STUDIES ON HERBACEOUS LAYER PRODUCTION IN <u>BURKEA AFRICANA</u> SAVANNA

By

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Supervisor: Prof. G.K. Theron

Co-supervisor: Prof. J.O. Grunow

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A point of view :

' Whether civilisation in South Africa
survives or not will be determined by
the way we manage our grasslands.'

A.W. Bayer, 1959.

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ABSTRACT

The effects of fire, woody vegetation and defoliation on components of the herbaceous layer in an area of *Burkea africana* savanna were studied for one year.
Biomass (live material) was significantly greater, over the year, in the open subhabitat than under the dominant *Burkea africana* trees and *Ochna pulchra* shrub clumps, in the case of the sward as a whole. Biomass of the palatable 'forage and intermediate' species group was, however, of the same order in the open as under *B. africana*, while that under *O. pulchra* remained less than in the open. Biomass of the non-forage species group was significantly greater in the open than in the two canopied subhabitats.
The amount of *in-vitro* digestible organic matter showed the same trends as the biomass, but there was more crude protein in forage and intermediate species under *B. africana* trees than in the open or under *O. pulchra* clumps.

An intense backfire applied in September 1978 resulted in a significant 29,4% less biomass over the following year, when compared with an unburnt area. This was largely due to the significant reduction in biomass and basal cover of the somewhat moribund non-forage species, mainly Eragrostis pallens, on the burnt plots. Basal cover and biomass of the leafier forage and intermediate species were not signicicantly affected by the backfire.

An eight-weekly clipping regime imposed on burnt plots resulted in a slower rate of biomass accumulation than was measured on burnt plots allowed unchecked regrowth. The slowest biomass accumulation rate was recorded, in the case of the sward as a whole, on unburnt, unclipped plots whilst the fastest was on burnt, unclipped plots. Burning followed by eight-weekly clipping reduced the biomass accumulation rate of the non-forage species relative to unburnt non-forage species, but stimulated the rate of accumulation of forage and intermediate species' biomass.

Exclusion of herbivores from burnt areas for differing periods resulted in the greatest peak standing crop occurring in those sites protected for the longest period (101 days) after the fire, in both Burkea africana and Acacia spp areas.

A six-weekly clipping interval resulted in relatively good dry matter yields of Digitaria eriantha ssp pentzii, both in a controlled and a natural environment, compared with more and less frequent clipping intervals. A similar clipping frequency also resulted in relatively good yields obtained from Brachiaria nigropedata, without adversely affecting carbohydrate reserves. A two cm clipping height resulted in greatest mortality of both species, whereas an eight cm height resulted in 100% survival.

An estimate of 71,87 g $m^{-2}yr^{-1}$ net grazeable annual above-ground production was obtained for the sward (on an oven-dry basis).

PRODUKSIESTUDIES OP DIE KRUIDLAAG VAN 'N BURKEA AFRICANA SAVANNE

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deur

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SAMEVATTING

Die invloed van vuur, houtagtige plantegroei en ontblaring op komponente van die kruidlaag van 'n stand in 'n *Burkea africana*-savanne is oor 'n periode van een jaar bestudeer.

Die lewende biomassa van die graslaag in geheel was deur die jaar betekenisvol groter in die oop subhabitat (buiteveld) as onder die dominante *Burkea africana* bome en *Ochna pulchra* struikgroepe. Die biomassa van die smaaklike 'voer en intermediêre spesies' was van dieselfde orde in die buiteveld as onder *B. africana* terwyl dié onder *O. pulchra* kleiner as in die buiteveld was. Die biomassa van nie-voer spesies was betekenisvol groter in die buiteveld as in die twee bedekte subhabitats.

Die hoeveelheid *in vitro* verteerbare organiese materiaal het dieselfde neiging as die biomassa getoon, maar die ruproteïengehalte van die voer- en intermediêre spesies was beter onder *B. africana* bome as in die buiteveld of onder *O. pulchra* struikgroepe.

