 72) Burkea africana, Combretum collinum and Combretum psidioides flowered profusely in September and October in the study area. Combretum collinum had already started in August (Fig. 6.7e). Thus only in the third season after the fire did the main tree species return to adequate flower production. Flowers of the tree species usually appeared before the adult leaves had formed and before the first rains of the season, although Terminalia sericea would appear to be an exception to this since flowers only appeared after formation of adult leaves (Fig. 6.7b).

In the study season, very few trees produced many fruits. Only Terminalia sericea appeared to produce a reasonably high ratio of fruit to flowers (Fig. 6.7b). Dombeya rotundifolia also fruited well (Fig. 6.7i) but Ozoroa paniculosa produced much fewer fruits than flowers (Fig. 6.7h), many of the fruits appearing infertile. Securidaca longepedunculata produced some fruit (Fig. 6.7f) which ripened from December to August. Combretum psidioides produced very little fruit (Fig. 6.7c) and that which was formed was infested by pupae. All flowers of Ochna pulchra aborted and no fruits were formed (Fig. 6.7d).

Since fruit production in most tree species was very low, determination of fruit fall could not be carried out accurately.

6.3.3.5 Rarer species

Forty-four rarer species were divided into 4 groups according to the degree of phenological knowledge concerning them.

(a) Some species were so rare that virtually no phenological data could be gathered about them. These species, which were very rarely recorded in the various sampling programmes used in previously mentioned sections, were:

- 1 Acacia mellifera
- 2 Aerva leucura
- 3 Asparagus africanus
- 4 Croton gratissimus
- 5 Eragrostis rigidior
- 6 Grewia flavescens
- 7 Heteropogon contortus
- 8 Maerua juncea
- 9 Melhania acuminata
- 10 Merremia tridentata
- 11 Pterococcus africanus
- 12 Solanum delagoense
- 13 Tragia dinteri
- 14 Ziziphus mucronata

(b) Species with incomplete phenological information:

1 Acacia species Only one individual about 1½ m high was found in the study area and appeared related to Acacia hebeclada. No generative parts were produced.

2 Clematis brachiata Only 2 of these woody-herbaceous climbers were seen on one mound. The leaves were still adult green in May but relatively few remained green by August when most had dried and fallen. Both individuals flowered in March with fruits forming in May, most of which had dropped by August.

3 Clematopsis scabiosifolia Only one individual was seen on the flats. The adult green leaf phase persisted until June, and in July leaves died off. The individual

flowered profusely in February and March and fruits were present from March until July. Much fruit fell in July and August.

4 Combretum apiculatum subspecies leutweinii This tree species, with individuals up to 5 m high, was very rarely found on the flats and mounds. Individuals were in the adult green leaf phase most of the year, leaves dying off in July and August. Very few fruits were seen in May and June.

5 Commelina benghalensis This herb, about 40 cm high, was only found in shade of Combretum collinum individuals on some mounds. It remained green until May, whereupon rapid die-off of leaves occurred. The flowers were seen in February and March but probably started to a slight degree in January. Very few fruits were found, only in March and April.

6 Grewia bicolor This very rare shrub, about 1 to 1½ m high on the flats, was in the adult green leaf phase until May. No generative parts were seen.

7 Leonotis dysophylla There was one small patch of individuals about 1 m high, that did not grow again from the base in the study season. They had flowered in earlier seasons.

8 Panicum maximum This grass species was only found on some mounds. It remained in the green adult leaf phase for longer (into May and June) than did the Digitaria polevansii of the surrounding flats.

9 Raphionacme burkei This shrub of about 35 cm height was very rarely seen but did scatter plumed disseminules in winter.

10 Rhynchosia sublobata This climber species was found on a few mounds. Flowers were not noticed, although a few fruits were found in winter.

11' Tephrosia lupinifolia This was a very rare ground level herbaceous species on which no generative parts were seen.

(c) Species with relatively more phenological information:

1 Acacia hereroensis Only a small group of these trees was found on one mound area. Vegetative development started in October although some green leaves were still present from the previous season. Some leaflets died off in November and

January and some fall of leaflets was noticed in March. No generative parts were seen.

2 Boscia albitrunca Only one low individual about 1 m high was found on a mound. Throughout the season its leaves remained grey-green. No new leaves were formed and very few leaves were lost. No generative parts were seen.

3 Eragrostis nindensis This species was rare and solitary on the flats. Vegetative growth started in October and the adult green leaf phase ended in April although die-off of leaves started in March and continued in April. Flowering occurred in January and February and one fruit was found in March. The individuals appeared to have a low vitality.

4 Eragrostis scopelophila This grass species was restricted to a few mounds but occurred socially on these mounds. Vegetative growth started in October and the adult green leaf phase ended in May with dying-off of leaves occurring in May and June. Most individuals flowered in January and February with fruits from April until about June.

5 Gloriosa virescens This straggling herbaceous species was found on several mounds. By December, individuals were in a frequently distinct adult green leaf phase that ended very abruptly in March, since, in April, all individuals were dead and prostrate. Individuals were in flower from December to March with the main flowering period in January and February. Two very young fruits were seen in March, but no ripe fruits were observed.

6 Hermannia tomentosa This rare creeping herbaceous species of the flats was in the adult green leaf phase until May and still at a slight degree, in a few individuals, in July. Main dying-off of leaves took place in April and May. No generative parts were seen.

7 Sphedamnocarpus puriens Individuals of this species were local and found mostly on some mounds. The adult green leaf phase lasted until June, die-off occurring gradually from March to June. Some degree of leaf drop occurred in August. Individuals flowered profusely in February and March and fruits were produced in April and were soon dropped.

8 Tarchonanthus camphoratus These shrubs, about 1 m high, were very rare on the flats and retained their green leaves throughout the year, although a slight die-off of leaves occurred in March and April and in August. A few dead flowers were seen in March.

9 Ximenia americana These very rare shrubs of the flats were about 60 cm high and remained evergreen, although some die-off and leaf-fall occurred, especially in July and August. No generative parts were seen.

(d) Aspect species that were visible above ground during only part of the year. These include 8 annual species. Often the start of the early phases was unknown in these species due to rapidity of appearance:

1 Bidens biternata This species was seen only at the edge of a mound and one individual was seen on the flats. It flowered until May and fruits were formed from April; some were retained until August.

2 Fimbristylis exilis This annual was not seen until January, 1971. Adult green leaves lasted until April with leaf die-off occurring from March to May. Flowering occurred until May while fruits were seen from March, some being retained until August. This species, although absent during much of the study year, was relatively common in some months, for example, 9300 individuals/ha in April.

3 Hibiscus fleckii This species, up to over 2 m high, occurred socially on 2 mounds. The adult green leaf phase lasted until June with die-off of leaves occurring mainly in the same month but also in July. Flowering occurred mainly in February and March and there was a separate flush of frequently distinct flowering in April that decreased to frequently slight in May. Fruits were observed from March until August and gradual fruit fall occurred from April onwards.

4 Kyphocarpa angustifolia This species of the flats, although not seen in the first half of the study season, was not uncommon when it occurred in autumn (900 individuals/ha in April) and winter. Leaves had fallen by May and fruits dropped from June to August.

5 Limeum fenestratum This herbaceous aspect species of the flats was not uncommon when it occurred, for example, 600 individuals/ha in June. Green leaves

were present until April whereupon they became shrivelled and dropped. Flowering occurred from February to May and included a new flush in April and May. Dead flowers from this flush were noted in June and July. Fruits (without wings) were observed from March until July and fruit fall occurred probably from April.

6 Limeum viscosum The vegetative pattern of this low prostrate rare herbaceous species of the flats appeared very similar to that of Limeum fenestratum, but flowers were very few and only seen in February and April. One fruit was seen in March and another in April.

7 Phyllanthus pentandrus This low annual herbaceous species of the flats was not uncommon when present (2 700 individuals/ha in April) and remained green only until May. Flowers and fruit were seen in April on the same individuals with fruits also in May.

8 Vernonia poskeana This herbaceous species was scattered over the flats area. No leaves were observed (probably already disappeared) but flowers were seen from April to June and fruits from June to August. Fruits dropped in the second half of winter.

9 Oxalis purpurascens This very social perennial aspect species was found on one mound. The vegetative phases ended in April but some adult green leaves still remained to a locally distinct degree in May. No generative parts were seen.

10 Pygmaeothamnus zeyheri This rare poisonous herbaceous species of the flats only produced a few leaves per individual and these died during April, the dead material disappearing soon afterwards. No generative parts were seen.

In summary, all the annual species flowered (mostly in April) and only the 2 perennial species did not. Late aspect species were Kyphocarpa angustifolia and Vernonia poskeana which flowered and fruited into winter, while Hibiscus fleckii and Limeum fenestratum were amongst the first of the annuals to start flowering (in February). The adult green leaf phase rarely continued after April, but in the 2 species found exclusively on the mounds, Oxalis purpurascens and Hibiscus fleckii, it lasted longer.

6.3.4 Phenology of species groups and communities

A comparison is made of the phenology of the previously mentioned groups: dominant grass species, common grass species, minor grass species, other herbaceous species, shrub species, tree species and aspect species. The other rare species of the study area are not included here. Phases referred to below occurred at the frequently distinct level for each species. Communities compared are those of the flats and mounds.

a Species groups

All the groups' main phenological phases are summarised in Fig. 6.8a - f.

i Vegetative phase (adult green leaf phase)

Species groups with many constituent species in an adult green leaf phase throughout the year, were only the tree group, shrub group and a small percentage of the other herbaceous group (Fig. 6.8f, e, d). The 3 grass groups and aspect species group did not remain in an adult green leaf phase throughout the year (Fig. 6.8a, b, c). The only groups, in which all constituent species were in an adult green leaf phase by November, were the tree and shrub groups (Fig. 6.8f, e). In the dominant and common grass groups, all species were in the adult green leaf phase by December, whereas in the minor grass group and the other herbaceous layer species group, all species were in this phase by January (Fig. 6.8a, b, c, d). The last month in which all species of a group were in the adult green leaf phase, was March in the case of shrubs and other herbaceous species groups, April for all grass species groups, and May for the tree group (Fig. 6.8e, d, a, b, c, f).

In the grass groups (except for the minor grasses group) and the other herbaceous species group the adult green leaf phase lasted for 5 months (where at least 95% of the species of the group were in this phase), from December to April (Fig. 6.8a, b, d). In the shrub group, this period was also 5 months but occurred earlier, that is from November to March, while in the tree group it was 7 months from November to May but for most tree species continued until July, that is a period of 9 months (Fig. 6.8e, f). For the minor grasses group this phase lasted only 4 months from January to April (Fig. 6.8c).

The group with the most concise adult green leaf phase was the dominant grass group (Fig. 6.8a).

ii Generative phase (flowering phase)

Only in the minor grass species group did all species flower simultaneously (in February), while about four-fifths of the common grass species flowered in February and March (Fig. 6.8c, b). In the dominant grass group and other herbaceous layer species group, only just over half of the species were flowering in the period February and March (Fig. 6.8a, d). The group which had least flowering was the tree group followed by the shrub group (Fig. 6.8f, e). Flowering started earliest in November in the other herbaceous species group, and was followed in December by the minor grass species group, the shrub species group and tree species group (Fig. 6.8d, c, e, f). The common grass species group only commenced flowering in January and the dominant grass species group in February (Fig. 6.8b, a). The peak flowering month was in February for all groups except the tree species group, while March was the next most important flowering month for all herbaceous groups. Flowering in a few tree species occurred in December and January, not in February and March, and again in April and May (Fig. 6.8f). From observations in the season following the study season, it became clear, however, that the dominant tree species that had not flowered or not flowered well in the study season, flower in September and October. In the common and minor grass species and shrub species groups, flowering ended in March, but extended into April in the dominant grass species group, and into June in the other herbaceous species group (Fig. 6.8b, c, e, a, d).

b Communities

The mound vegetation and vegetation of the flats differed in some respects in their community phenology. Cenchrus ciliaris, Dicliptera eeni, Rhynchosia venulosa, Commelina benghalensis, Oxalis purpurascens and Hibiscus fleckii continued in the adult green leaf phase longer than many herbaceous species on the flats. The difference in the vegetative phenology of the mound community and community of the flats was clearly discerned in May, June and even July, when the mound areas stood out greener than the vegetation of the herbaceous layer of the surrounding flats. The prolonged adult green leaf phase in the mound species is probably related to greater water retention in the mound soil and to the shade provided by the relatively broad-leaved Combretum collinum and Dombeya rotundifolia trees which retained

their leaves for most of the study year.

Most of the herbaceous species on the mounds flowered over several months and not only for a short period as was usually the case in the species of the flats.

6.3.5 Phenology in relation to climatic factors and productivity

6.3.5.1 Relation of phenological phenomena to some climatic factors

There were few clear relationships between the changes in monthly mean daily temperature and frequency of phenological phases. However, the relatively steep increase in number of species with an adult green leaf phase at a frequently distinct level, from September to November, corresponded with a rise in temperature from a monthly mean daily temperature of $20,5^{\circ}\text{C}$ to $23,0^{\circ}\text{C}$. The initiation of the vegetative phase in the tree species corresponded with the most rapid rise in monthly mean daily temperature in the year, that is from about 16°C in August (based on study year's records) to $20,5^{\circ}\text{C}$ in September.

Flowering appeared to be less dependent upon the distribution of rainfall in the study year than were the vegetative phases. Flowering at a frequently distinct level corresponded, in most species, to the period of maximum monthly average rainfall and not to the study year's rainfall, where the below average rainfall in March coincided with full flowering in many species. The high incidence of flowering in February and March corresponded closely to the high monthly mean daily relative humidity of these months (76% and 57% respectively), although, the humidity did not prevent die-off of some vegetative parts in some species in March.

The above-average rains of October, followed only by average rains in November and no effective rain in the first 3 weeks of December, apparently resulted in a partial die-off and scorching of leaf tips referred to previously (Section 6.1). The only month of the rainy season with a below-average rainfall was March. This appeared to create a water deficit toward the end of March which resulted in another partial die-off and scorching of leaf tips in several species and some flowers in a few species (Section 6.1). The relatively high temperatures in November, December

and March (Fig. 2.9) probably also contributed to creating the water deficits. The relative water deficit in March was followed by a relative water surplus in April that appeared to result in a new flush of vegetative growth and some generative growth, in April and May (Section 6.1). In some species (Section 6.1) the late flush of flowers was withered shortly afterwards by the onset of the severe water deficit from May onwards. The periods of water deficit, recognised by phenological reaction in December and March, are independently indicated in a climate diagram (after Walter, 1962) (Fig. 2.8), although it appears that the December reaction was a delayed reaction depending upon conditions in November.

Many of the culms of Andropogon gayanus that were still erect in early August, were broken and laid on the ground by winds in late August.

The above-average rainfall of the study year (Fig. 2.6), which was in contrast to the below-average rainfall of the previous year and following year, had various effects upon the vegetation. Many species, especially the tree species, extended their period of adult green leaf phase almost till the end of winter in the study season (Fig. 6.8f), which was in contrast to the preceding season and following season, where many leaves had dropped by mid-winter. Some normally deciduous species were only slightly deciduous in the study season, for example, Lonchocarpus nelsii and Combretum collinum (Fig. 6.7g, e). In the year following the study year, some annual species, for example Limeum fenestratum, were almost absent while some, for example Kyphocarpa angustifolia, were not seen. These species may be more restricted to early stages in pyric succession but might also have been present or more common in the study year because of the above-average rains of that year.

6.3.5.2 Relation of phenology to productivity

Lieth (1970) has discussed the relation of phenology to productivity studies and points out that in recent years, a quantitative approach to phenology has been made that is referred to as phenometry. Phenometry and growth analysis are very similar, only their goals are slightly different. "Growth analysis is mainly concerned with physiological processes or plant properties; phenometry searches for environmental relationships, using plant growth as a microclimatic indicator."

Thus seasonal growth rates, accumulation and turn-over of biomass and energy in the field, are but a few examples which can be evaluated by phenometry concepts. It is phenometrically important to relate some of the previously defined phenological phases to the productivity data.

To relate phenology to productivity, data from 2 grass species with the most reliable productivity data, that is, Digitaria polevansii and Brachiaria nigropedata, the dominant non-grass species, Tephrosia cephalantha, and the dominant shrub species, Grewia avellana, were used.

In Digitaria polevansii and Brachiaria nigropedata, the period of maximum productivity of new material (Fig. 5.8a, b) occurred 3 and 2 months respectively, after the start of the frequently distinct level of adult green leaf phase (Fig. 6.2a, b); in both species maximum biomass (Fig. 5.6a, b) was attained after 6 months of this phase. In the other herbaceous species, Tephrosia cephalantha, the corresponding periods were longer, 6 and 9 months respectively, (Figs. 5.8d; 6.5a; 5.4h), but in the shrub species, Grewia avellana, they were shorter, 1 and 4 to 5 months respectively, (Figs. 5.8c; 6.6c; 5.4g). Only in the 2 grass species did the end of the frequently distinct adult green leaf phase coincide with the start of new material decrease (Figs. 6.2a, b; 5.6a, b). In the other herbaceous species and shrub species, the phase continued, for a few months, into the period of biomass decrease (Figs. 6.5a; 6.6c; 5.4h, g).

Frequently distinct flowering coincided with the month of maximum productivity of new material in both grass species (Figs. 6.2a, b; 5.8a, b), but in Tephrosia cephalantha flowering occurred 2 to 3 months before its maximum productivity period (Figs. 6.5a; 5.8d).

In Digitaria polevansii, the amount of generative material was relatively small during the period of frequently distinct flowering; maximum mass of generative material was attained when fruits were forming and flowering was only locally distinct (Figs. 5.10a; 6.2a). Tephrosia cephalantha (Figs. 6.5a; 5.10c), as well as the next most common other herbaceous species, Cyperus margaritaceus (Figs. 6.5b; 5.10b),

also flowered mainly before maximum mass of generative material was attained; the fruiting phase was concurrent with the maximum mass of this material. After fruit drop, associated generative structures still remained and in this period generative mass was still relatively high in, for example, Tephrosia cephalantha (Fig. 5.10c, d).

6.3.6 Other seasonal changes in the ecosystem

An attempt was made to record the seasonal change in amount of litter on the ground and the damage, caused mainly by insects, on leaf margins and lamina on plants.

Apart from noting a white mildew-like fungus on leaves of some individuals of Combretum collinum in winter, no attention was given to fungus diseases.

a Litter

Determination of changes in litter on the ground through the year was found to be difficult. At the base of each tagged herbaceous individual, the depth and nature of the litter layer (if present) was recorded. From analysis it became evident that the thickness of the litter layer was very variable through the year due to frequent redistribution of loose-lying leaves. This indicates that use of litter traps in the study area would result in measuring artificially stabilised litter.

The species with more than half the individuals having some litter around their bases throughout the year were Commelina africana, Dicliptera eonii and Mariscus laxiflorus. The only grass species with a modicum of litter cover at the base of some of their individuals throughout the year were Triraphis schinzii, Rhynchelytrum species and Panicum kalahareense.

b Insect damage

Some leaves were apparently very badly damaged by insects, usually at night.

Those species with the most damaged leaves were the 3 tree species that remained virtually evergreen throughout the study year; viz., Ochna pulchra, Combretum collinum and Lonchocarpus nelsii. Other species with damaged leaves were Combretum psidioides, Terminalia sericea and Burkea africana, and to a lesser degree the other tree species Securidaca longepedunculata and Ozoroa paniculosa. The only shrub species that were affected to some degree, were Grewia avellana and Ancylanthos bainesii. The herbaceous species with the most damaged leaves were Rhynchosia venulosa and Turbina oblongata.

The least damaged leaves were those of Cyperaceae; Cyperus margaritaceus and Mariscus laxiflorus, as well as the grass species Pogonarthria squarrosa and Aristida meridionalis. Some other very little damaged species were Anthospermum ericoideum, Cassia biensis and Polygala kalaxariensis. In some species such as Cyperus margaritaceus, Andropogon gayanus, Cenchrus ciliaris, Aristida congesta and Aristida stipitata, care had to be taken not to confuse scorching of leaf tips in December or March with insect damage.

Most insect damage to leaves took place in the early summer or over the whole summer. Main damage to species such as Turbina oblongata, Commelina africana and Securidaca longepedunculata occurred from November to March. Damage to most tree species started earlier: Combretum psidioides and Combretum collinum leaves became increasingly damaged in November while main damage to Terminalia sericea occurred in December. Severe damage to leaflets of some Burkea africana individuals by Crina forda occurred in December and extended into January, with one isolated occurrence in March. Ochna pulchra leaves were already partially eaten in the previous year, and no pronounced increase in damage to these leaves occurred during the study year. However, as soon as the new flush of leaves appeared in May, many leaves were severely damaged in the same month. Species with damage occurring soonest after appearance of the new leaves, were Ochna pulchra, Combretum psidioides and to a lesser degree Terminalia sericea.

In all species, the leaf margin was more damaged than the rest of the lamina. Grass species and species of Cyperaceae, had almost no damage on the lamina. However, in

species such as Combretum collinum, Lonchocarpus nelsii and Grewia avellana, which were relatively broadleaved species, damage on the central parts of the lamina was almost as severe as on the margin, and leaves were clearly perforated.

Some individuals of Terminalia sericea had a type of leaf curl present in summer while in some leaves of many individuals of Securidaca longepedunculata, localised translucent areas became apparent in late summer.

The generative structures of only a few of the grass species appeared to be attacked by insects. This was most clearly seen in some individuals of Andropogon gayanus where much inflorescence development was arrested by insect damage, mainly in February but also in March. This occurred to a much lesser extent in Aristida stipitata, Aristida congesta and Andropogon schirensis in February. Some fruits of some species, for example, Combretum psidioides, were rendered infertile by infestation with pupae.

Fig. 6.1 (on following page) Standardized views, taken from 1,65 m height above ground, of part of the study vegetation: the upper is just before new growth in spring (11.00 hrs, 25.10.1970) and the lower is at the time of maximum biomass of the herbaceous layer in autumn (11,40 hrs, 20.4.1971). Visible are Combretum psidioides at near left, Terminalia sericea at middle back, Burkea africana at upper right, Grewia avellana in middle foreground, and the tall grass in autumn is Andropogon gayanus. Part of a dead and fallen Burkea africana is visible in the foreground.



Fig. 6.1

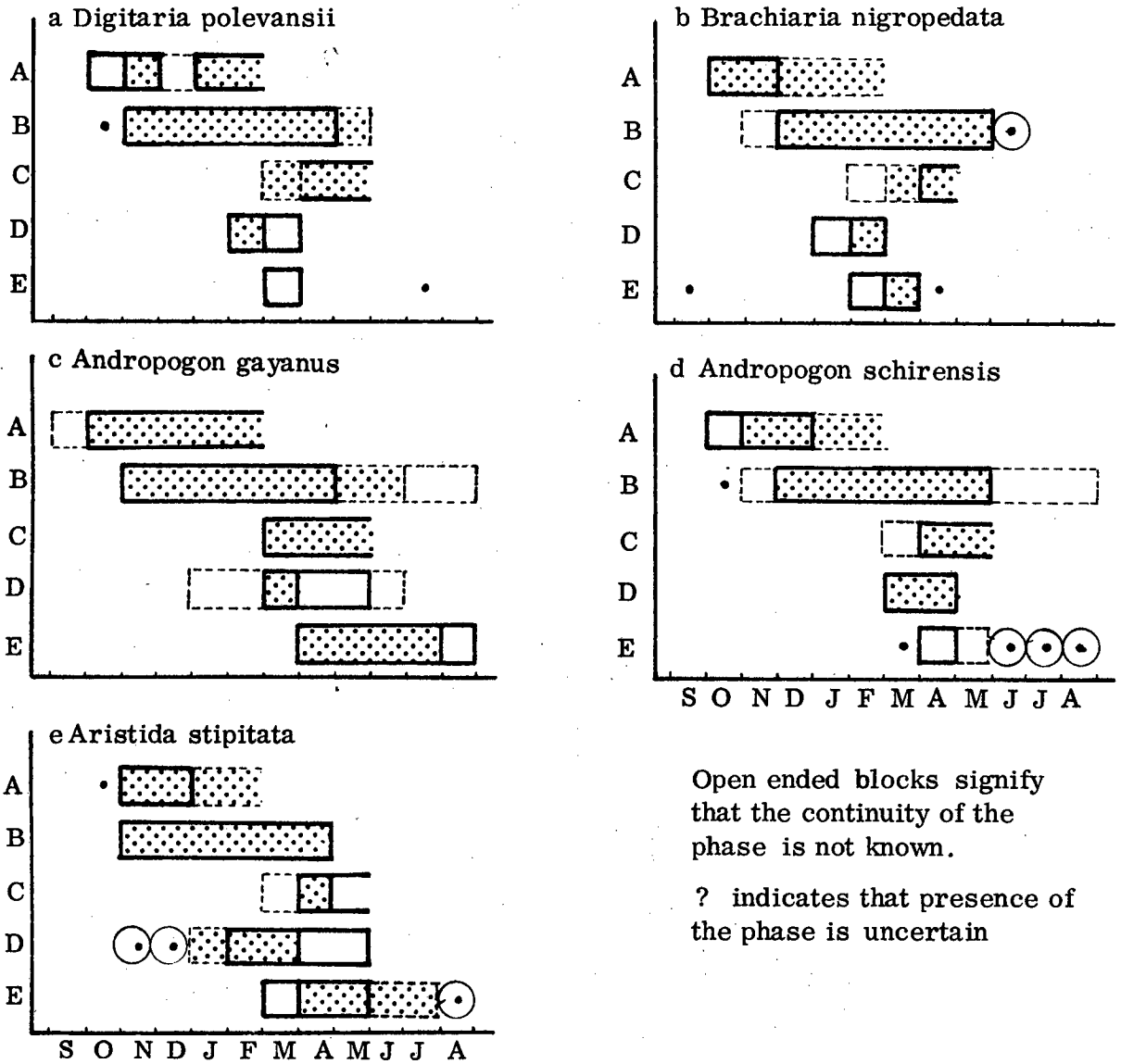


Fig. 6.2 Phenological phases of dominant grass species

- | | | | |
|----------------|---------------------------------------|--|---------------------------|
| A | Initiation of vegetative growth phase | | Frequently distinct |
| B | Adult green leaf phase | | Locally distinct |
| C | Initiation of die-off of leaves | | Frequently slight |
| C ₁ | Period of dead leaves on plant | | Locally slight |
| D | Flowering phase | | Few records in population |
| E | Fruit phase | | One record in population |
| X - Axis: | Months | | Y - Axis: Phases |

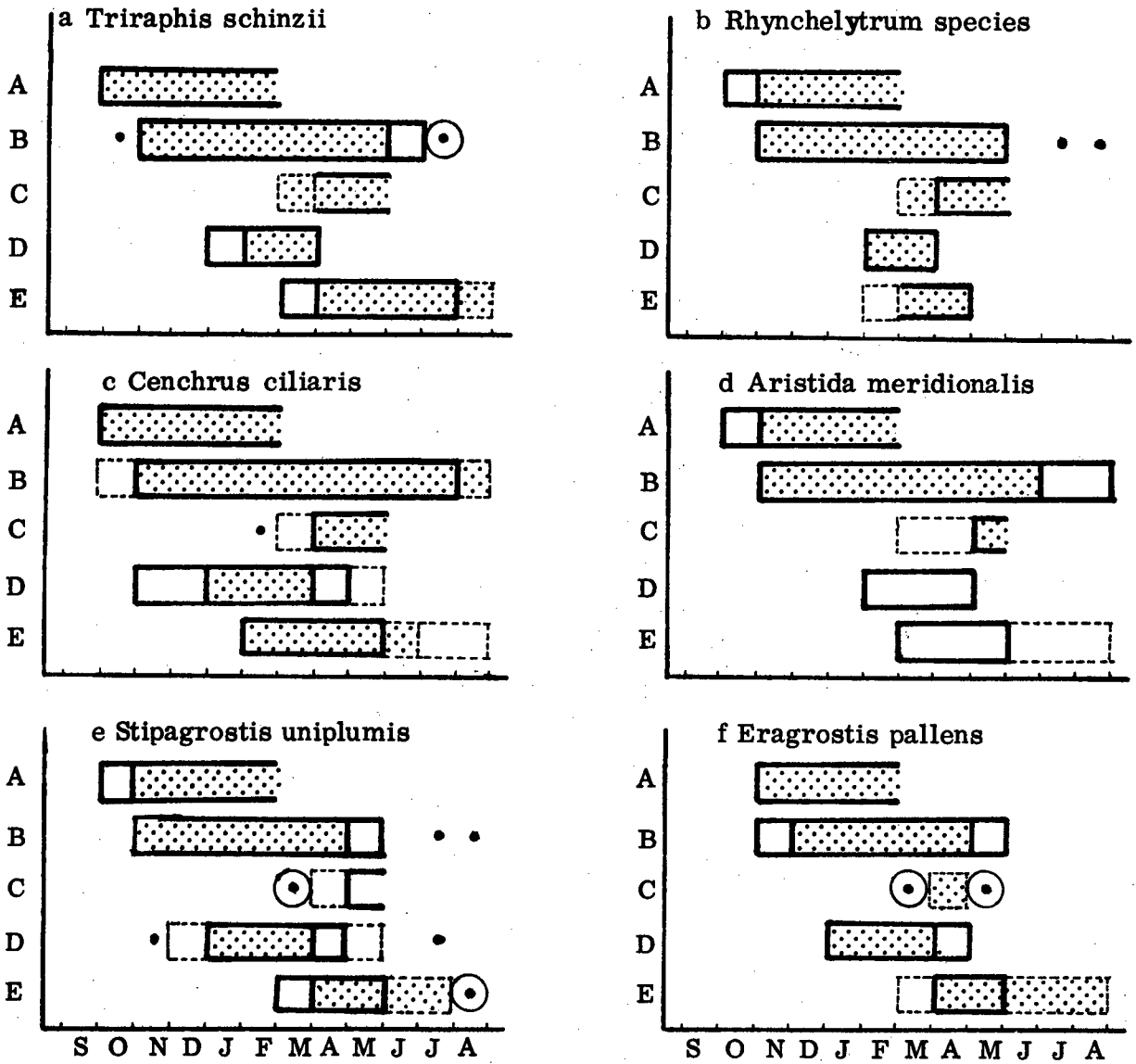


Fig. 6.3 Phenological phases of common grass species

(Legend as in Fig. 6.2)

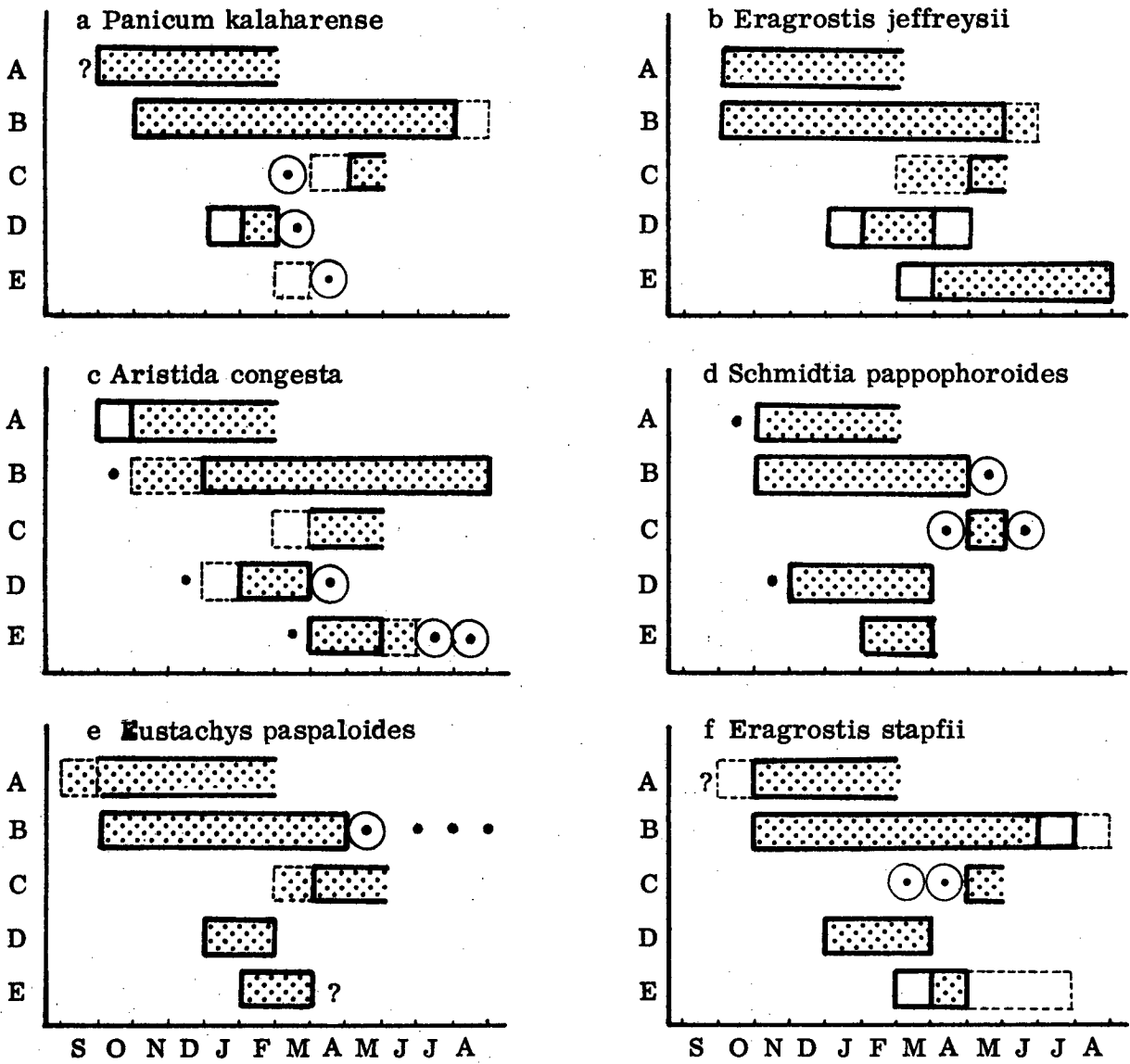


Fig. 6.4 Phenological phases of minor grass species

(Legend as in Fig. 6.2)

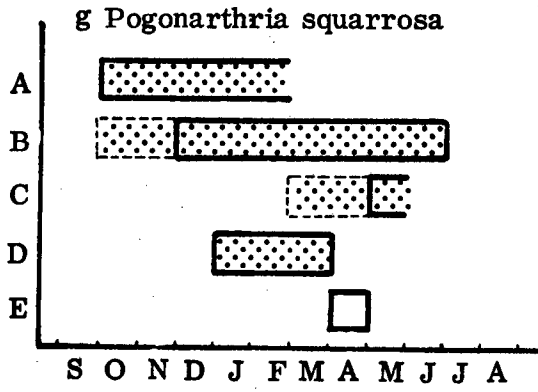


Fig. 6.4 (continued) Phenological phases of minor grass species

(Legend as in Fig. 6.2)

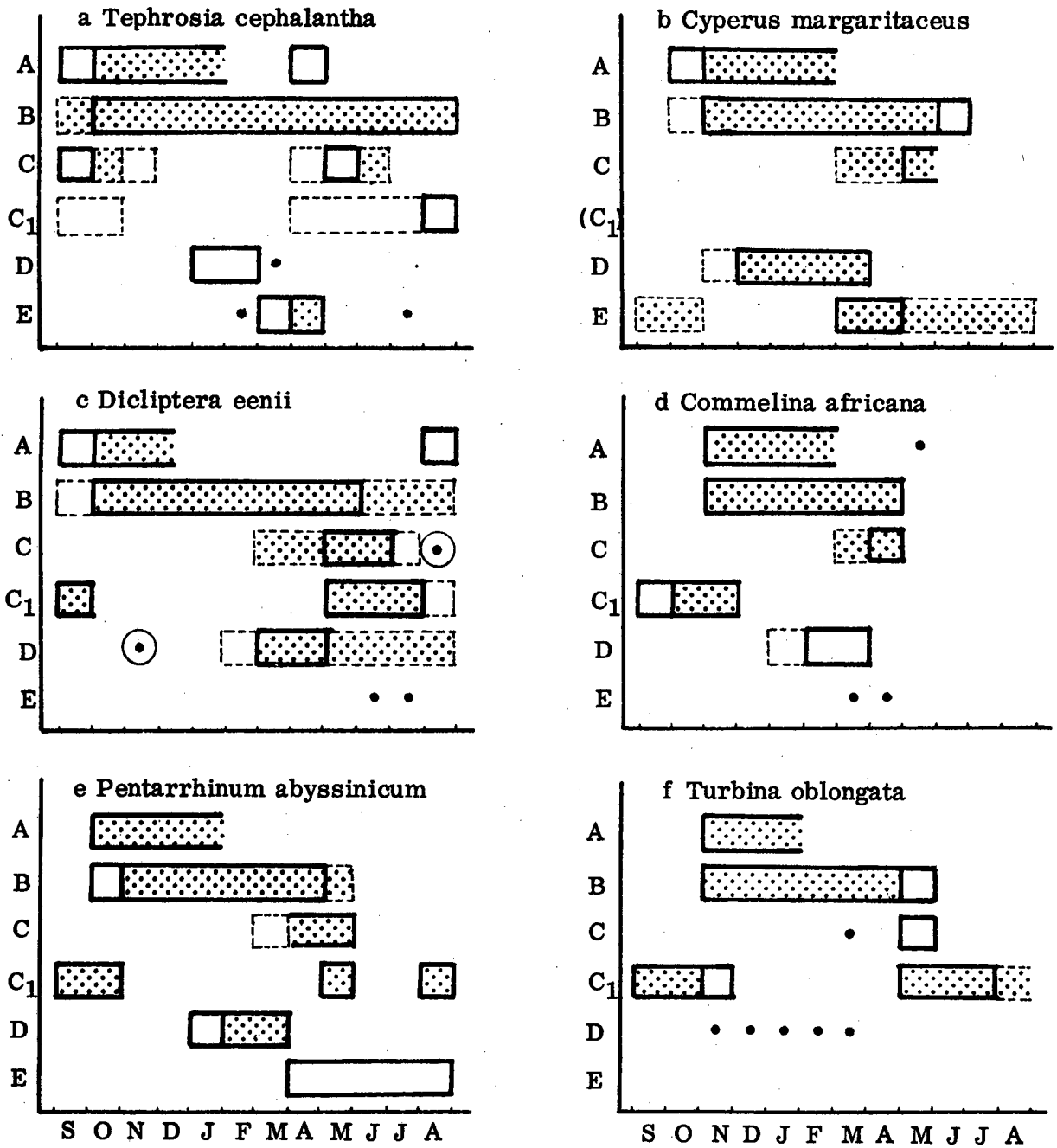


Fig. 6.5 Phenological phases of ground layer species (excepting grass species)

(Legend as in Fig. 6.2)