'n Warm windop vuur gedurende September 1978 het 'n betekenisvolle kleiner biomassa van 29,4% in die daaropvolgende jaar in vergelyking met 'n ongebrande gebied tot gevolg gehad. Dit kan grootliks

toegeskryf word aan die betekenisvolle kleiner biomassa en basale bedekking van die nie-voer spesies met 'n laer lewenskragtigheid, waarvan Eragrostis pallens die belangrikste is, op die gebrande persele. Die basale bedekking en biomassa van die blaarryker voer-en intermediêre spesies is nie betekenisvol deur die windop vuur beinvloed nie.

'n Agtweeklikse snyprogram op die brandpersele het 'n stadiger biomassa akkumuleringstempo tot gevolg gehad in vergelyking met wat op die brandpersele waar onversteurde groei toegelaat is, gemeet is. Die stadigste biomassa-akkumuleringstempo vir die graslaag in geheel is op die ongebrande, ongesnyde persele aangeteken en die vinnigste op die gebrande ongesnyde persele. Brand gevolg deur 'n agtweeklikse snyprogram het 'n verlaging in die biomassa-akkumuleringstempo van die nie-voer spesies relatief tot ongebrande nie-voerspesies tot gevolg gehad, terwyl die biomassa-akkumuleringstempo van voer en intermediêre spesies gestimuleer is.

Die uitsluiting van herbivore vir verskillende periodes vanaf gebrande gebiede het tot gevolg gehad dat in beide die Burkea africana en Acacia spp—savannes die groter staande biomassa verkry is op daardie persele wat vir 'n periode van 101 dae (langste periode) na die brand beskerm is.

'n Sesweeklikse snyinterval het in vergelyking met 'n meer of minder dikwels ontblaringsprogram gunstige droëmateriaalopbrengste van Digitaria eriantha ssp pentzii in beide gekontroleerde en natuurlike omgewings tot gevolg gehad. In die geval van Brachiaria nigropedata het soortgelyke ontblaringsfrekwensies ook betreklik goeie droëmateriaalopbrengste gegee, sonder om die koolhidraatreserwes nadelig te beinvloed. 'n Twee sentimeter snyhoogte het die grootste mortaliteit van beide grassoorte tot gevolg gehad, terwyl 'n 8 cm snyhoogte 'n 100% oorlewing gegee het.

'n Beraamde 71,87 g $m^{-2}jr^{-1}$ netto beweibare jaarlikse bogrondse biomassaproduksie, op 'n oonddroë basis, is vir die ongebrande graslaag gekry.

ACKNOWLEDGEMENTS

I wish to sincerely thank both Professor G.K. Theron and Professor J.O. Grunow, under whose supervision the field work was undertaken, for constant support, advice and interest.

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CURRICULUM VITAE

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INTRODUCTION

This study formed part of the inter-disciplinary South African Savanna Ecosystem Project conducted on the Nylsvley Provincial Nature Reserve under the aegis of the Council for Scientific and Industrial Research. The terms of reference and objectives of the Ecosystem Project have been summarized as being '... to develop the understanding necessary to predict changes in the ecosystem's stability induced by various natural and man-made stresses.' (Anon, 1978(a)). As Whittaker (1970) has stated '... perhaps the most fundamental dimension of an ecosystem is its productivity', the need to consider this aspect of ecosystem functioning is apparent. Furthermore, it has been stated that the value of the Savanna Ecosystem Project will be judged '... both on its scientific merit and practical benefits' (Anon 1978 (a)). Within this context, the objectives of the present study were to quantify the structural and functional components of above-ground herbaceous layer vegetation (particularly in regard to productivity) in a variety of situations pertinent to the particular savanna vegetation type. The study was therefore a direct contribution to the producer component research groups' efforts in the overall project.

Major aspects investigated were the influence of woody vegetation, fire and defoliation on herbaceous layer biomass cycles and accumulation rates, and the effects of defoliation regimes on regrowth. Such information is basic to the needs of the consumer and decomposer component research groups as well as providing data to land-users which may be of value in determining land-use management strategies.

Although primary production ecology is not, per se, a new field of study, this aspect of ecosystem function has not generally been investigated in southern Africa to the extent that it has in many other biogeographical regions. As a result, the ambiguity in terminology and conceptualization which is apparent throughout relevant literature is a real problem insofar as comparing data, both within the region and elsewhere, is concerned. Phrases such as 'shrewd guesses', 'simplifications' and 'appropriate adjustments', quoted by Rutherford (1978), often form the basis for estimates of production. It is therefore both appropriate and desirable to discuss the present study within the context of primary production ecology, and to define the concepts pertaining to this study.