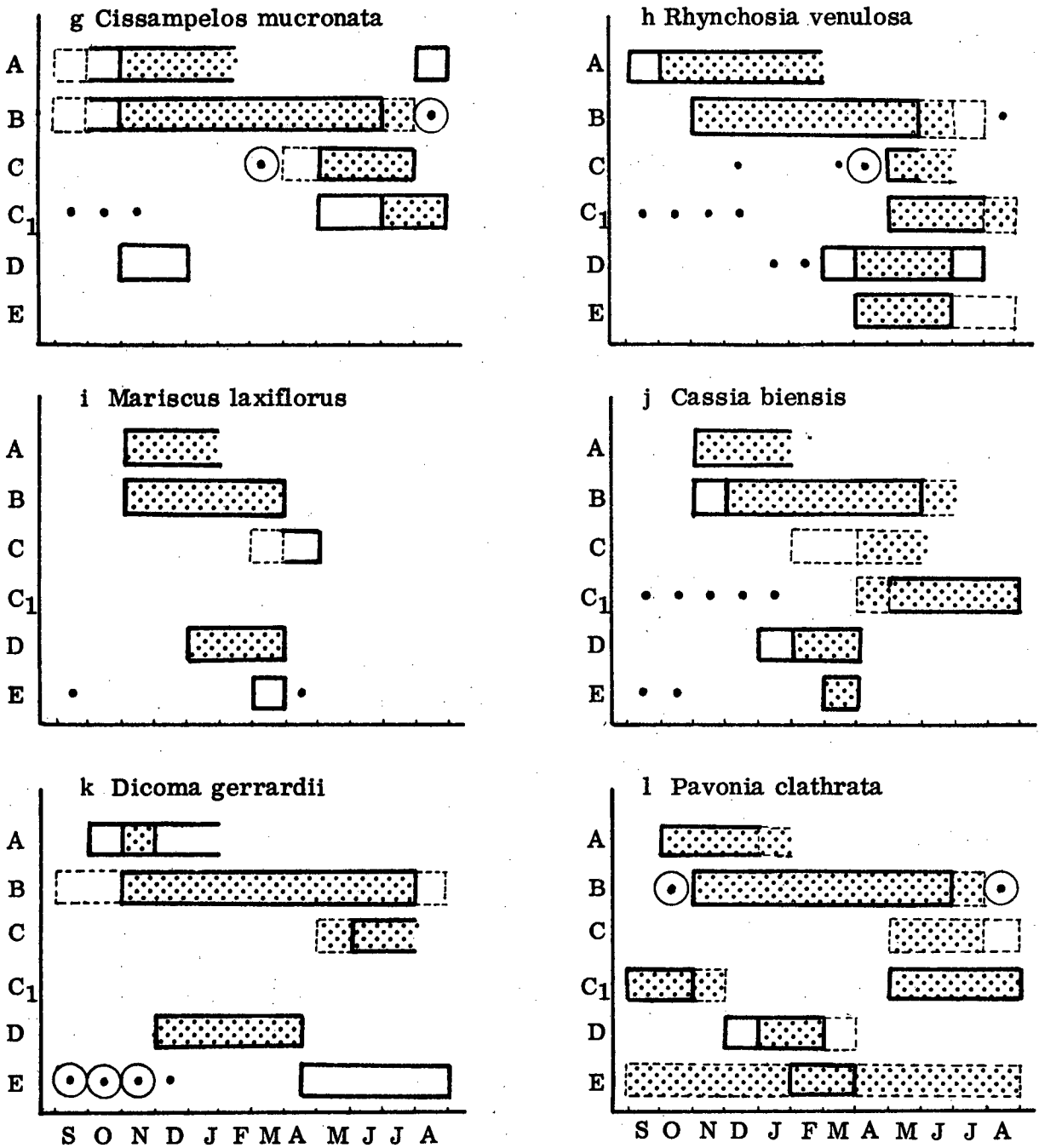


Fig. 6.5 (continued) Phenological phases of ground layer species (excepting grass species)

(Legend as in Fig. 6.2)

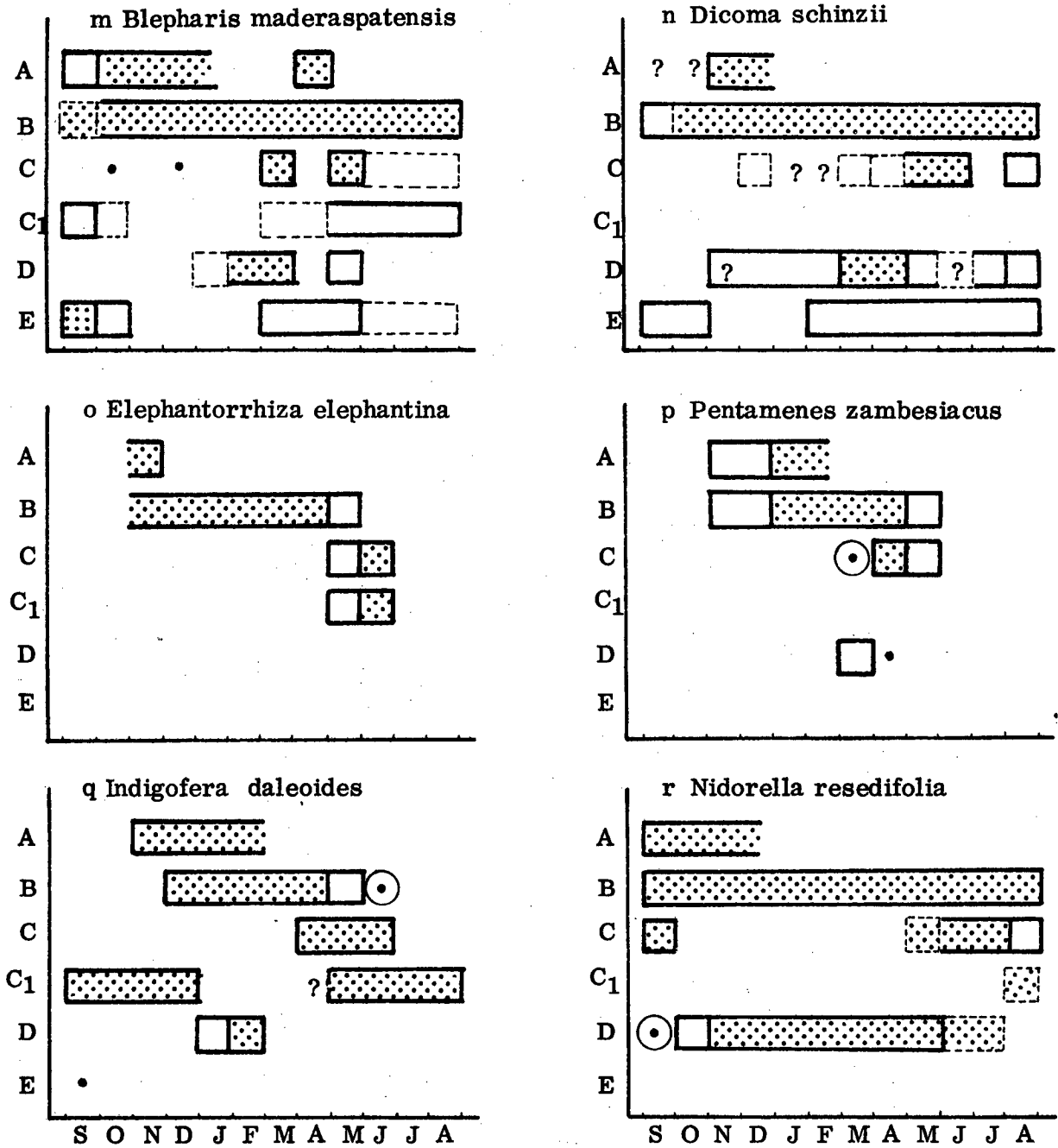


Fig. 6.5 (continued) Phenological phases of ground layer species (excepting grass species)

(Legend as in Fig. 6.2)

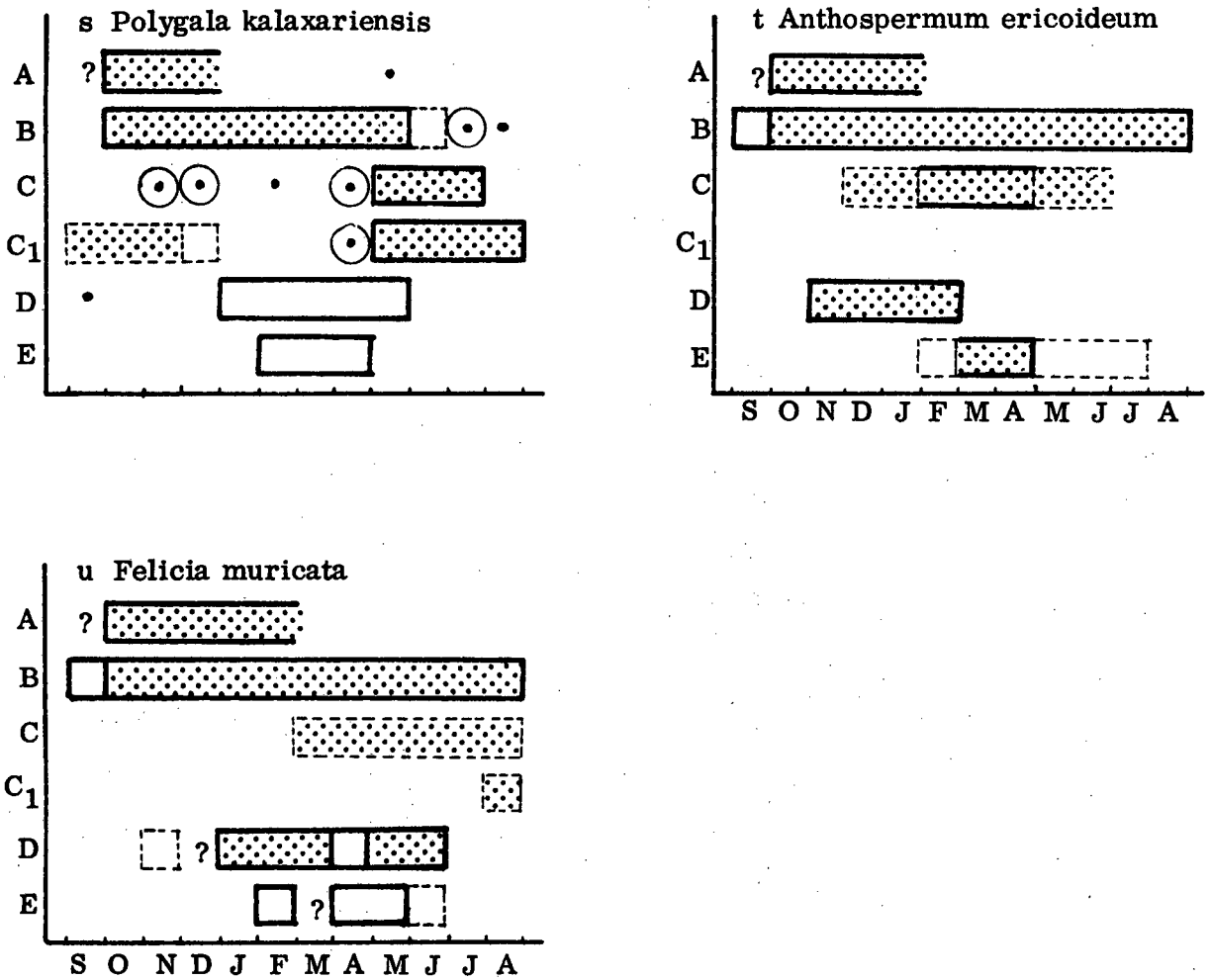


Fig. 6.5 (continued) Phenological phases of ground layer species (excepting grass species)

(Legend as in Fig. 6.2)

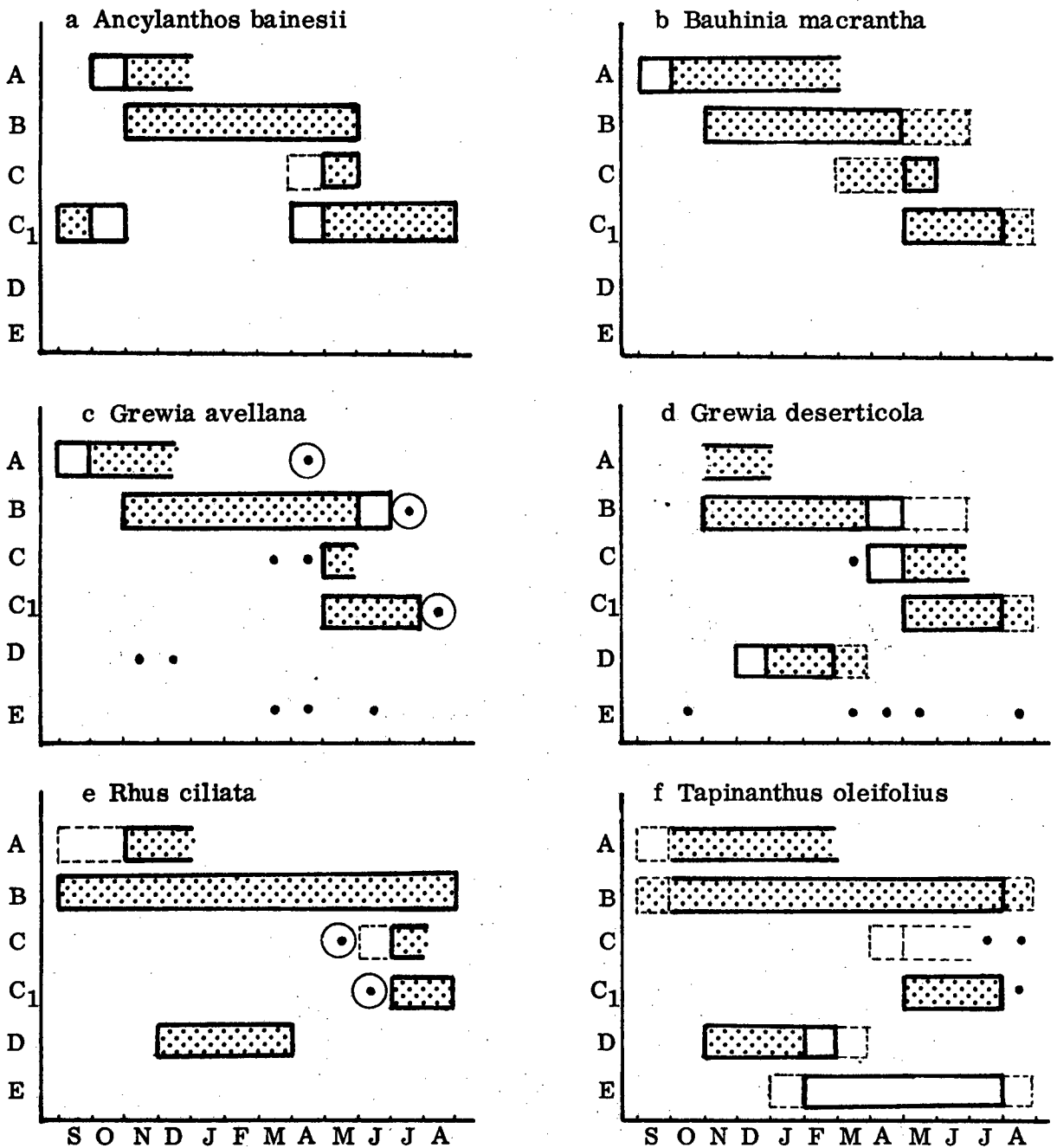


Fig. 6.6 Phenological phases of shrub species (alphabetical)

(Legend as in Fig. 6.2)

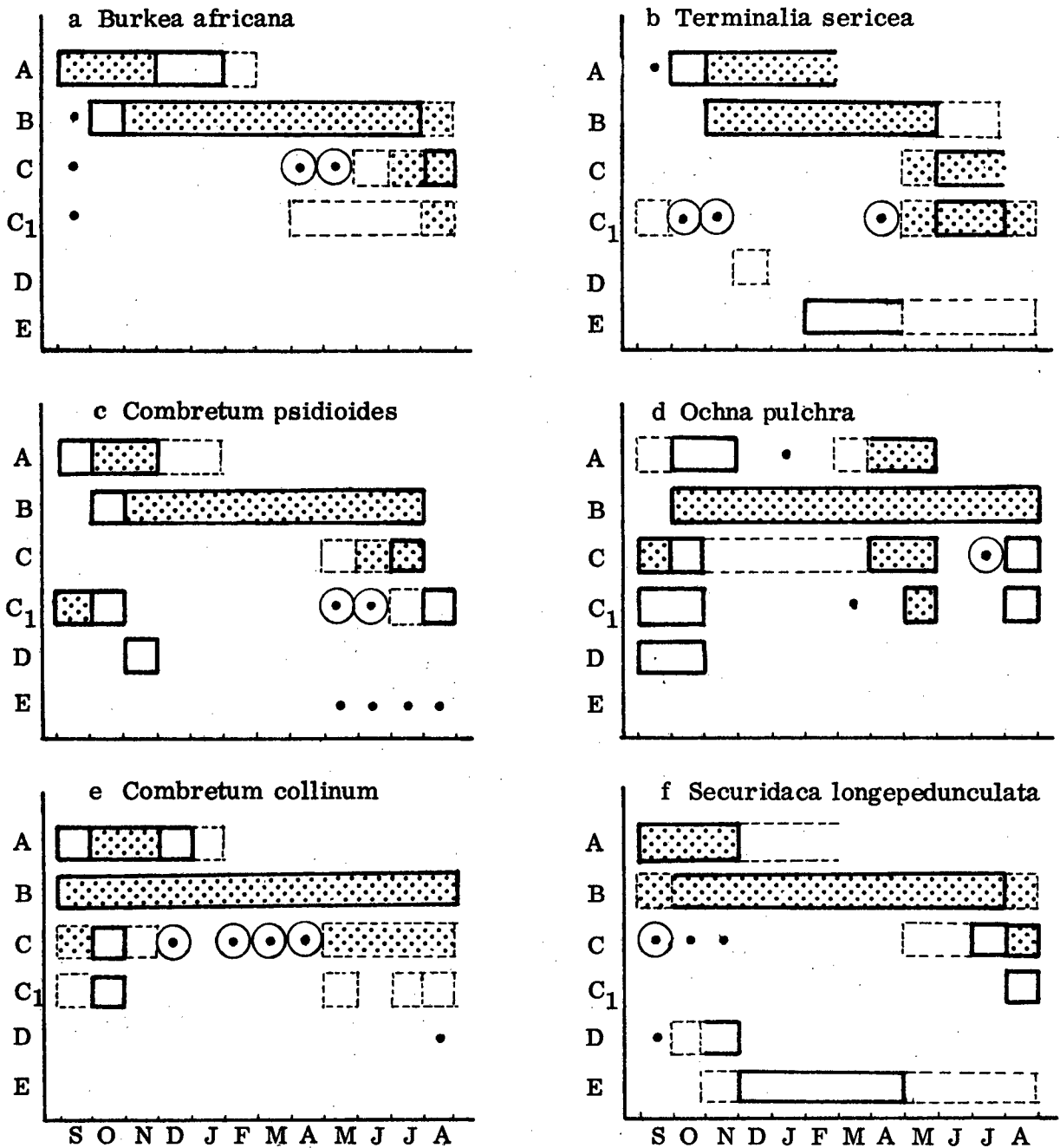


Fig. 6.7 Phenological phases of tree species

(Legend as in Fig. 6.2)