In southern Africa, the most widely used technique for attempting to quantify above-ground herbaceous layer production has been the destructive harvest method (Rutherford, 1978). Net above-ground annual production has been variously equated with peak biomass (live material) peak biomass and necromass (live and dead material) and biomass increment over a season (Williamson, 1976). However, as Williamson (1976) observed, production need not be equivalent to any of these measurements:-
no account is taken of losses through mortality, consumption, leaching, exudation, translocation and loss of plant matter to the litter compartment.

Insofar as several studies are of a purely practical nature, with the objective of gaining a crude estimate of, for example, available graze, or evaluating the effects of fertilizer applications, the limitations referred to above are of a less critical nature. However, increasing requirements for plant-based products demand a more precise understanding of primary production within various biogeographical areas. Such an understanding is a prerequisite for the most efficient utilization of an ecosystem. Refined physiological techniques (e.g. Sestak, Catsky and Jarvis, 1971) involving measurements of carbon assimilation in relation to environmental variables have an important contribution to make in this respect, as have 'whole-plant' studies, examining translocation and exudation (Cresswell, Ferrar, Rutherford, Grunow and Grossman, 1979). However, such studies are often impracticable under natural conditions, and the difficulties relating to such techniques are compounded in a heterogeneous, perennial sward.

In this study, the sequential harvest technique was selected as being the most practicable method of quantifying biomass and necromass. The variables which may be quantified by this method are:

(i) Biomass - defined as the mass of green, attached aerial plant matter,

(ii) Necromass - the mass of dead, attached aerial plant matter,

(iii) Biomass accumulation rate - the resultant of simultaneously occurring accretions due to growth, and losses due to all or any of the loss factors described above, largely manifested as change in amount of green material over time,

(iv) Necromass accumulation rate - the net result of inflow of biomass to necromass and outflow of necromass to litter, and

(v) Litter accumulation rate - the net result of inflow of necromass to litter and outflow of litter to soil organic matter (c f Grunow, Groeneveld and du Toit, 1980).

((i) and (ii) are structural variables, (iii) to (v) are functional variables (*sensu* Odum, 1962)). As stubble was not included in biomass estimates, all amounts refer to plant material potentially grazeable by larger herbivores. Biomass accumulation rate (BAR), by definition, is not synonymous with net annual aerial production (NAAP). This concept (NAAP) is elaborated on in Chapter 6, in which estimates of NAAP are presented.

The term 'standing crop' is used in the traditional sense to describe biomass plus necromass. The use of this term has been criticized as being ambiguous and scientifically imprecise (Rutherford, 1978), but no wholly acceptable alternative is readily apparent.

In a treatise on herbaceous layer production, it is not considered necessary to qualify the above terms by use of the prefix 'phyto' (e.g. phytobiomass).

Biomass and necromass are expressed in the unit $g\ m^{-2}$. This unit is readily convertible to other units

$g\ m^{-2} \times 10 = kg\ ha^{-1}$
$g\ m^{-2} \div 100 = t\ ha^{-1}$
$kg\ ha^{-1} \div 1000 = t\ ha^{-1}$

CHAPTER 2

THE STUDY AREA

2.1 Locality and topography

The study area occupies approximately 750 hectares of the Nylsvley Provincial Nature Reserve, near Naboomspruit, Transvaal ($24^{o}29'$S, $28^{o}41'$E). Most of the study area forms part of a gently sloping sandy upland at 1 100 m above sea level bounded on the north western edge by the Nyl river drainage (vlei) system (1 080 m above sea level). A prominent rocky outcrop (Maroelakop 1 140 m above sea level) occupies approximately 100 hectares near the centre of the study area.