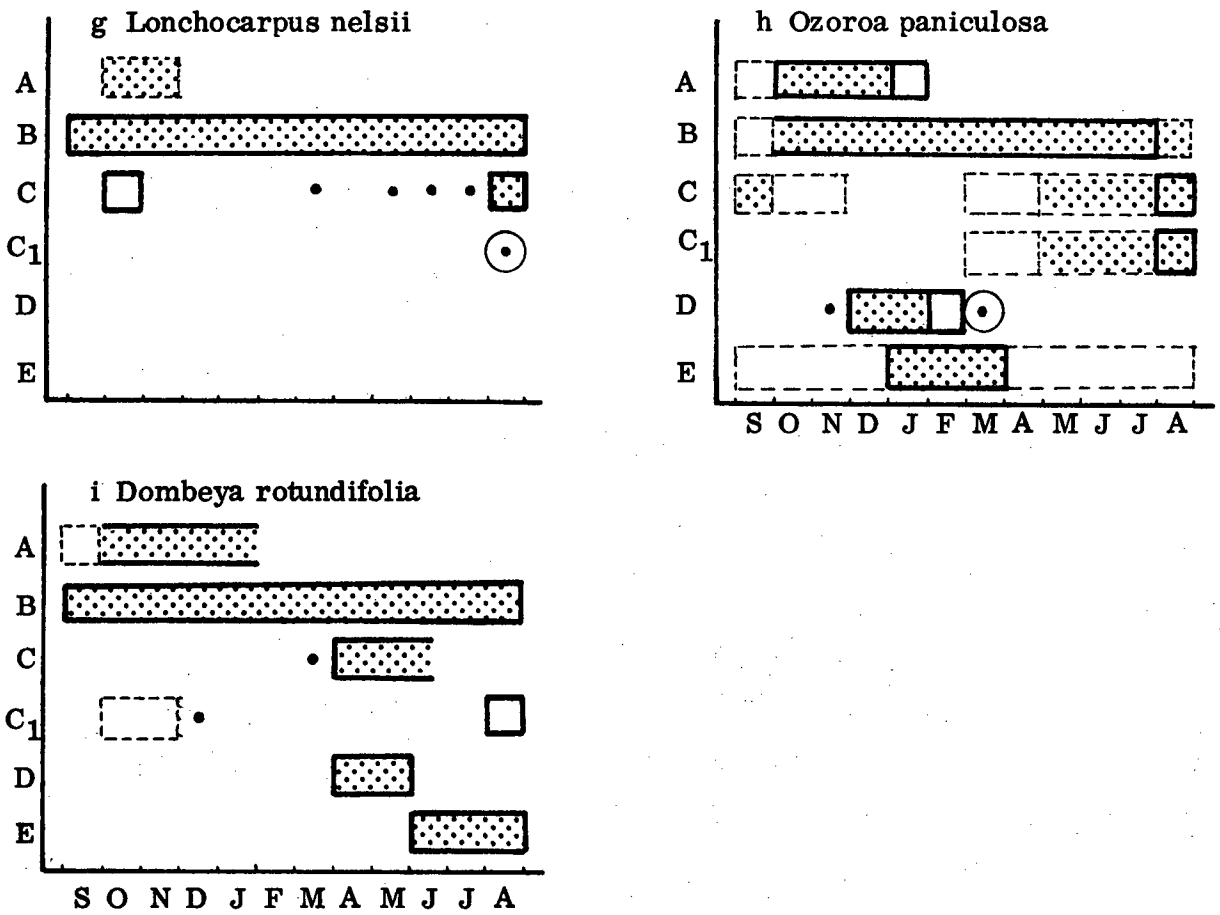
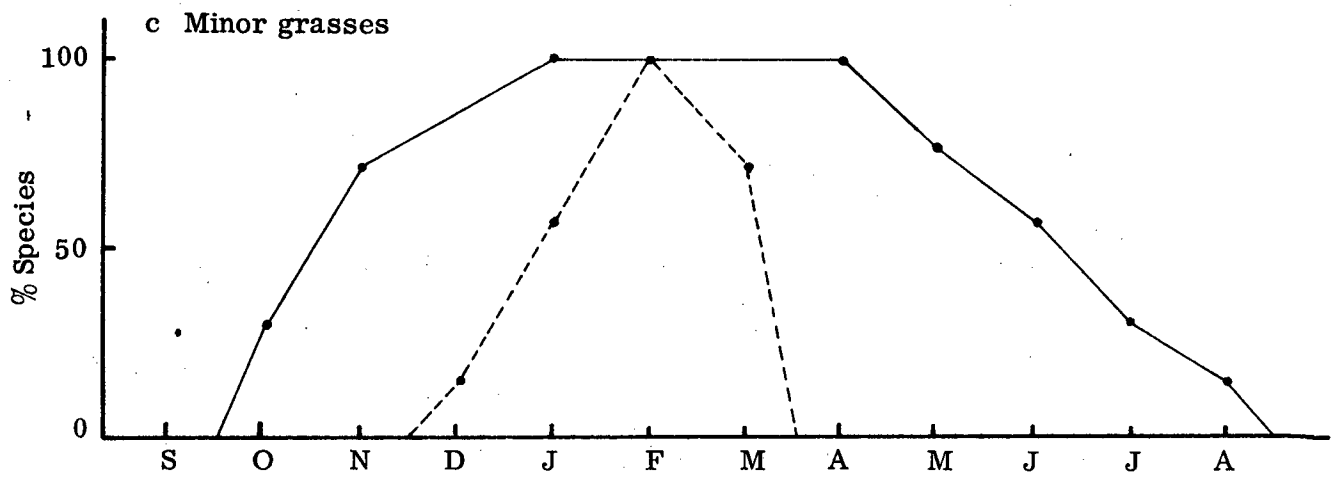
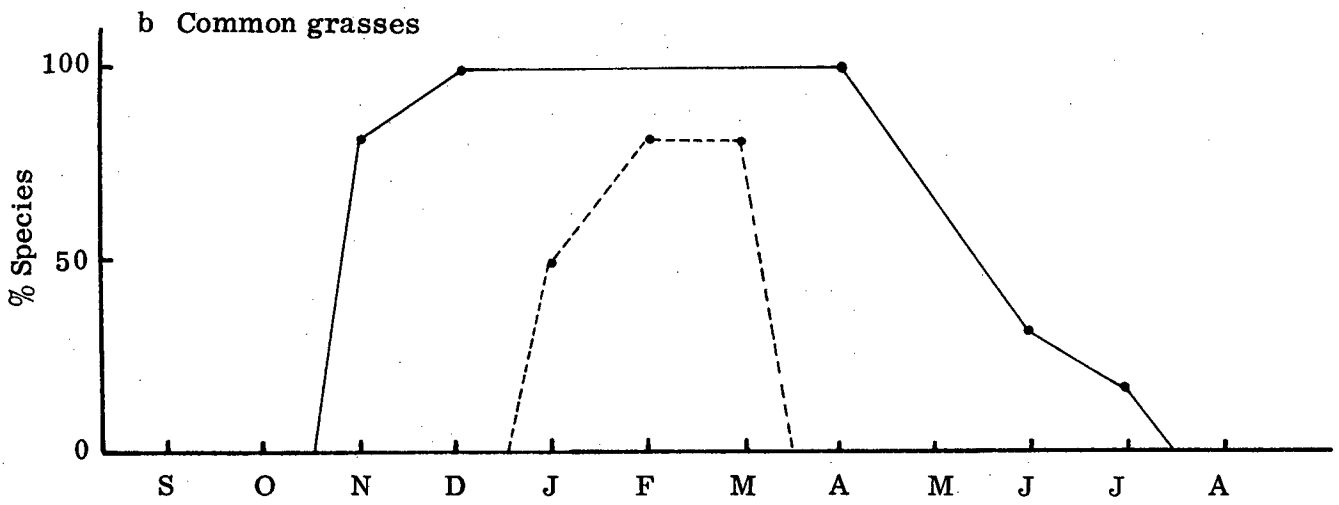
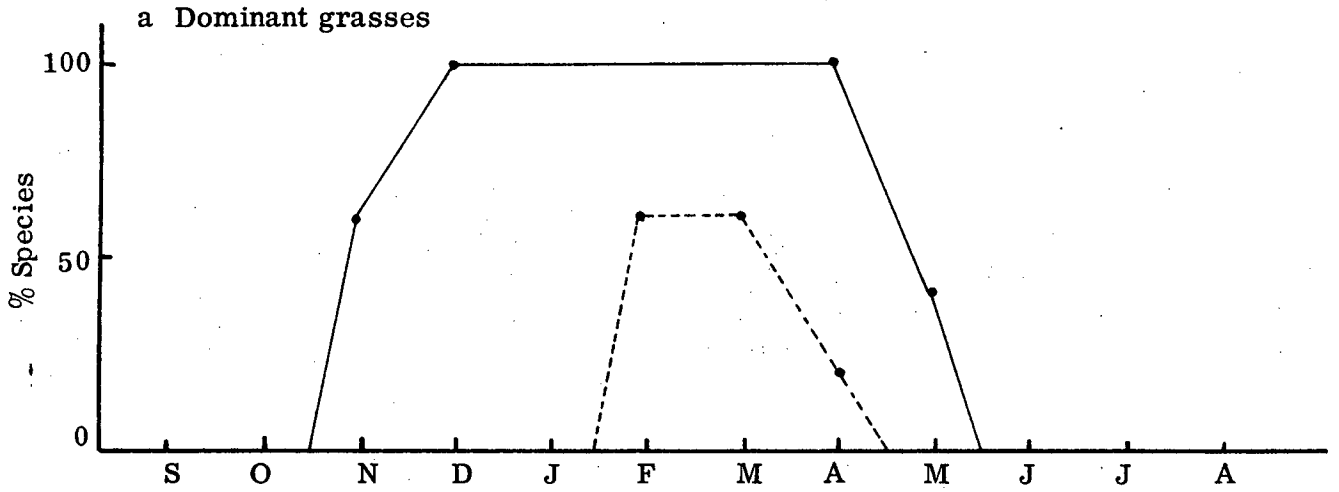


Fig. 6.7 (continued) Phenological phases of tree species

(Legend as in Fig. 6.2)



— Adult green leaf phase (frequently distinct level)
 - - - Flowering phase (frequently distinct level)

Fig. 6.8 Percentage of species in main phenological phases for various species groups in the study area during 1970-71

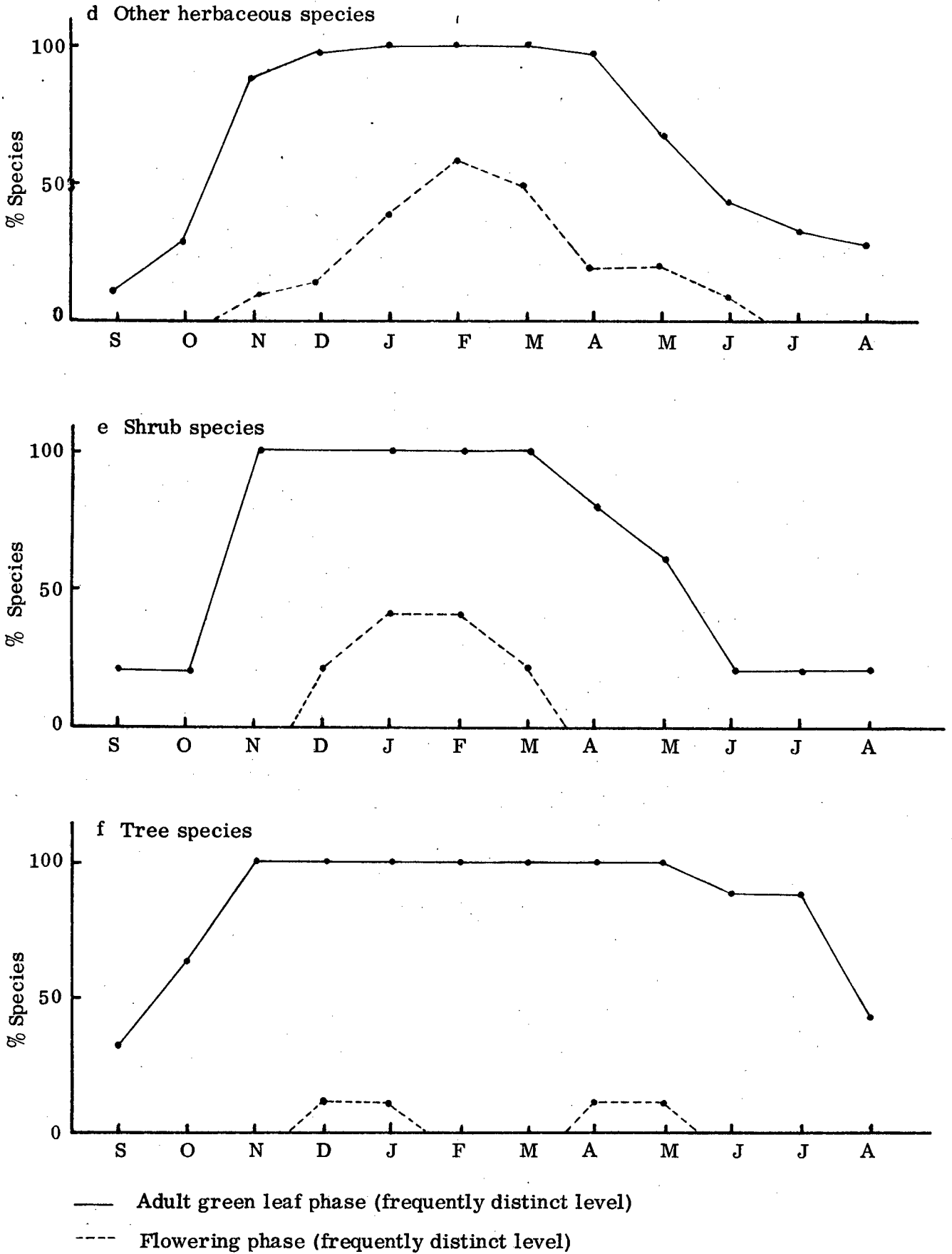


Fig. 6.8 (continued) Percentage of species in main phenological phases for various species groups in the study area during 1970 - 71

7 FIRE

7.1 Introduction

Throughout the study in 1970 and 1971, various effects of the fire that occurred in November, 1969, were noted. The study thus provided a good opportunity to record some phenomena such as regeneration, mortality and vegetation dynamics after fire.

Due to the effective fire-break provided by the encircling cliffs, fires on the Omuverume Plateau have probably only been started by lightning at intervals of several years. The 1969 fire was probably a relatively hot fire, since:

(i) there was accumulation of dead material due to lack of grazing by larger mammals; (ii) the fire occurred at the end of a long, almost rainless period when the vegetation was at its driest and (iii) there was present in the litter layer, some highly inflammable leaves of, for example, Burkea africana. Although it is likely that many of the tree species were already in leaf at the time of the fire, burning occurred early enough to be not too damaging, especially to the herbaceous layer, and new growth of all species could take place in the same season.

Most of the results pertaining to fire were obtained from observations made while studying other aspects of the vegetation.

7.2 Results of fire

7.2.1 General effects

Burning of leaf litter, herbaceous layer (with above-average biomass) and tree leaves, probably resulted in an accelerated addition and availability of nutrients to the soil. Since the study area was level and the soil had a good internal drainage, no erosion - usually associated with fire - occurred. Temperatures were probably relatively higher in the 1969 - 70 growth season, especially in newly bared and unshaded areas; the below-average rainfall of the season, probably also contributed to

bringing about higher temperatures. The low number of animals seen in the study year, was probably due to destruction of smaller above-ground animals by the fire and the retarding of recolonisation by removal of protective cover and loss of essential food.

The fire helped to maintain the predominantly 2-layered savanna stratification of the vegetation by suppressing shrubs. Fire is widely used in savanna vegetation to maintain grass dominance in the lower layer (Cook, 1939). Basal cover of the herbaceous layer apparently decreased after the fire, due to death of all or parts of individuals of, for example in the latter case, Brachiaria nigropedata and Triraphis schinzii. This partial baring of the soil surface allowed some change in vegetation dynamics to take place.

The productivity of the herbaceous layer was probably increased after the fire. Apart from direct stimulation by the heat of the fire (Daubenmire, 1968b), removal of superfluous material from old ungrazed, smothered and moribund individuals, which were observed in unburned and protected sandy pockets of the rocky perimeter belt of the plateau, often stimulates new growth (Anderson, 1964). Thus the biomass change of 500 kg/ha in the herbaceous layer from beginning to end of the study year was probably relatively high, not only because of the above-average rainfall, but also the removal of accumulated dead material.

Only in the third season after the fire, did all the main tree species return to a pattern of adequate flower production. In the first season (judging by fruit production), only Ozoroa paniculosa flowered. In the second season (the study year), only Ozoroa paniculosa and a few individuals of Securidaca longepedunculata, Terminalia sericea, Ochna pulchra and Combretum psidioides flowered. Combretum collinum and Burkea africana only flowered in the third season, and here flowering was prolific.

7.2.2 Regeneration and mortality after fire

Although the temperature of burning tussocks can exceed 600°C, temperatures at

lower levels rise relatively little (Cook, 1965) and the duration of maximum temperature is so brief in African grasslands, that the effect on the soil would appear negligible (Daubenmire, 1968b). The highest temperatures are often so elevated above ground level that short unburned stubble remains after the fire has passed and, in consequence, shallowly placed buds and seeds escape damage (Daubenmire, 1968). Unburned stubble was often observed in the study area, especially in species such as Brachiaria nigropedata, Andropogon gayanus and Panicum kalaharensis. Since the bottom parts and roots of plants are subjected to relatively little heat during a fire, it is not unexpected that most burned plants can regenerate from the base, afterwards.

A common property of the growth form of some species was the presence of underground parts connecting several adjacent apparent individuals to one another. This was probably due to successive modification of the individual by past fires and not only to the effect of the last fire. Difficulties in determining the density of individuals in some species were due to this underground connecting of apparent individuals. Apparent individuals of Combretum collinum were often connected underground to adjacent ones on the same mound and often formed a thicket on the mounds due to fire induced basal shoots. This effect has been observed in several woody species, after fires, in the Kruger National Park (Brynard, 1965). Underground connecting parts were also often encountered in the shrub species Grewia avellana (Fig. 4.2) and Ancylanthos bainesii. In some individuals of the dominant tree species of the study area, the probable long-term effect of fire was seen in the formation of a few double or triple-stemmed individuals, for example in Combretum psidioides, Terminalia sericea and Burkea africana (Fig. 4.1).

Recordings were made in the winter of 1970 of the regeneration which had occurred in the summer of 1969 - 70, soon after the fire. Mortality in species individuals that were killed by the fire itself and those that regenerated after the fire but died after one season of growth, was distinguished from each other.

7.2.2.1 Herbaceous layer

a Regeneration

Estimates of the ratio of vegetative to generative regeneration were derived from inspection of the bases of the 10 individuals of each species tagged for phenological observation.

Regeneration from the base after the fire could not always be determined with certainty in all individuals. However, all tagged individuals of the grass species appeared to have regenerated vegetatively from the base after the fire. Runners sent out from individuals of Digitaria polevansii (up to 3 m in length were measured) only appear to have occurred in the study year and not in the season immediately following the fire. Species that had only a few individuals growing from seed after the fire were: Indigofera daleoides, Cassia biensis, Rhynchosia venulosa and Cyperus margaritaceus. Species that appeared to regenerate almost exclusively from seed were Tephrosia cephalantha and Polygala kalaxariensis, as well as the 8 annual species mentioned in the section on phenology (Section 6.3.3.5). Thus, the greater part of the herbaceous layer vegetation's biomass was derived from basal vegetative regeneration after the fire and not from generative regeneration.

b Mortality

Mortality that had occurred at the time of the fire was not readily determinable, but mortality that occurred after one season's growth after regeneration, was estimated using monthly density counts (concurrent with the production measures of 1970 and 1971) in which live individuals were counted separately from dead individuals. It was not always possible to distinguish dormant individuals from dead individuals in the period September to January, since late resumption of growth after dormancy still occurred in this period. It was thus not possible to obtain a reliable indication of mortality from density data of this period. Confusion of old dead with recently dead individuals, as well as the loss of old dead individuals by weathering in the period April to August, rendered density data of this period unsuitable for the determination

of mortality. The mortality figures given were thus derived from the counts made in February and March, although some addition of new season's seedlings result in an underestimate of the percentage plants that had died in the previous season. To maintain a sample of adequate size for the mortality estimates only species with more than 80 individuals counted in this period, were included.

Five species had at least the following percentages of dead individuals: Andropogon schirensis, 21,0%; Aristida meridionalis, 14,3%; Rhynchelytrum species, 12,3%; Aristida stipitata, 5,9% and Digitaria polevansii, 0,6%. Of all the species in the sample, only 2 other species (Ochna pulchra and Polygala kalaxariensis) showed slight mortality in the season following regeneration. This extremely low number of species with any mortality appears to indicate, either that very few annual forms grew in the season after the fire, or that these had virtually all disappeared just before the study season and sample period. Of the 5 above-mentioned species with definite mortality after one season following regeneration, only Andropogon schirensis showed some decrease in density of individuals over the study season.

7.2.2.2 Tree layer

a Regeneration

It was evident that most tree individuals regenerated vegetatively, while, with the exception of Ochna pulchra and Combretum psidioides, very few had grown from seed. In the section on growth forms of trees (Section 4.3.2), several growth forms were defined according to their regeneration shoots, because of the commonness of this phenomenon in the vegetation under study. The different regeneration types were summarised in the table on growth forms (Table 4.5). The data in Table 4.5 was then rearranged to summarise regeneration from the base and in the canopy of trees (Tables 7.1; 7.2).

i Basal

Table 7.1 gives, in 2 tree height classes, the basal regeneration of individuals with

canopies (canopied) and those which had the upper parts killed (non-canopied). Individuals above 2 m are called tall, while those below 2 m are called small. The number of individuals which regenerated from the base is expressed as a percentage of the total number of individuals of each of the 4 resulting groups.

It was not possible to determine exactly how many small non-canopied individuals had regenerated from the base, since seedlings could be confused with small non-canopied individuals with basal regeneration but with their dead material broken off and missing. Therefore, 2 alternatives were possible: (i) the inclusion of all doubtful individuals as small basal regenerative individuals, or, (ii) their exclusion. In the 4th column of Table 7.1 their inclusion is given as the upper limit and their exclusion as the lower limit of the percentage basal regeneration. In the 4 species Combretum collinum, Securidaca longepedunculata, Lonchocarpus nelsii and Ozoroa paniculosa, no seedling-like individuals were seen and consequently only one figure is given.

For both tall and small canopied individuals, the highest percentage (44,0 and 60,8% respectively) of basal regeneration in a more common tree species was found in Combretum psidioides. Terminalia sericea also had a relatively high percentage (40,8 and 47,4% respectively). High percentages (42,9 and 71,4%) of basal regeneration were also found for the few canopied Securidaca longepedunculata individuals. The relatively low percentages (28,6 and 26,3%) of the canopied Combretum collinum individuals do not necessarily indicate a low basal regenerative capacity in canopied individuals of this species, since many of the "individuals" themselves, are regenerative shoots from previous fires. The lowest percentages of basal regeneration in canopied individuals were found in the dominant tree species, Burkea africana (7,8 and 20,0%) and in the few canopied Ochna pulchra individuals (6,7 and 17,9%).

All non-canopied individuals (both tall and small) of Combretum collinum regenerated from the base. All the non-canopied individuals of Securidaca longepedunculata, Lonchocarpus nelsii and Ozoroa paniculosa were small and regenerated from the base. Almost all non-canopied individuals (tall and small) of Combretum psidioides regenerated from the base while almost all small non-canopied individuals of Burkea

africana, Terminalia sericea and Ochna pulchra regenerated from the base. Basal regeneration for the tall non-canopied individuals was only 79,3% for Terminalia sericea, 44,4% for Ochna pulchra and 31,0% for Burkea africana.

ii Canopy

Since it could only be established with reasonable certainty that the fire had burned all parts of each individual under 2 m in height, only in these small individuals could a real estimate be made of canopy regeneration after the fire. For the same reasons of uncertainty in seedling identification given in the previous section on basal regeneration of this group, canopy regeneration is given as a range of percentages.

It will be seen from Table 7.2 that all small individuals of the 6 main tree species had relatively low percentages of canopy regeneration, with the exception of Combretum collinum (48,7%). Ochna pulchra had the lowest percentage (8,8 to 12,0%) while Combretum psidioides had the highest (21,4 to 23,0%).

Although perhaps an overestimate of canopy regeneration, since it is possible that not all canopies of the tallest trees were burned by the fire, the percentage of tall individuals with canopies is also given for rough comparison in Table 7.2. Possible canopy regeneration of tall individuals was higher than 80% for Burkea africana, Combretum psidioides and Terminalia sericea. All tall individuals of Securidaca longepedunculata were canopied. Canopies were found on 72,4% of the tall individuals of Combretum collinum and on 62,5% of the tall individuals of Ochna pulchra. The fire resulted in several twigs with leaves being formed on the thicker branches of some tall individuals of Burkea africana.

b Mortality

The evidence of new litter below trees at the beginning of the study season indicated that, in contrast to species in the herbaceous layer, no mortality appeared to have occurred in tree species after one season after regeneration. Only in years prior to the fire, and at the time of burning, did mortality in trees occur.

Although some indication of mortality can be obtained from consideration of non-canopied individuals that had no basal regeneration, that is, of individuals with no regeneration, information of mortality of the whole population cannot be obtained directly from Table 7.1, where each percentage is relative to each specific column. To include information on different types of mortality in trees, dead individuals, standing and prostrate, were counted in the 2 ha area which was surveyed for determination of frequency of tree growth forms (Section 4.3.2). For convenience, dead individuals were divided into 3 classes. Dead individuals still standing were considered as probably being trees killed by the fire. Prostrate trees, which were much burned at the base and on one side of the upper portions, were considered to be trees that were dead but standing before the fire, and which were felled by the fire. Much charred, loose-lying stumps were considered as being dead and prostrate trees at the time of the fire. This latter form was rarely encountered, but some examples of it may have been entirely burned away.

Dead, standing trees, expressed as a percentage of the probable number of living trees at the time of the fire, were 6,5% of Burkea africana individuals, of which 16,7% were small (below 2 m height) and 83,3% tall (greater than 2 m in height); 2,9% of Terminalia sericea individuals, of which 33,3% were small and 66,6% tall; 2,1% of Ochna pulchra individuals, of which 81,5% were small and 18,5% tall; 1,1% of Combretum psidioides, of which 66,6% were small and 33,3% tall; 4,3% of Lonchocarpus nelsii individuals, of which all were tall, and 63,6% of Tapinanthus oleifolius individuals. Mortality in individuals of small trees was only greater than in tall trees in the species Ochna pulchra and Combretum psidioides. The high percentage of mortality for Tapinanthus oleifolius individuals appears closely connected with the fact that, of the eleven Tapinanthus individuals found in the sample, all the 7 dead individuals were found on some of the 23 tall dead trees of Burkea africana and Combretum psidioides. Mortality in Tapinanthus oleifolius after a fire may thus depend only upon the death of the host individuals. That about a quarter of all the tall dead individuals of Burkea africana and Combretum psidioides had Tapinanthus oleifolius individuals present, might have been due to the relatively greater age of these tree individuals which would have provided Tapinanthus oleifolius with an increased opportunity for colonisation.

The only dead prostrate trees in the sample, were 13 tall individuals of Burkea africana per hectare. Also taking into account the 6,5% (this includes 10 tall individuals per hectare) dead standing individuals, it is clear that Burkea africana had the greatest mortality of tall individuals before and at the time of the fire.

7.2.3 Vegetation dynamics after fire

The dominant species, Digitaria polevansii and Brachiaria nigropedata, in the herbaceous layer of the study area, are amongst the vegetational climax species on the sand of the north east of South West Africa. This, together with the relatively dense stabilised tree canopy, indicates that the vegetation had probably reached the culmination of its community development. The association of the more common species on the mounds might be of great age since the soil profile is relatively mature.

The high percentage of regeneration in the burned herbaceous species did not readily provide an opportunity for colonisation and changes recorded in seasons after the fire appeared to be localised. Although virtually no changes in floristic composition occurred, there were changes in the abundance of several species individuals.

a Changes from winter 1970 to winter 1971 (study period)

At the start of the study year, the frequency of Tephrosia cephalantha individuals was about 20% but doubled to between 40% and 50% at the end of the period (Fig. 7.1). For most of the other species a slight increase of frequency occurred, while in no species (with the possible exception of Polygala kalaxariensis) did there appear to be a decrease in frequency. In Andropogon schirensis, however, there was an apparent slight decrease in density of individuals.

b Changes from winter 1971 to winter 1972

In the year following the study year, another survey (of 100 m² size) was carried out in June to record the frequency of each species in square metre quadrats.

The frequency of a species in June, 1972 was compared with its frequency in the same period in the study season. To increase the sample size for the purpose of comparison by means of a Chi-squared test, samples were taken ranging over 2 months either side of June (that is April to August) in the study year. This increased the sample size in the study year to 500 m². The only changes in frequency that were significantly different were the following:

A decrease in Aristida meridionalis, Cassia biensis and Cyperus margaritaceus ($P \leq 0,05$); and a decrease in Aristida congesta and Fimbristylis exilis ($P \leq 0,1$). All these were significantly associated members of the Aristida congesta species association (Section 4.2.6) which is further evidence that this was a localised pioneer association which in the third season after a fire, was being disrupted. The sample size taken in 1972 was, however, too small to show a significant decrease in frequency of the rare species, Kyphocarpa angustifolia and Limeum fenestratum. In 1972, no individuals of Kyphocarpa angustifolia, and only a few individuals of Limeum fenestratum were observed, but none occurred in the sampling quadrats. The decrease of the 2 species, Kyphocarpa angustifolia and Limeum fenestratum, might have been due to a below average rainfall of the season following the study season and not due to the fire. When carrying out relatively short term studies vegetation dynamics after a disturbing influence, such as that of fire, in an area with a fairly erratic annual rainfall, it is difficult to distinguish the effect of the disturbance from that of an abnormal rainfall pattern.

Although no significant increases occurred, it was clear that the frequency of species, such as Digitaria polevansii and Andropogon gayanus did not decrease. Virtually no change in frequency was found in Tephrosia cephalantha and Andropogon schirensis.

Table 7.1 Percentage (relative to total number of individuals for a particular species in a specific column) basal regeneration in canopied, non-canopied individuals, above and below 2 m height for each tree species. Canopied and non-canopied individuals as well as the figure ranges in the 4th column are explained on pages 213 - 214.

Species	Canopied individuals		Non-canopied individuals	
	Tall (>2m)	Small (< 2 m)	Tall (>2m)	Small (< 2 m)
<i>Burkea africana</i>	7,8	20,0	31,0	82,4-95,5
<i>Terminalia sericea</i>	40,8	47,4	79,3	96,9-97,2
<i>Combretum psidioides</i>	44,0	60,8	94,9	97,7-97,9
<i>Ochna pulchra</i>	6,7	17,9	44,4	97,9-98,1
<i>Combretum collinum</i>	28,6	26,3	100,0	100
<i>Securidaca longepedunculata</i>	42,9	71,4	-	100
<i>Lonchocarpus nelsii</i>	23,1	-	-	100
<i>Ozoroa paniculosa</i>	-	-	-	100

Table 7.2 Percentage (relative to total number of individuals for a particular species in a specific column) tree species individuals with live canopies which relates to regeneration subject to conditions on page 215.

Species	Small individuals (<2 m)	Tall individuals (>2 m)
<i>Burkea africana</i>	10,1 - 23,8	89,3
<i>Terminalia sericea</i>	14,8 - 16,4	84,4
<i>Combretum psidioides</i>	21,4 - 23,0	87,4
<i>Ochna pulchra</i>	8,8 - 12,0	62,5
<i>Combretum collinum</i>	48,7	72,4
<i>Securidaca longepedunculata</i>	10,9	100,0

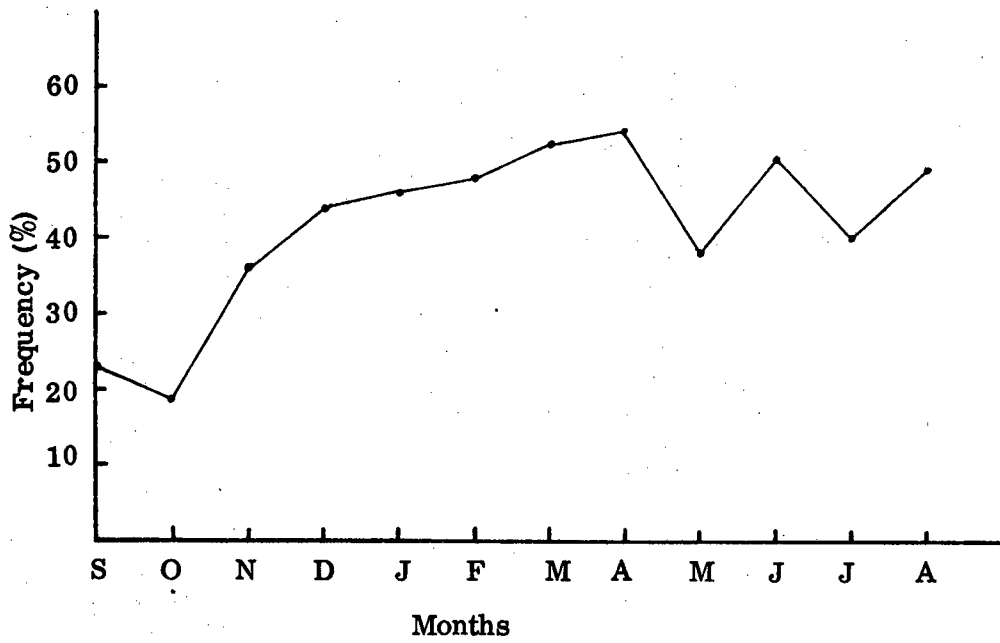


Fig. 7.1 Changes in frequency of Tephrosia cephalantha over the study year

8 VEGETATION UTILIZATION

The vegetation of the area studied is a variation of the large vegetation type of the north-eastern sector of South West Africa. The correct use of such a large area is of prime importance. The rainfall over much of the area is too low for dry land crops but is suitable for cattle ranching, which is wholly dependent upon natural vegetation. Various facets of importance in using the vegetation are its nutritive value and its reaction to removal of upper parts of plants. Comparisons of grazed areas and adjacent ungrazed areas also show in which direction vegetation dynamics move under stress. Some of these aspects are discussed in relation to information from previous sections.

8.1 Nutritive value of the vegetation

The vegetation of the study area is a "sourish bushveld" type owing to unpalatability of many grasses in winter. The dominant palatable grasses are Brachiaria nigropedata, Digitaria plevansii and, in the green state, the two Andropogon species. Aristida stipitata is unpalatable. Although most of the vegetation is probably in a climax state, the productivity of the herbaceous layer, even with the stimulus of the fire, is probably below that of several judiciously grazed grassland areas with lower rainfall. However, the above-mentioned palatable grass species are dominant in this layer and the layer only forms a minor part of the vegetation (including trees) of the study area.

In Section 5.3 main reference was made to analyses of plant material for phosphorus and calcium content. Other determinations of direct importance to utilization included protein, fibre and fat. Results of each determination are found in Appendix 3.

The quantities of phosphorus, and especially calcium (Section 5.3), in the vegetation are, according to Du Toit et al. (1940), adequate for cattle grazing purposes, although phosphorus content becomes deficient in the winter months. The important nutritive component, protein content, is highest in new growth (for example, more than 20% of new material in Brachiaria nigropedata in October), but falls rapidly as the season progresses (Fig. 8.1). A table summarising the differences in protein content in the new material of January, February and March, and that in the material in the winter months of June, July and August, is given for the 5 dominant grass species, 5 tree species' leaves and one shrub species.

	Average % protein in 2 different seasons for 3 plant groups	
	Summer new material Jan. - March	Winter total material June - Aug.
Grasses	6,9 (5,0 - 7,9)	2,9 (2,3 - 3,5)
Shrub (<u>Grewia avellana</u>)	15,3	5,6
Trees (leaves)	13,8 (10,5 - 16,7)	8,8 (6,8 - 12,6)

It is seen that in each group there is a decided decrease in protein content from summer to winter. The woody species, especially the leaves of the tree species, have a relatively high protein content in both seasons. From other analyses it appeared that the tree species usually had a higher nutritive value than the grass species, not only in respect of phosphorus, calcium and protein, but also in respect of fat. The leaves of the dominant tree species had an average fat content of 2 - 4% in comparison with 1,5 - 2,5% in the dominant grass species. Ochna pulchra and Aristida stipitata both had a lower average fat content (0,5 - 1,5%) than the above. The leaves of the tree species (with the exception of Ochna) also had a lower average fibre content (20 - 30%) compared to that of the dominant grass species and Ochna (30 - 40%). There appeared to be no great seasonal variation in fibre or fat content in the materials of the species analysed.

The general decrease in, for example, protein and phosphorus content, as the season progressed, as well as the increased unpalatability of grasses, such as Andropogon gayanus in winter, are reasons why this vegetation is sometimes referred to as "sourish bushveld". Although tree leaves have a higher average nutritive value in the study area, the majority of leaves are so distributed (see Section 4.3.4) that they are above the reach of cattle and the leaves of some species are also of doubtful palatability.

8.2 Effect of clipping time on regeneration

The height (5 cm) at which clippings were taken for productivity determinations corresponds well to the usual grazing level of cattle (T.J. Kotze - personal

communication)*. Although the topsoil in the quadrats was disturbed while harvesting and counting density, this appeared to have had no effect upon the sandy soil porosity.

Some of the clipped quadrats were revisited on the 1st October, 1971, to determine what effect clipping in different months had upon individuals of the dominant herbaceous species. The height of re-growth and presence of new generative material on the revisited quadrats, was recorded. Regrowth was measured as the height of extension above clipping level. Results were obtained for the populations of each of the 5 dominant grass species.

Formation of re-growth generative material ceased in Andropogon schirensis and Digitaria polevansii when clipping after December, in Brachiaria nigropedata when clipping after January, and in Andropogon gayanus and Aristida stipitata when clipping after February. Regenerative growth, of at least 10 cm in height, ceased in Andropogon schirensis when clipping after January, in Aristida stipitata when clipping after February and in Digitaria polevansii and in Brachiaria nigropedata when clipping after March. In Andropogon gayanus the 10 cm level of regeneration was just reached after clipping in August. Any lower level regenerative growth (under 10 cm) ceased in Digitaria polevansii when clipping after May, in Andropogon schirensis and Aristida stipitata when clipping after June, and in Brachiaria nigropedata when clipping after July.

From the above, it appeared that Digitaria polevansii and Andropogon schirensis were relatively sensitive to clipping and might not be expected to flourish after grazing. Aristida stipitata and Andropogon gayanus appeared to be less sensitive. Seed setting is adversely affected if (i) the whole aboveground plant is grazed before normal seed production has taken place, and (ii) if grazing takes place too late for formation of new seed by regeneration. When both these conditions are present, seed production is severely retarded, for example, if grazing the 2 dominant grass species, Digitaria polevansii and Brachiaria nigropedata takes place in February.

*Department of Agricultural Technical Services, Windhoek, S.W.A.

8.3 Effect of intensive grazing and frequent fires

Some indication of the direction in which vegetation structure and floristic composition can change when subjected to grazing and more frequent fires, could be obtained by comparing vegetation of the protected study area with that of the adjacent main Waterberg Plateau. Until very recently, intensive cattle farming had taken place on large areas of the main Waterberg Plateau. Frequent fires had also occurred, which often spread widely, due to lack of effective firebreaks. A comparison between the vegetation of these 2 areas appears justified, since the geology, soils, topography and climate of these areas are very similar. The original floristic composition of both areas also appears to have been similar, since remnants of the dominant grass species (Brachiaria nigropedata, Digitaria polevansii and Andropogon schirensis) of the study area are found in areas of the main plateau that have been less intensively grazed. All the woody species of the study area are also found on the main plateau. A woodland savanna structure, similar to that of the study area, is seen in isolated belts on the main plateau.

In all the grazed areas of the main plateau there appears to have been a major change in composition of the herbaceous layer. The palatable dominant species, Digitaria polevansii and Brachiaria nigropedata of the study area, are almost entirely absent. The unpalatable grasses Aristida stipitata and Eragrostis pallens (with average fibre content exceeding 40% in both cases - see Appendix 3), that made up approximately 2% of the relative basal cover of the study area, apparently increased under grazing conditions on the main plateau, to almost 100% of the basal cover of the herbaceous layer. In many parts of the farmed areas, there was a lower occurrence of mature tree individuals of Burkea africana, Combretum psidioides and Terminalia sericea. Combretum collinum, which is present in the study area almost exclusively in thicket form on the mounds, occurs more frequently on the main plateau, especially in the form of large trees. The very few Combretum collinum thickets seen on the main plateau had been trampled at the bases, so that any traces of specifically associated vegetation had been almost eliminated. The apparent greater occurrence of Bauhinia macrantha and the lower occurrence of Grewia avellana, Tephrosia cephalantha and possibly Securidaca longepedunculata might be due to differences in

geographical plant distribution and not necessarily to the effect of grazing.