2.2 Soils

The soils of the study area have been mapped and fully described by Harmse (1977) according to the South African Soil Classification System (McVicar, de Villiers, Loxton, Verster, Lambrechts, Merryweather, le Roux and Harmse, 1977). They are generally non-calcareous, well drained sandy soils of poor nutrient status, derived from sandstone, conglomerates and grits of the underlying Waterberg system. The dominant forms are Hutton, Clovelly and Mispah, the Hutton form dominating the study area latosols. The profile of this form comprises an orthic A horizon, generally of 50 to 300mm depth, underlain by a red apedal B horizon of from 300 to 1 300 mm depth. Of the several series of this form identified in the study area, most are low in available phosphate content and have a pH of about 5. An exception is the eutrophic Portsmouth series which occurs in a few scattered patches, thought to be the sites of early indigenous settlements. The clay content of the Hutton form is less than 16%.

These sandy soils generally hold little water, with plant available water ranging from 3% to 6% volumetrically (van Rooyen, 1978).

2.3 Climate

A mean annual rainfall of 640 mm, over 40 years, has been reported for Mosdene, a farm 10 km north-east of the study area (Huntley and Morris, 1978). Eighty per cent of this rainfall falls during the period November through March. Short term records for Nylsvley (Fig. 1) demonstrate the variability in distribution of rainfall, both between and within years.

From April through August, mean daily air temperatures are from 12 to 20°C, rising to from 14 to 22°C during September and October. From November through March, mean daily air temperatures are from 20 to 25°C. The extreme maximum temperature reached in the growing (rainy) season from October through April for Nylstroom, a town situated 25 km to the south west, over a 40 year period was 38,9°C. The extreme minimum for the dry season (May through September)over the same period was -6,1°C (Huntley and Morris, 1978).

Ground frosts occur on about 20 days in most years and have been recorded in all months from May to September (Huntley and Morris, 1978).

The average total radiation in January and June during 1977 to 1979 was 24,3 and 14,2 $Mjm^{-2}d^{-1}$ respectively. Approximately 50% of radiation was photosynthetically active (Huntley and Morris, 1978).