In areas of the main plateau which had been intensively farmed, the typical two-layer stratification of the study area, was rarely seen (Fig. 8.2). In some of the grazed areas (for example above the "Plantage") Terminalia sericea and Burkea africana trees were scattered either singly or in groups. Ochna pulchra was a dominant small tree, between one and 2 m in height. The grass cover was made up almost entirely of Aristida stipitata (Fig. 8.2). In other more damaged areas on the main plateau further to the east, the vegetation tended towards open shrubland (Fig. 8.4) with a few infrequently scattered Combretum collinum trees. This highly damaged area seems to have the potential to evolve into a woodland savanna similar to that of the study area, since it appears to exist only in a suppressed state at the present time. Terminalia sericea was present in the form of 2 to 3 m high regeneration shoots and Burkea africana and Combretum psidioides were found in the form of frequently encountered low, half metre high, burned back tussocks. In other farmed areas of the Agter Waterberg, where the formation dips below the Kalahari sand in the north east, the vegetation structure over large areas consists of a dense mass of Terminalia sericea shrubs, about 2 to 3 m high, and widely isolated tall individuals of Burkea africana (Fig. 8.3).

It is thus clear that shrub forms of tree species tend to dominate in areas where large scale damage from fire and grazing has occurred. Although, the herbaceous layer in the damaged areas usually has a low basal cover and is composed largely of unpalatable grasses, the modification from tree to shrub form results in an increased availability of browsing material.

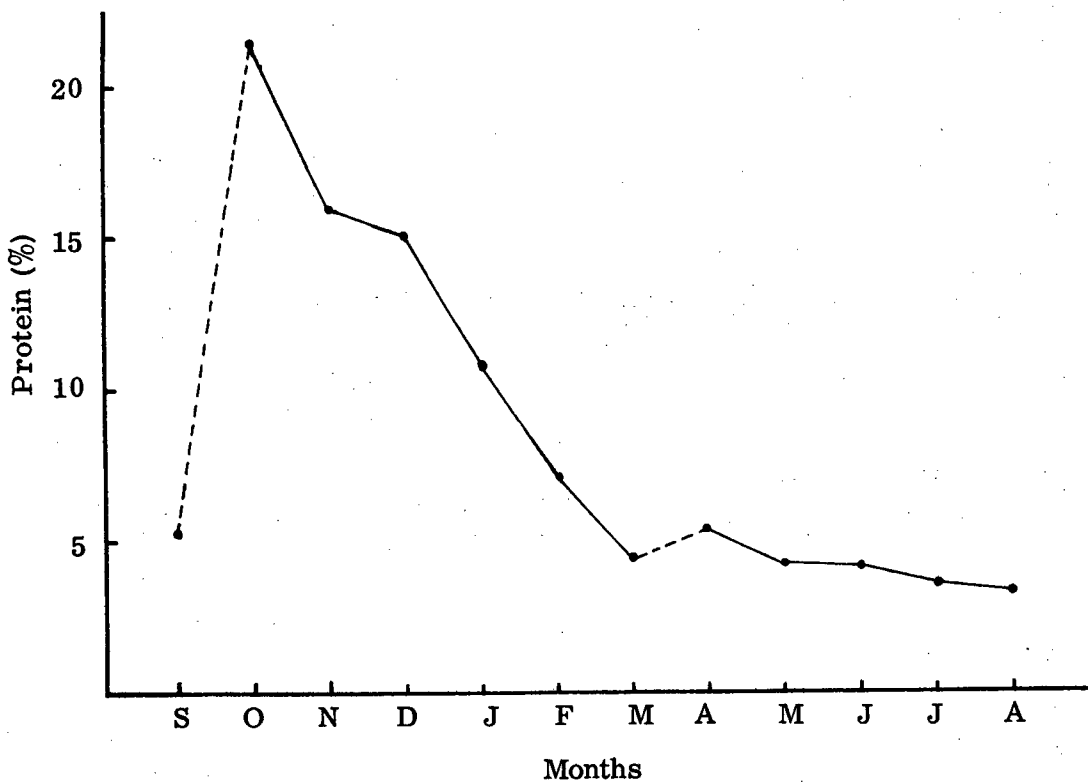


Fig. 8.1 Relationship between % protein content of vegetative material of *Brachiaria nigropedata* and time (months) (new material: Oct. - March; old and new material: Sept.; April - Aug.) The dotted lines signify discontinuities owing to changes in the type of material analysed.

Fig. 8.2 (on following page) Part of a heavily grazed and burned area (April, 1971) on the main part of the Great Waterberg Plateau above the "Plantage", showing scattered dead individuals of Burkea africana, a fairly dense shrub layer of Ochna pulchra and an herbaceous layer consisting almost entirely of Aristida stipitata.

Fig. 8.3 (on following page) A few large Burkea africana individuals scattered over a 2 to 3 m high shrub layer dominated by Terminalia sericea on the farmed areas of the Agter-Waterberg, near Okandjindi (July, 1971).

Fig. 8.4 (on following page) A farmed and frequently burned area (July, 1972) on the central part of the main Waterberg Plateau, showing Terminalia sericea with dead upper parts and only basal regeneration, amongst several half-metre high regenerating individuals of Combretum psidioides and Burkea africana.



Fig. 8.2



Fig. 8.3



Fig. 8.4

9 GENERAL CONCLUSIONS AND RECOMMENDATIONS

Specific conclusions have been made in the relevant sections. Some general conclusions, however, are:

- (a) Methods of sampling were found to be adequate for the stated purposes, although tagging of adequate numbers of rare individuals was difficult to achieve.
- (b) Average biomass, as an importance value of a species, was found to be an appropriate standard for comparing species in most sections.
- (c) Detailed analysis of physiognomic structure makes valuable deductions of the effects of fire and the availability of browsing material possible.
- (d) The phenomenon of aggregation is so frequent in common species that the suspected relation between aggregation of individuals of species and the productivity of the individuals should be further investigated.
- (e) Properly selected regressions are invaluable for calculation of productivity rates for direct comparison between species at any particular time.
- (f) Seasonal changes in total biomass of an herbaceous species give, especially in the early part of the growth season, little indication of the exact progress of new growth that is masked by the rapid decline of old dead material.
- (g) Measurements of circumference of trunk below general branching height, at a set level above ground, provide for usable regressions of trunk circumference on dry mass of trees.
- (h) The energy values of material from tree and herbaceous layers differ sufficiently to make it necessary for mass to be converted to standardized energy units for future production values to be properly compared.

(i) Phenology is commonly a so widely defined field of study that there is a maximum limit to the amount of detail, beyond which, the phenology cannot be presented integrally and coherently.

(j) When herbaceous species were grouped and subdivided according to average biomass, description of phenology was facilitated and some natural functional groups could be recognized.

Since within the extensive stock farming areas of South West Africa, the vegetation of the study area is almost unique in being virtually undisturbed by the effects of man yet situated on extensive level soil, a recommendation for its continued conservation is made. The vegetation of the Omuverume Plateau needs total protection against disturbing factors, other than those that have prevailed in the past, since the vegetation on the plateau now provides (i) an indication of the probable mature development of the woodland savanna vegetation type in the European farmed area of South West Africa, (ii) a standard by which structure and grazing potential of other areas of this vegetation type can be assessed, and (iii) an opportunity for the study of long term undisturbed phytosociological relationships between plant species of this vegetation type.

To restore the commonly encountered deteriorated structure and composition of much of the vegetation in the north-eastern sector of South West Africa to a probable climax woodland savanna structure, it appears that (i) protection by some form of fire-break against the spread of the too frequent fires that occur is necessary and (ii) numbers of grazing animals should be restricted due to the apparent sensitivity of the dominant species of the stated climax herbaceous layer.

SUMMARY

I Purpose

The purpose of the study was to obtain a knowledge of functional aspects of a terrestrial South West African ecosystem, with particular regard to the seasonal changes in the vegetation over a period of one year (September, 1970 - August, 1971). Emphasis was to be laid on productivity and phenology, although relevant structural analyses were also to be included.

The 13 ha study area was to be selected so that the vegetation would be structurally and functionally simple yet representative of other larger areas. The area chosen was situated on the Omuverume Plateau in the Otjiwarongo district; the vegetation consisted of part of a protected woodland savanna which, although ungrazed by larger herbivours, was subject to fires.

II Methods

One thousand two hundred one meter square quadrats were randomly distributed over the study area so that seasonal data of the vegetation could be taken according to a destructive method, in 100 m² areas each month for the year. These sample areas were used for determinations of frequency and density of individuals and productivity. The density counts were made by method of removal.

There were separate sampling programmes for information on mounds and flats, physiognomic structure and basal cover using additional random quadrats, belt transects and wheel-points, respectively.

Harvest methods were used for productivity and biomass determinations on a monthly dry mass basis. All herbaceous layer species were treated separately and generative, vegetative, previous season's material and the study seasons' material were handsorted. Changes in the biomass of species were expressed

using regressions. A method for estimating the rate of change of the study season's new material is presented using graph segments and derived regressions. Determinations of biomass of the main tree species were made by using curvilinear regressions of trunk diameter on dry mass. Energy determinations of plant material were made using a bomb calorimeter.

Standard and modified equipment was used for recording rainfall, temperature and relative humidity throughout the study period.

The phenology of each species was recorded using tagged individuals and was expressed taking into account the intensity on the individual and the frequency in the population, of each of the 6 defined phenological phases.

Effect of fire and grazing on the vegetation was deduced from the data obtained, using many of the above methods, although other measurements, some in additional quadrats, were made.

III Results and conclusions

- 1 The soil was a relatively uniform deep, loamy sand. That of the few scattered mounds was richer in nutrients and was less acidic than the soil of the flats.
- 2 About 97% of the average annual rainfall (ca. 514 mm) falls between the 1st of October and the 30th of April. In the study year, 807,3 mm was recorded. The average (mean daily) relative humidity for the study year was about 40%. The average annual temperature of the area was estimated at about 20°C with a relatively low annual range of mean monthly temperature. No frost was recorded in the study year.
- 3 The vegetation was 2-layered: an herbaceous layer with Digitaria polevansii, Brachiaria nigropedata, Andropogon gayanus and Grewia avellana, and a tree layer with Burkea africana, Terminalia sericea and Combretum psidioides as dominant species. The dominant species on the mounds were Cenchrus ciliaris and Combretum collinum.

- 4 Average biomass as a measure of importance of a species was usually more reliable than frequency and density.
- 5 A large number of the species were rare in the study area.
- 6 A greater number of dominant species than subdominant species was indicated using frequency and density data.
- 7 Dominant and more common species tended to aggregate more than less common species.
- 8 Aristida congesta associations (on a 1 m^2 scale) were less stable, had a lower biomass but had a higher species density and richness than Dicliptera eonii associations.
- 9 The mounds made up about 2% of the study area and had vestigial characteristics of some termitaria. The flora of the mounds and that of the flats differed greatly.
- 10 Analysis of the frequency of growth forms and heights of trees showed various effects of fire on the regeneration and mortality of individuals and the physiognomy of different parts of the community. Vertical distribution of leaf mass was indicative of the canopy shape of tree species individuals.
- 11 Basal cover of the herbaceous layer was 7,82%. The wheel-point method for estimating basal cover of less common species was inefficient.
- 12 Basal cover as a measure of biomass of different species could not be reliably used because of large differences in surface area utilization between herbaceous species.
- 13 With certain exceptions, those species with an average density of greater than 3 000 individuals per hectare or a frequency of greater than 19% (in 1 m^2 quadrats), provided satisfactory data for clear seasonal changes in biomass when using a 100 m^2 sample each month.
- 14 Growth functions such as the logistic, were found unsuited for describing seasonal change in new material under field conditions.
- 15 The maximum mean rate of increase of biomass of the herbaceous layer was attained in February ($15,90 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$) and the maximum biomass was

29 During the rainy season, a below average rainfall month resulted in varying forms of leaf scorching with subsequent flushing of vegetative and some generative parts.

30 In the 2 dominant grass species, maximum productivity was attained after 2 to 3 months in the defined frequently distinct level of the adult green leaf phase while maximum biomass was attained after 6 months in this phase.

31 Insect damage to plant organs forms part of the seasonal change in the ecosystem. Insect damage occurred, to the greatest degree, in the tree species' leaves, while members of Cyperaceae were amongst those least damaged.

32 Fire resulted in limited changes in the abundance of species individuals and in almost complete vegetative regeneration of individuals although some degree of mortality of some species individuals was noted one year after regeneration had taken place.

33 The grazing potential of the vegetation was high in summer but in winter, certain grass species became less palatable and the plant material's nutrient content, such as protein, decreased sharply.

34 Measurements of heights of regrowth in cut quadrats showed widely differing reaction to time of clipping between grass species.

35 In the vegetation type studied, excessive grazing pressures and frequent fires radically alter the composition of the herbaceous layer from Digitaria to Aristida and the structure from woodland savanna to mixed scrubland savanna.

OPSOMMING

I Doel

Die doel van hierdie ondersoek was om 'n kennis van die funksionele aspekte van 'n landelike Suidwes-Afrikaanse ekosisteem, met spesiale verwysing na die seisoensveranderinge in die plantegroei oor 'n tydperk van een jaar (September 1970 - Augustus 1971) te verkry. Besondere aandag moes aan produktiwiteit en fenologie verleen word, alhoewel relevante strukturele analise ook ingesluit moes word.

Die 13 hektaar studiegebied moes volgens kriteria van relatiewe eenvoudigheid van struktuur en funksie uitgesoek word, alhoewel dit ook verteenwoordigend van ander groter gebiede moes wees. Die uitgesoekte studiegebied is op die Omuverume Plato in die Otjiwarongo distrik geleë en het 'n gedeelte van 'n beskermende digte boomsavanna uitgemaak. Alhoewel onbeweis deur groter herbivore, was die plantegroei aan vuur blootgestel.

II Metodes

Eenduisend-twee-honderd kwadrate van een meter vierkant is ewekansig oor die studie-area versprei, sodat seisoensdata van die plantegroei vir elke maand van die jaar in 100 m² gebiede volgens 'n vernietigende metode ingesamel kon word. Hierdie monsters is gebruik vir bepaling van frekwensie en digtheid van individue en produktiwiteit. Digtheidstellings is deur middel van die verwyderingsmetode gemaak.

Daar is afsonderlike monsters vir inligting oor heuweltjies en vlaktes, fisiognomiese struktuur en basale bedekking geneem deur gebruik te maak van addisionele ewekansige kwadrate, strooktransekte en wielpunte, respektiewelik.

Snymetodes is vir die bepaling van produktiwiteit en biomassa op 'n maandelikse droëmassa basis gebruik. Die bepaling is vir elke kruidlaag soort afsonderlik uitgevoer en generatiewe, vegetatiewe, vorige seisoensmateriaal en die studie-

seisoenmateriaal is met die hand gesorteer. Regressies is gebruik om die verandering in die biomassa van soorte uit te druk. Deur van grafiek segmente en afgeleide regressies gebruik te maak, word 'n metode aangetoon waarvolgens die veranderings-tempo van nuwe seisoensmateriaal vir die studiejaar bepaal is. Bepalings van biomassa van die hoof boomsoorte is gemaak deur gebruik te maak van "curvilinear" regressies van die stamdeursnee op droë massa. Energiebepalings van plantmateriaal is gemaak deur gebruik te maak van 'n bomkalorimeter.

Standaard en gewysigde toerusting is gebruik vir die aanteken van reënval, temperatuur en relatiewe humiditeit in die studietydperk.

Die fenologie van elke soort is aangeteken deur van permanent gemerkte individue gebruik te maak. Die intensiteit van elk van die 6 gedefinieerde fenologiese fases op die individue, asook hul frekwensie in die populasie is in berekening gebring met die bepaling van die fenologie.

Die effek van vuur en beweiding op die plantegroei is afgelei uit die data verkry deur gebruik te maak van bogenoemde metodes, alhoewel ander metings, sommige in addisionele kwadrate, ook gemaak is.

III Resultate en gevolgtrekkings

1 Die grond was 'n relatief uniforme diep leemsand. Die grond van die beperkte aantal lae, verspreide heuweltjies was ryker aan voedingstowwe en minder suur as die grond van die gelyker dele.

2 Ongeveer 97% van die gemiddelde jaarlikse reënval (ca. 514 mm) kom vanaf die 1ste Oktober tot die 30ste April voor. In die studiejaar is 807,3 mm reën verkry. Die gemiddelde (daaglikse gemiddeldes) relatiewe humiditeit van die studiejaar was 40%. Die gemiddelde jaarlikse temperatuur van die gebied is beraam op ongeveer 20°C met 'n relatief lae jaarlikse variasie van gemiddelde maandelikse temperatuur. Geen ryp is gedurende die studiejaar aangeteken nie.

3 Die plantegroei het bestaan uit 2 strata: 'n kruidlaag met Digitaria polevansii,

Brachiaria nigropedata, Andropogon gayanus en Grewia avellana en 'n boomlaag met Burkea africana, Terminalia sericea en Combretum psidioides as die dominante soorte. Die dominante soorte op die heuweltjies was Cenchrus ciliaris en Combretum collinum.

4 Gemiddelde biomassa, as 'n meting van belangrikheid van 'n soort, was gewoonlik meer betroubaar as frekwensie en digtheid.

5 'n Groot aantal van die soorte was seldsaam in die studie-area.

6 Deur van frekwensie en digtheidsdata gebruik te maak, is 'n groter aantal dominante soorte as subdominante soorte aangedui.

7 Dominante en meer algemene soorte het 'n groter neiging getoon om te aggregeer as minder algemene soorte.

8 Aristida congesta assosiasies (op 'n 1 m^2 skaal) was minder stabiel, het 'n laer biomassa, maar het 'n hoër soortedigheid en rykheid as Dicliptera eenii assosiasies gehad.

9 Die heuweltjies het ongeveer 2% van die studie-area beslaan en het rudimentêre eienskappe van sekere termitaria besit. Die flora van die heuweltjies en die gelyker dele het skerp verskil.

10 Analise van die frekwensie van groeivorms en boomhoogtes het verskeie effekte van vuur op regenerasie, mortaliteit van individue en die fisiognomie van verskillende dele van die gemeenskap aangetoon. Die vertikale verspreiding van blaarmassa was 'n aanduiding van die kruinvorm van boomsoorte.

11 Die basale bedekking van die kruidlaag was 7,82%. Die wiewpuntmetode om basale bedekking van die minder algemene soorte te bepaal was ondoeltreffend.

12 Basale bedekking as 'n meting van biomassa van verskillende soorte kon nie betroubaar gebruik word nie, aangesien daar groot verskille in die oppervlaktebenutting tussen kruidagtige soorte was.

13 Deur elke maand van 'n 100 m^2 ewekansige monster gebruik te maak, is dit gevind dat, met sekere uitsonderings, soorte met 'n gemiddelde digtheid van meer as 3 000 individue/ha of 'n frekwensie van meer as 19%, voldoende inligting vir duidelike

seisoensveranderinge in biomassa gegee het.

14 Groeifunksies, soos byvoorbeeld die logistiese funksie, is nie geskik gevind vir die beskrywing van seisoensveranderinge in nuwe materiaal onder veldtoestande nie.

15 Die maksimum gemiddelde toename van biomassa in die kruidlaag is in Februarie bereik ($15,90 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{dag}^{-1}$) en die maksimum biomassa in April ($1\,420 \text{ kg/ha}$). Die vinnigste gemiddelde afname van biomassa was in Junie ($-5,54 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{dag}^{-1}$).

16 Die variasie in biomassa van die kruidlaag (ongeveer 900 kg/ha) het die netto toename (ongeveer 500 kg/ha) in die studiejaar aansienlik oortref.

17 Die maksimum seisoensvariasie in die biomassa van die meer belangrike kruidlaagsoorte het vanaf $1,6\%$ tot 72% van hul respektiewelike maksimum biomassa verskil.

18 Die tempo van afname in die vorige seisoensmateriaal het aansienlik gevarieer tussen die verskillende meer belangrike grassoorte.

19 Die maandelikse biomassa van die kruidlaag, in die tydperk van toename in biomassa, was ongewoon gekorreleerd met die gemiddelde reënval van die vorige maand.

20 Die gemiddelde biomassa van die kruidlaag was $912,85 \text{ kg/ha}$ vir die studiejaar. Die totale biomassa van die boomlaag was beraam as $22\,290 \text{ kg/ha}$.

21 Blaarbiomassa van die boomlaag was ongeveer dieselfde as die biomassa van die kruidlaag.

22 Die blaarafval wat gedurende die studiejaar tot die grondoppervlakte toegevoeg is, was ten minste twee keer soveel as dié van die materiaal van die kruidlaag.

23 Die energiewaardes van die kruidlaag en die boomblare was respektiewelik ongeveer $17\,550$ en $20\,500 \text{ J/g}$.

24 Die fosfor en kalsiumkonsentrasies in boomblare was hoër as dié in die materiaal van die kruidlaag.

25 Relatief hoë kalsiumkonsentrasies is in die plantegroei en die grond van die heuweltjies gevind. Hierdie verskynsel werp waarskynlik meer lig op die ontwikkeling van die heuweltjies.

- 26 'n Swak omgekeerde verwantskap tussen die gemiddelde biomassa van die grassoorte per eenheidsoppervlakte en die duur van die volwasse groenblaarfase het bestaan.
- 27 Die lengte van die blomfase was gewoonlik korter by die dominante grassoorte as by die minder belangrike grassoorte.
- 28 Blomvorming in die studiejaar het by die meerderheid soorte in die kruidlaag voorgekom, maar slegs by 'n beperkte aantal boom- en struiksoorte. Laasgenoemde verskynsel word toegeskryf aan 'n onlangse vuur in die studie-area.
- 29 'n Maand met minder as gemiddelde reënval in die reënseisoen, het verskillende vorme van blaarskroeiing en daaropvolgende uitloping van vegetatiewe en sommige generatiewe dele tot gevolg gehad.
- 30 In die 2 dominante grassoorte is maksimum produktiwiteit bereik nadat die soorte vir 2 tot 3 maande in die gedefinieerde frekwentatiewe duidelike volwasse groenblaarfase was, terwyl maksimum biomassa na 6 maande in hierdie fase bereik is.
- 31 Insekteskade van plantorgane vorm deel van die seisoensverandering in die ekosisteem. Insekteskade het grotendeels op die blare van die boomsoorte voorgekom. Lede van die Cyperaceae was die minste beskadig.
- 32 Vuur het slegs beperkte veranderinge in die talrykheid van soort-individue tot gevolg gehad, asook feitlik volledige vegetatiewe regenerasie van individue na die vuur. 'n Sekere mate van mortaliteit na afloop van een jaar na die regenerasie is by sommige soort-individue waargeneem.
- 33 Die weidingspotensiaal van die plantegroei was hoog in die somer, maar in die wintermaande het sekere grassoorte onsmaklik geword en die voedingskonsentrasie in die plantmateriaal, soos proteïne, het skerp afgeneem.
- 34 Bepalings van die hoogte van hergroei in afgesnyde kwadrate het 'n uiteenlopende reaksie van verskillende grasse op die tydstip van ontblaring getoon.
- 35 Oorbeweidings en gereelde vure het oënskynlik 'n radikale verandering in die samestelling van die studieplantegroeitipe gehad, naamlik vanaf Digitaria na Aristida. Die struktuur het vanaf 'n digte boomsavanna na 'n digte gemengde struiksavanna verander.

ACKNOWLEDGEMENTS

I wish to record my sincere appreciation for the help given in this study by, amongst others, the following persons or organizations:

The Department of Agricultural Technical Services for allowing me to use a departmental project for degree purposes and for seconding me to the University of Stellenbosch to process the data.

The Department of Nature Conservation and Tourism in South West Africa for granting permission to work on the Waterberg (Omuverume) site.

My promoter, Dr. J.G. Smith for his ready help and interest in the work in the field and during the writing up.

My former superiors, Mr. T.J. Kotze and Dr. L. Mostert for their help and advice and for making the study possible.

Drs. D. Edwards, J.W. Morris and O.J.H. Bosch of the Botanical Research Institute in Pretoria for constructive criticism of parts of the text.

The South West Africa Herbarium, in particular Mr. W. Giess, for immediate service obtained in the identifications of the plant specimens collected; the National Herbarium in Pretoria and Dr. O. Almborn of Lund, Sweden for other identifications.

The Institute for Soils and Irrigation in Pretoria for chemical analysis of the plant samples.

The Department of Soil Science at the University of Stellenbosch, in particular, Mr. J.J.N. Lambrechts and Dr. H.W. Weber, for analysis of the soil samples.

The Weather Bureau in Windhoek, in particular Mr. Boshoff, for ready advice and

the loan of a Stevenson screen.

Dr. Dirk van Schalkwyk for the considerable time taken up with the statistical analyses and Mr. Conradie for making the Wang Programmable Calculator available.

Also in South West Africa, the technical assistants of the South West Africa Region of the Department of Agricultural Technical Services, in particular Mr. D.S. de Bruin, for unstinting help in the field; Mr. W.G. Klein and Dr. J.A. Steyn for making laboratory equipment available in Windhoek; Mr. Schneider-Waterberg for access to the study area and for full co-operation in the study; Myne Wilischita for willing help in the field.

Also in Stellenbosch, Proff. P.G. Jordaan and J.A. du Bruyn of the Department of Botany for their contributions; Prof. F.J. van der Merwe of the Department of Animal Science for the use of the bomb calorimeter; the Departments of Entomology and Botany for identifications and other help received; Dr. H. Geertsema for some insect identifications; Mr. Crafford of the Department of Botany for the timely printing of the photographs.

Also in Pretoria, Prof. J.O. Grunow of the Department of Pasture Science at the University of Pretoria for advice while on the study site and to Dr. G.K. Theron of the Department of Botany at the same university for his contribution; technicians of the Botanical Research Institute for help received; Mrs. A. Lessing for the patient and able typing of this work.

Finally, my mother for the rapid typing of the provisional copy; my late father for constant encouragement and many helpful suggestions in the initial writing up stages; my wife, Thea for the drawing of most of the figures and the checking of the entire text and for other valued help and encouragement at all stages.

LITERATURE CITED

- Anderson, K.L. 1964. Burning Flint Hills bluestem ranges. Tall Timbers Fire Ecol. Conf. 3:89-103.
- Barnard, W.S. 1963 - 65. 'n Kaart van die klimaatstreke van Suidwes-Afrika. South West Africa Scientific Society Journal 18 and 19:74-84.
- Boaler, S.B. 1966. Ecology of a miombo site, Lupa North Forest Reserve, Tanzania. II. Plant communities and seasonal variation in the vegetation. J.Ecol. 54:465-479.
- Boaler, S.B. and Sciwale, K.C. 1966. Ecology of a miombo site, Lupa North Forest Reserve, Tanzania. III. Effects on the vegetation of local cultivation practices. J.Ecol. 54:577-587.
- Bourlière, F. and Hadley, M. 1970. The ecology of tropical savannas. Ann.Rev. Ecol.Syst. 1:125-152.
- Bowden, B.N. 1964. Studies on Andropogon gayanus Kunth, III. An outline of its biology. J.Ecol. 52:255-271.
- Boyd, C.E. 1970. Production, mineral accumulation and pigment concentrations in Typha latifolia and Scirpus americanus. Ecology 51:285-290.
- Brown, D. 1954. Methods of surveying and measuring vegetation. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks., England.
- Brynard, A.M. 1965. The influence of veld burning on the vegetation and game of the Kruger National Park. p.371-393. In D.H. Davis (ed.) Ecological studies in Southern Africa. W. Junk, The Hague.
- Carlisle, A., Brown, A.H.F. and White, E.J. 1966. The organic matter and nutrient elements in the precipitation beneath a sessile oak (Quercus petraea) canopy. J.Ecol. 54:87-98.
- Cook, L. 1939. A contribution to our information on grass burning. S.Afr. J. Sci. 36:270-282.
- Cook, L. 1965. Note upon burning experiments at Frankenwald, Transvaal, South Africa. Tall Timbers Fire Ecol. Conf. 5:96-97.
- Daubenmire, R. 1968a. Plant communities. A textbook of plant synecology. Harper and Row, New York.

- Daubenmire, R. 1968b. Ecology of fire in grasslands. *Advances Ecol. Res.* 5:209-266.
- Du Toit, P.J., Louw, J.G. and Malan, A.I. 1940. A study of the mineral content and feeding value of natural pastures in the Union of South Africa. *Onderstepoort Journal of Veterinary Science and Animal Industry* 14:123-327.
- Evans, F.C. 1967. The significance of investigations in secondary terrestrial productivity. p. 3-15. In K. Petrusewicz (ed.), *Secondary productivity of terrestrial ecosystems*. Vol. 1. Kraków, Warsawa.
- Evans, G.C. 1972. The quantitative analysis of plant growth. In D.J. Anderson et al. (eds.), *Studies in Ecology*. Vol. 1. Blackwell Scientific Publications, Oxford.
- Gevers, T.W. 1937. The Etjo beds of northern Hereroland, South West Africa. *Trans. Geol. Soc. S. Afr.* 39:317-330.
- Giess, W. 1971. A preliminary vegetation map of South West Africa. *Dinteria* 4:5-114.
- Golley, F.B. 1961. Energy values of ecological materials. *Ecology* 42:581-584.
- Goodall, D.W. 1952. Quantitative aspects of plant distribution. *Biol. Rev.* 27:194-245.
- Greig-Smith, P. 1964. *Quantitative plant ecology*, 2nd ed. Butterworths, London.
- Hartmann, G. 1904. Karte des nordlichen Teiles von deutsch Südwestafrika. Map 4. Friederischen, Hamburg.
- Holland, P.G. 1969. Weight dynamics of Eucalyptus in the mallee vegetation of South East Australia. *Ecology* 50:212-219.
- Hopkins, B. 1962. Vegetation of the Olokemeji Forest Reserve, Nigeria. 1. General features of the reserve and the research sites. *J. Ecol.* 50:559-598.
- Hopkins, B. 1966. Vegetation of the Olokemeji Forest Reserve, Nigeria. 4. The litter and soil with special reference to their seasonal changes. *J. Ecol.* 54:687-703.
- Hopkins, B. 1968. Vegetation of the Olokemeji Forest Reserve, Nigeria. 5. The vegetation of the savanna site with special reference to its seasonal changes. *J. Ecol.* 56:97-115.
- Hughes, M.K. 1971. Seasonal calorific values from a deciduous woodland in England. *Ecology* 52:923-926.
- Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577-586.
- Jäger, F.R. and Waibel, L. 1921. Beiträge zur Landeskunde von Südwestafrika.

- Teil 2. Mitteilungen aus den deutschen Schutzgebieten, Ergänzungsheft 15.
Map 4 in "Teil 1".
- Jones, R.M. 1968. Seed production of species in the Highveld secondary succession. *J.Ecol.* 56:661-666.
- Jordan, C.F. 1971. Productivity of a tropical forest and its relation to a world pattern of energy storage. *J.Ecol.* 59:127-142.
- Kershaw, K.A. 1964. Quantitative and dynamic ecology. Edward Arnold, London.
- Kucera, C.L., Dahlman, R.C. and Koelling, M.R. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. *Ecology* 48:536-541.
- Lawson, G.W., Jeník, J. and Armstrong-Mensah, K.O. 1968. A study of a vegetation Catena in Guinea savanna at Mole Game Reserve (Ghana). *J.Ecol.* 56:505-522.
- Leistner, O.A. 1967. The plant ecology of the Southern Kalahari. Botanical Survey Memoir No. 38. The Government Printer, Pretoria.
- Lieth, H. 1970. Phenology in productivity studies. p. 29-46. In D.E. Reichle (ed.), Analysis of temperate forest ecosystems. Ecological studies 1. Springer-Verlag, Heidelberg.
- Lieth, H. 1972. Über die Primärproduktion der Pflanzendecke der Erde. *Angew. Bot.* 46:1-37.
- Likens, G.E., Bormann, F.H., Johnson, N.M. and Pierce, R.S. 1967. The calcium, magnesium, potassium and sodium budgets for a small forested ecosystem. *Ecology* 48:772-785.
- Louw, A.J. 1968. Bemesting van natuurlike veld op rooi-leemgrond van die Springbokvlakte. 2. Invloed van ammonium-sulfaat- en superfosfaatbemesting op lugdroë-materiaalopbrengs en die minerale-inhoud daarvan. *S.Afr. Tydskr. Landbouwet.* 11:629-636.
- Maignien, R. 1964. Survey of research on laterites. Humid Tropics Research Programme. UNESCO/NS/HT 125.
- Medwecka-kornás, A. 1967. Estimation of primary production as a basis for studies of secondary production. p. 83-95. In K. Petrusiewicz (ed.), Secondary productivity of terrestrial ecosystems. Vol. 1. Kraków, Warsawa.
- Merxmüller, H. 1966-72. Prodröm einer Flora von Südwestafrika. J. Cramer, Lehre.
- Milner, C. and Hughes, R.E. 1968. Methods for the measurement of the primary production of grasslands. I.B.P. Handbook no. 6. Blackwell Scientific Publications, Oxford and Edinburgh.

- Munsell soil color chart. 1954. Munsell Color Co., Baltimore, Maryland.
- Newbould, P.J. 1967. Methods for estimating the primary production of forests. I.B.P. Handbook no. 2. Blackwell Scientific Publications, Oxford and Edinburgh.
- Odum, E.P. 1959. Fundamentals of ecology. W.B. Saunders Company, Philadelphia and London.
- Olson, J.S. 1964. Gross and net production of terrestrial vegetation. *J. Ecol.* 52 (Suppl.):99-118.
- Oosting, H.J. 1956. The study of plant communities, 2nd ed. W.H. Freeman and Co., San Francisco, Calif.
- Ovington, J.D. 1962. Quantitative ecology and the woodland ecosystem concept. *Advances Ecol. Res.* 1:103-192.
- Ovington, J.D., Heitkamp, D. and Lawrence, D.B. 1963. Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosystems in central Minnesota. *Ecology* 44:52-63.
- Penfound, Wm. T. 1964. Effects of denudation on the productivity of grassland. *Ecology* 45:838-845.
- Peterken, G. F. and Newbould, P.J. 1966. Dry matter production by Ilex aquifolium L. in the New Forest. *J. Ecol.* 54:143-150.
- Petrusewicz, K. 1967a. Concepts in studies on the secondary productivity of terrestrial ecosystems. p. 17-49. In K. Petrusewicz (ed.), Secondary productivity of terrestrial ecosystems. Vol. 1. Kraków, Warszawa.
- Petrusewicz, K. 1967b. Suggested list of more important concepts in productivity studies (definitions and symbols). p. 51-58. In K. Petrusewicz (ed.), Secondary Productivity of terrestrial ecosystems. Vol. 1. Kraków, Warszawa.
- Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley-interscience, John Wiley and Sons, New York.
- Porter, C.L. Jr. 1967. Composition and productivity of a subtropical prairie. *Ecology* 48:937-942.
- Post, L.J. 1970. Dry matter production of Mountain Maple and Balsam Fir in northwestern New Brunswick. *Ecology* 51:548-550.
- Radford, P.J. 1967. Growth analysis formulae - their use and abuse. *Crop Science* 7:171-175.

- Ratray, J.M. 1960. The habit, distribution, habitat, forage value and veldt indicator value of the commoner Southern Rhodesian grasses. *Rhodesia Agric. J.* 57:424 (and 6 tables).
- Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography.* Clarendon Press, Oxford.
- Richards, F.J. 1969. The quantitative analysis of growth. p. 3-76. In F.C. Steward (ed.), *Plant physiology. A treatise.* Vol. 5A. Analysis of growth: behaviour of plants and their organs. Academic Press, New York.
- Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978-983.
- Riley, H.P. 1963. *Families of flowering plants of Southern Africa.* University of Kentucky, Kentucky.
- Rodin, L.E. and Bazilevich, N.I. 1967. *Production and mineral cycling in terrestrial vegetation.* Oliver and Boyd, Edinburgh and London.
- Russel, E.J. 1968. *Soil conditions and plant growth,* 9th ed. Longmans, London.
- Rutherford, M.C. 1972. Notes on the flora and vegetation of the Omuverume Plateau-Mountain, Waterberg, South West Africa. *Dinteria* 8:3-55.
- Schinz, H. ca. 1891. *Deutsch Südwestafrika Forschungsreisen durch die deutschen Schutzgebiete Gross-Nama- und Hereroland nach dem Kunene, dem Ngami-See und der Kalahari, 1884-1887.* Schulze, Oldenburg and Leipzig.
- Schnelle, F. 1955. *Pflanzen-Phänologie. Probleme der Bioklimatologie.* Bd. 3. Akad. Verlagsges., Leipzig.
- Schulze, B.R. 1965. *Climate of South Africa. Part 8. General survey.* W.B. 28. The Government Printer and Weather Bureau, Pretoria.
- Tidmarsh, C.E.M. and Havenga, C.M. 1955. The wheel-point method of survey and measurement of semi-open grasslands and Karoo vegetation in South Africa. *Botanical Survey Memoir No. 29.* The Government Printer, Pretoria.
- Van der Eyk, J.J., Macvicar, C.N. and De Villiers, J.M. 1969. *Soils of the Tugela basin.* Natal Town and Regional Planning Reports. Vol. 15. Interpak. (Pty.) Ltd., Durban.
- Van der Schijff, H.P. 1971. Die plantegroei van die drie distrikte Potgietersrus, Pietersburg en Soutpansberg in die Noordelike Transvaal. *Tydskr. vir Natuurwet.* 11:108-144.
- Van Dyne, G.M., Vogel, W.G. and Fisser, H.G. 1963. Influence of small plot size and shape on range herbage production estimates. *Ecology* 44:746-759.

- Vedder, H. 1938. South West Africa in early times. Oxford University Press, London.
- Volk, O.H. 1965-66. Die Florenggebiete von Südwestafrika. South West Africa Scientific Society Journal 20:25-58.
- Walter, H. 1939. Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. Jb.wiss.Bot. 87:750-860.
- Walter, H. 1962. Die Vegetation der Erde in ökologischer Betrachtung. Band 1. Die tropischen und subtropischen Zonen. Vess Gustav Fischer Verlag, Jena.
- Walter, H. and Volk, O. 1954. Grundlagen der Weidewirtschaft in Südwestafrika. Eugen Ulmer, Stuttgart z.Z. Ludwigsburg.
- Watson, D.J. 1963. Climate, weather, and plant yield. p. 337-350. In L.T. Evans (ed.), Environmental control of plant growth, Academic Press, New York and London.
- Watson, J.P. 1967. A termite mound in an iron age burial ground in Rhodesia. J.Ecol. 55:663-669.
- Weather Bureau, 1954. Climate of South Africa. Part 1. Climate statistics. WB 19. The Government Printer, Pretoria and Cape Town.
- Westlake, D.F. 1963. Comparisons of plant productivity. Biol.Rev. 38:385-425.
- Whittaker, R.H. and Woodwell, G.M. 1969. Structure, production and diversity of the oak-pine forest at Brookhaven, New York. J.Ecol. 57:155-174.
- Wiegert, R.G. and Evans, F.C. 1964. Primary production and the disappearance of dead vegetation on an old field. Ecology 45:49-63.
- Williams, R.F. 1964. The quantitative description of growth. p. 89-101. In C. Barnard (ed.), Grasses and grasslands. Macmillan, London.
- Yarranton, G.A. 1971. Mathematical representations and models in plant ecology: response to a note by R. Mead. J.Ecol. 59:221-224.

APPENDIX 1 Species list

The following is a list of the angiosperm species found on the 13 ha study area and is arranged according to Merxmüller (1966 - 72). Abbreviations of author names are mostly after the same authority. Species were identified by the South West Africa Herbarium in Windhoek and the National Herbarium in Pretoria. Representatives of most species collected in the study area and surrounding area (Rutherford, 1972), are housed in the first mentioned herbarium with some in the latter herbarium. Four species, rarely recorded on the central summit sand of the plateau, were not recorded in the study area itself (see Section 6.3.2) while one unidentified sterile Acacia species (possibly A. hebeclada) individual was found (see Section 6.3.3.5).

Rhynchelytrum repens (Willd.) C.E. Hubbard and the annual R. villosum (Parl. ex Hooker) Chiov. were both present, but were so similar (see remark under R. repens in Merxmüller, 1966 - 72) that it was found impracticable to distinguish them, in all their growth phases, in the field. For purposes of the study, both species were treated as one Rhynchelytrum species. From several collections, it became apparent the R. repens was far more abundant than R. villosum.

All fruits of Limeum fenestratum (Fenzl) Heimerl in the study area did not have the expected developed wing present.

All individuals of Stipagrostis uniplumis (Licht. ex Roemer & Schultes) De Winter were exceptionally robust in form.

Non-angiosperm species that were noted during the study year only included, one moss and one hepatic in January, and basidiomycete fruiting bodies from December to March, with average density and frequency of the latter species, for this period, about 250 per hectare and 1,75% (in 1 m² quadrats) respectively. Usually on the south facing side of several trunks of Terminalia sericea (but not on Burkea africana and Combretum psidioides), lichens belonging to the genera, Parmelia and Physcia, were conspicuous.

OLACACEAE

Ximenia americana L. var. microphylla Welw. ex Oliver

LORANTHACEAE

Tapinanthus oleifolius (Wendl.) Danser

MOLLUGINACEAE

Limeum fenestratum (Fenzl) Heimerl

L. viscosum (J. Gay) Fenzl subsp. viscosum

AMARANTHACEAE

Aerva leucura Moq.

Kyphocarpa angustifolia (Moq.) Lopr.

RANUNCULACEAE

Clematis brachiata Thunb.

Clematopsis scabiosifolia (DC.) Hutch.

MENISPERMACEAE

Cissampelos mucronata A. Richard

OCHNACEAE

Ochna pulchra Hooker subsp. pulchra

CAPPARACEAE

Boscia albitrunca (Burch.) Gilg & Benedict

Maerua juncea Pax subsp. juncea

MIMOSACEAE

Acacia hereroensis Engler

A. mellifera (Vahl) Bentham subsp. detinens (Burch.) Brenan

A. sp.

Elephantorrhiza elephantina (Burch.) Skeels

CAESALPINIACEAE

Bauhinia macrantha Oliver

Burkea africana Hooker

Cassia biensis (Steyaert) Mendonça & Torre

FABACEAE

Indigofera daleoides Bentham ex Harvey

Lonchocarpus nelsii (Schinz) Schinz ex Heering subsp. nelsii

Rhynchosia sublobata (Schuhmacher) Meikle

R. venulosa (Hiern) K. Schum.

Tephrosia cephalantha Welw. ex Baker var. decumbens Welw. ex Baker

T. lupinifolia DC.

OXALIDACEAE

Oxalis purpurascens Salter

EUPHORBIACEAE

Croton gratissimus Burch.

Phyllanthus pentandrus Schumacher & Thonning

Pterococcus africanus (Sonder) Pax & K. Hoffm.

Tragia dinteri Pax

MALPIGHIACEAE

Sphedamnocarpus pruriens (A. Juss.) Szyszyl.

POLYGALACEAE

Polygala kalaxariensis Schinz

Securidaca longepedunculata Fresen.

ANACARDIACEAE

Ozoroa paniculosa (Sonder) R. & A. Fernandes

Rhus ciliata Licht. ex Roemer & Schultes

RHAMNACEAE

Ziziphus mucronata Willd. subsp. mucronata

TILIACEAE

Grewia avellana Hiern

G. bicolor Juss.

G. deserticola Ulbr.

G. flavescens Juss.

MALVACEAE

Hibiscus fleckii Gürke

Pavonia clathrata Mast.

STERCULIACEAE

Dombeya rotundifolia (Hochst.) Planchon

Hermannia tomentosa (Turcz.) Schinz ex Engler

Melhania acuminata Mast.

COMBRETACEAE

Combretum apiculatum Sonder subsp. leutweinii (Schinz) Exell

C. collinum Fresen.

C. psidioides Welw. subsp. dinteri (Schinz) Exell

Terminalia sericea Burch. ex DC.

PERILOCACEAE

Raphionacme burkei N.E.Br.

ASCLEPIADACEAE

Pentarrhinum abyssinicum Decne

RUBIACEAE

Ancylanthos bainesii Hiern

Anthospermum ericoideum Krause

Pygmaeothamnus zeyheri (Sonder) Robyns

CONVOLVULACEAE

Merremia tridentata (L.) Hall. f. subsp. angustifolia (Jacq.) Ooststr.

Turbina oblongata (E. Meyer ex Choisy) Meeuse

LAMIACEAE

Leonotis dysophylla Bentham

SOLANACEAE

Solanum delagoense Dunal

ACANTHACEAE

Blepharis maderaspatensis (L.) Heyne ex Roth

Dicliptera eenii S. Moore.

ASTERACEAE

Bidens biternata (Lour.) Merr. & Scherff

Dicoma gerrardii Harvey ex Wilson

D. schinzii O. Hoffm.

Felicia muricata (Thunb.) Nees

Nidorella resedifolia DC. subsp. resedifolia var. rapunculoides (DC.) Harvey

Tarchonanthus camphoratus L.

Vernonia poskeana Vatke & Hildebr.

LILIACEAE

Asparagus africanus Lam.

Gloriosa virescens Lindley

IRIDACEAE

Pentamenes zambesiacus (Baker) N. E. Br.

COMMELINACEAE

Commelina africana L.

C. benghalensis L.

GRAMINEAE

Andropogon gayanus Kunth

A. schirensis Hochst. ex A. Richard

Aristida congesta Roemer & Schultes

A. meridionalis Henrard

A. stiptata Hackel

Brachiaria nigropedata (Munro ex Fical. & Hiern) Stapf

Cenchrus ciliaris L.

Digitaria polevansii Stent

Eragrostis jeffreysii Hackel

E. nindensis Fical. & Hiern

E. pallens Hackel

E. rigidior Pilger

E. scopelophila Pilger

E. stapfii De Winter

Eustachys paspaloides (Vahl) Lanza & Mattei

Heteropogon contortus (L.) Beauv. ex Roemer & Schultes

Panicum kalaharensis Mez

P. maximum Jacq.

Pogonarthria squarrosa (Licht. ex Roemer & Schultes) Pilger

Rhynchelytrum repens (Willd.) C.E. Hubbard

R. villosum (Parl. ex Hooker) Chiov.

Schmidtia pappophoroides Steudel

Stipagrostis uniplumis (Licht. ex Roemer & Schultes) De Winter

Triraphis schinzii Hackel

CYPERACEAE

Cyperus margaritaceus Vahl

Fimbristylis exilis (Humb., Bonpl. & Kunth) Roemer & Schultes

Mariscus laxiflorus Turrill

APPENDIX 2 Results of analysis of soil samples from the study area on Omuverume, carried out by the Department of Soil Science at the University of Stellenbosch (methods used for analysis see text page 14)

Sample No.	Sample position	Sample depth (m)	Texture					pH (in 1N KCl)	Carbon (%)	Resistance ohms (20°C)	Calcium me/100g	Magnesium me/100g	Sodium me/100g	Potassium me/100g
			Rough sand (%)	Medium sand (%)	Fine sand (%)	Silt (%)	Clay (%)							
1	Mound 1	0,1	0,17	8,11	78,43	4,60	8,69	4,55	1,08	3150	2,22	0,67	sp	0,27
2	"	0,2	0,13	7,44	72,77	4,83	14,83	6,05	1,36	1270	7,62	1,56	0,01	0,29
3	"	0,5	0,14	8,39	75,16	4,20	12,11	5,85	0,88	1280	6,50	1,27	0,06	0,18
4	"	1,0	0,33	14,71	67,49	3,28	14,19	6,20	0,67	1700	4,37	1,08	0,01	0,11
5	"	1,5	0,15	9,55	73,81	2,50	13,99	6,25	0,62	1840	4,37	1,00	sp	0,13
6	"	2,5	0,25	10,78	72,49	3,52	12,96	7,00	0,15	1270	12,25	0,69	0,10	0,16
7	"	2,8	0,37	9,37	73,08	3,63	13,57	6,80	0,14	1050	11,62	0,60	0,02	0,20
8	Mound 2	0,1	0,26	10,76	74,18	5,27	9,53	5,20	1,56	2290	6,25	1,33	sp	0,65
9	"	0,2	0,11	5,39	78,22	3,91	12,37	6,15	0,76	2100	7,25	1,60	0,02	0,57
10	"	1,0	0,11	10,58	71,95	4,91	12,45	6,65	0,85	1700	8,75	1,44	0,01	0,35
11	"	3,0	0,24	10,88	72,69	2,89	13,30	7,15	0,08	1400	12,25	1,54	0,01	0,29
12	Flats	0,1	0,17	10,45	78,81	3,13	7,44	4,15	0,90	6200	0,82	0,29	sp	0,18
13	"	0,1	0,18	15,57	74,01	2,52	7,72	3,70	0,66	11500	0,12	0,04	sp	0,06
14	"	0,1	0,13	18,76	71,32	2,82	6,97	3,85	1,36	3300	0,87	0,29	sp	0,17
15	"	0,1	0,32	15,83	74,30	2,42	7,11	3,80	0,58	11000	0,12	0,04	sp	0,10
16	"	0,1	0,29	11,97	77,35	2,89	7,50	4,50	0,62	4800	1,37	0,31	0,01	0,24
17	"	0,2	0,12	5,80	82,40	2,34	9,34	4,10	0,46	7100	0,45	0,21	sp	0,14
18	"	0,5	0,19	8,42	79,23	1,79	10,37	4,05	0,16	12700	0,32	0,19	0,01	0,10
19	"	1,0	0,17	6,07	81,17	2,08	10,51	4,00	0,10	11000	0,25	0,25	sp	0,10
20	"	2,0	0,16	7,35	75,42	5,96	11,11	4,15	0,10	7200	0,35	0,44	0,02	0,10

Stellenbosch University <http://scholar.sun.ac.za>

APPENDIX 3 Chemical analyses of plant material of more important species of the study area (methods of determination are mentioned on page 124)

Species	Type material	Month	P %	Ca %	Protein %	Fibre %	Fat %	Ash %
<i>Brachiaria nigropedata</i>	Total vegetative	Sept.	0,028	4,12	5,4	28,8	1,5	4,80
"	New vegetative	Oct.	0,250	0,27	21,5	24,0	2,1	8,50
"	"	Nov.	0,140	0,31	15,9	23,0	3,7	8,90
"	"	Dec.	0,130	0,33	15,0	27,0	2,0	6,00
"	"	Jan.	0,083	3,33	10,9	13,2	2,1	6,49
"	"	Feb.	0,083	2,66	7,1	41,3	1,0	6,06
"	"	March	0,083	2,66	4,4	33,3	1,5	7,65
"	Total vegetative	April	0,053	2,79	5,2	33,6	2,0	6,84
"	"	May	0,039	3,33	4,2	32,1	2,1	9,94
"	"	June	0,025	2,79	4,0	30,8	1,7	11,03
"	"	July	0,025	3,19	3,4	32,2	2,5	6,90
"	"	Aug.	0,023	3,99	3,0	30,9	1,9	7,16
<i>Digitaria plevansii</i>	Total vegetative	Sept.	0,039	5,59	4,6	33,8	2,5	5,80
"	New vegetative	Nov.	0,100	0,35	13,6	28,2	3,1	8,00
"	"	Dec.	0,110	0,30	14,3	29,6	2,6	8,40
"	"	Jan.	0,108	4,00	10,1	35,6	2,5	8,38
"	"	Feb.	0,092	3,33	7,5	37,3	2,1	8,70
"	Previous season's vegetative	Feb.	0,062	5,59	6,9	36,5	2,7	6,36
"	New vegetative	March	0,070	3,06	6,1	37,3	2,4	9,62

Species	Type material	Month	P %	Ca %	Protein %	Fibre %	Fat %	Ash %
<i>Digitaria polevansii</i>	Generative	March	0,050	2,53	4,7	43,1	1,1	5,17
"	Total vegetative	April	0,056	3,59	4,8	35,9	1,9	7,75
"	"	May	0,023	3,19	2,3	40,4	1,6	4,63
"	"	June	0,025	4,92	2,6	36,9	2,4	7,55
"	"	July	0,028	3,86	2,7	38,6	1,9	5,02
"	"	Aug.	0,023	3,86	2,7	39,5	2,7	5,02
<i>Andropogon gayanus</i>	Total vegetative	Sept.	0,050	4,39	4,9	33,4	1,8	4,88
"	New vegetative	Nov.	0,120	0,44	11,5	27,3	2,4	6,20
"	"	Jan.	0,105	4,39	10,2	31,7	1,6	6,62
"	"	Feb.	0,095	3,06	8,2	37,9	1,4	6,89
"	"	March	0,073	3,19	4,9	40,4	1,9	4,05
"	Generative	March	0,070	1,20	5,1	41,1	1,3	3,83
"	Total vegetative	April	0,045	2,79	3,6	37,2	1,6	3,83
"	"	May	0,023	3,19	2,7	36,7	2,0	3,52
"	"	June	0,031	2,79	3,0	40,3	2,3	4,36
"	"	July	0,020	3,06	2,0	42,2	1,8	2,52
"	"	Aug.	0,023	3,99	2,0	38,4	1,4	3,40
<i>Andropogon schirensis</i>	New vegetative	Jan.	0,070	2,79	8,0	32,4	1,9	5,72
"	Previous season's vegetative	Jan.	0,022	1,60	4,5	34,7	1,4	3,12
"	New vegetative	Feb.	0,075	2,53	6,0	38,3	1,7	5,11
"	"	March	0,048	2,79	4,8	36,1	1,9	6,80

Species	Type material	Month	P %	Ca %	Protein %	Fibre %	Fat %	Ash %
<i>Andropogon schirensis</i>	Total vegetative	June	0,028	2,79	3,9	34,1	2,0	5,80
"	"	July	0,020	3,19	2,8	35,7	2,2	4,78
"	"	Aug.	0,020	3,33	2,7	34,0	2,0	4,20
<i>Aristida stipitata</i>	New vegetative	Jan.	0,056	1,60	6,0	41,6	1,1	3,64
"	"	Feb.	0,053	1,41	4,9	43,0	1,0	3,51
"	"	March	0,050	1,20	4,1	41,6	0,8	3,15
"	Total vegetative	June	0,025	0,27	3,1	41,1	1,2	3,28
"	"	July	0,023	0,93	2,5	43,2	1,1	2,44
"	"	Aug.	0,023	1,20	2,6	40,9	1,1	2,54
"	Generative	Aug.	0,023	1,20	2,8	38,4	1,2	3,04
<i>Grewia avellana</i>	Vegetative	Jan.	0,119	12,77	18,0	33,6	2,3	7,86
"	"	Feb.	0,112	12,77	15,8	34,2	3,3	10,63
"	"	March	0,092	13,70	12,1	30,4	3,1	8,76
"	"	June	0,050	7,85	6,5	41,0	1,5	4,28
"	"	July	0,053	9,98	5,2	43,0	0,7	4,40
"	"	Aug.	0,050	9,71	5,1	43,3	1,0	4,22
<i>Burkea africana</i>	Leaves	Jan.	0,095	3,06	16,5	26,3	2,7	2,37
"	"	Feb.	0,092	3,19	14,0	30,0	1,8	2,48
"	"	March	0,086	4,20	15,2	14,7	2,0	3,65
"	"	June	0,071	3,72	10,6	26,1	2,7	2,65
"	"	July	0,034	3,82	8,8	24,1	2,0	2,37

Species	Type material	Month	P %	Ca %	Protein %	Fibre %	Fat %	Ash %
<i>Burkea africana</i>	Leaves	Aug.	0,048	3,86	9,1	28,1	2,1	2,48
<i>Terminalia sericea</i>	Leaves	Jan.	0,114	8,65	12,8	23,2	2,2	4,32
"	"	Feb.	0,098	11,70	12,7	23,5	2,7	5,11
"	"	March	0,089	10,13	12,0	18,4	3,7	4,73
"	"	June	0,067	12,32	8,5	20,2	4,1	4,72
"	"	July	0,034	13,08	6,9	20,8	3,8	4,24
"	"	Aug.	0,034	14,23	5,0	17,3	2,4	5,26
<i>Combretum psidioides</i>	Leaves	Jan.	0,117	7,32	13,1	30,9	2,8	4,41
"	"	Feb.	0,105	7,18	14,0	29,1	3,8	4,38
"	"	March	0,105	7,85	13,5	29,0	3,9	5,12
"	"	June	0,050	9,18	7,6	25,7	5,2	3,84
"	"	July	0,044	12,54	7,4	29,7	3,2	3,51
"	"	Aug.	0,050	15,69	7,2	34,3	3,9	5,36
<i>Ochna pulchra</i>	Leaves	Jan.	0,100	5,99	11,5	38,4	0,9	3,15
"	"	Feb.	0,098	7,98	10,0	36,7	0,9	3,92
"	"	March	0,101	5,03	10,0	37,2	1,2	2,52
"	"	June	0,095	6,66	9,1	38,2	1,0	2,94
"	"	July	0,071	5,32	6,7	36,9	1,2	3,12
"	"	Aug.	0,062	6,38	7,6	36,5	1,1	2,58
<i>Combretum collinum</i>	Leaves	Jan.	0,117	10,91	16,3	25,5	2,3	6,24
"	"	Feb.	0,112	11,44	16,7	24,0	2,6	5,77

Species	Type material	Month	P %	Ca %	Protein %	Fibre %	Fat %	Ash %
<i>Combretum collinum</i>	Leaves	March	0,107	12,15	17,0	20,7	3,9	6,19
"	"	June	0,098	13,94	11,6	22,3	3,8	5,57
"	"	July	0,067	13,17	14,0	20,9	5,1	6,60
"	"	Aug.	0,075	14,89	12,2	20,1	5,6	6,36
<i>Cenchrus ciliaris</i>	New vegetative	Jan.	0,053	1,30	9,1	37,5	1,6	8,90
"	"	Feb.	0,092	4,39	7,4	40,5	1,2	10,47
"	"	March	0,064	2,79	6,3	41,5	1,0	9,94
"	Total vegetative	Aug.	0,050	4,79	6,0	38,7	1,4	5,52
<i>Commelina africana</i>	New vegetative	Jan.	0,168	11,44	15,3	23,4	1,6	16,72
"	"	Feb.	0,105	11,57	9,7	21,3	1,5	9,95
"	"	March	0,090	12,77	5,6	31,0	1,6	8,65
<i>Triraphis schinzii</i>	New vegetative	March	0,062	2,53	5,1	44,2	1,7	4,30
"	Generative	March	0,142	2,00	10,1	40,1	1,3	5,21
<i>Rhynchelytrum species</i>	Total vegetative	June	0,025	2,13	3,0	37,9	1,1	6,93
"	Generative	June	0,025	2,39	2,4	36,5	0,9	4,88
<i>Eragrostis pallens</i>	New vegetative	March	0,031	1,46	2,8	45,1	1,0	4,32
"	Generative	March	0,078	2,00	4,0	41,0	1,4	4,07
<i>Securidaca longepedunculata</i>	Leaves	Jan,	0,115	2,47	15,6	30,9	4,0	2,54
"	"	Feb.	0,119	2,42	13,9	22,4	4,9	3,19
"	"	March	0,128	2,66	17,7	30,7	3,5	2,43
"	"	April	0,089	2,39	11,1	39,0	4,6	1,39
"	"	Aug.	0,073	2,53	7,9	37,1	3,7	1,56