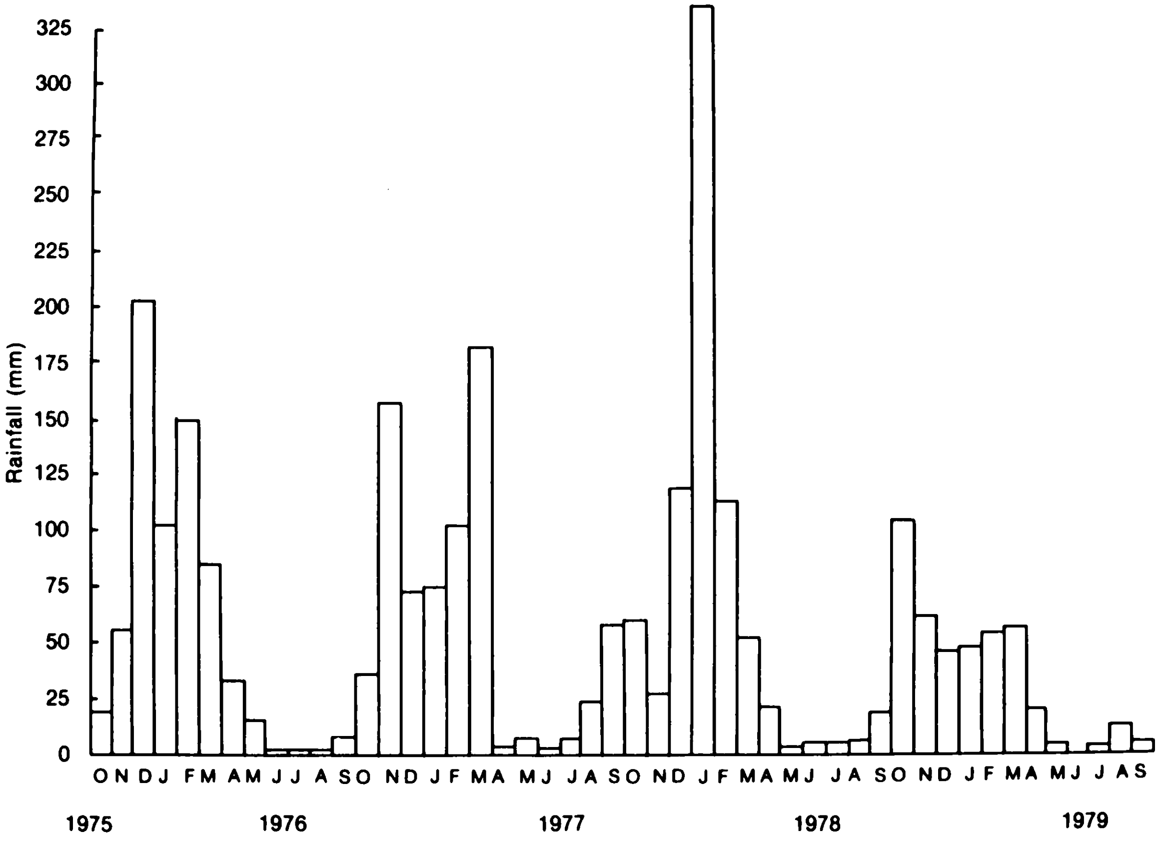

Fig. 1. Monthly rainfall recorded at Nylsvley from October 1975 to September 1979.

The relative humidity of the air is consistently low in the early afternoon (14h00), dropping to below 15% from July through September. Mean values at 08h00 for these months ranged from 57% to 70% while mean monthly values for the same time during the wet months of October through March ranged from 65% to 86% (Huntley and Morris, 1978).

Meteorological data, obtained from a weather station adjacent to the study site, are shown in Table 1, for the period July 1978 to September 1979.

Table 1 : Relevant meteorological data from Station 2 * Nylsvley, between July 1978 and September 1979

Month	Monthly rainfall mm	Monthly evaporation mm	Mean relative humidity %	Air Temperature			
				Mean of daily maximum °C	Mean of daily minimum °C	Mean of daily temp. °C	Mean grass minimum °C
1978							
July	0.0	141,7	47,5	21,4	8,4	14,9	-2,4
August	5,2	287,6	42,6	27,4	11,3	19,3	3,6
September	23,0	231,6	40,4	27,7	11,9	19,8	5,5
October	104,7	259,5	47,4	29,0	14,0	21,5	9,9
November	63,6	222,3	56,5	28,6	15,4	22,0	11,8
December	49,4	275,5	51,9	30,4	15,9	23,2	8,9
1979							
January	49,1	256,5	52,7	30,4	16,5	23,4	10,4
February	57,2	259,1	59,0	30,6	16,8	23,7	10,5
March	59,6	334,3	53,1	30,0	14,8	22,4	6,5
April	19,0	228,0	51,5	28,3	16,2	22,3	7,6
May	0,6	198,6	52,7	24,7	11,4	18,0	3,0
June	NA**	NA	NA	NA	NA	NA	NA
July	0,0	NA	51,3	21,4	5,7	13,6	NA
August	12,5	176,0	48,8	22,9	8,4	15,6	1,7
September	1,4	242,8	40,5	28,2	11,2	19,6	5,6

* Station 2 - the station automatically and continuously recording meteorological data, adjacent to game-proof fenced study site described.

** NA - data not available.

2.4 Vegetation

The reserve lies within Acocks' (1975) Mixed Bushveld Veld Type. A detailed phytosociological classification has been done and described by Coetzee, van der Meulen, Zwanziger, Gonsalves and Weisser (1977). The vegetation of the study area comprises a mosaic of broadleaf communities on deeper latosols and small scattered areas of leptophyllous thorn savanna on more compacted soils with higher amounts of N, P and K (Harmse, 1977).

The most commonly occurring community within the study area is the *Eragrostis pallens* - *Burkea africana* tree savanna, differentiated by such woody species as *Grewia flavescens*, *Strychnos pungens* and *Strychnos cocculoides*, the grasses *Eragrostis pallens*, *Aristida argentea*, *Aristida stipitata*, and the toxic woody geophyte *Dichapetalum cymosum*. Of the variations identified within this community, the most extensive, and that in which the majority of the work described in this study was done, is the *Eragrostis pallens* - *Dombeya rotundifolia* variation. This variation occurs on well-drained soils of the Hutton and Mispah forms. *Burkea africana*, *Terminalia sericea* and *Combretum molle* are the dominant species in the tree stratum, the dominant shrubs being *Grewia flavescens* and *Ochna pulchra* (Coetzee *et al*., 1977). Tree canopy spread cover varies from 20 - 60% and averages 27,5% (Van Rooyen and Theron, 1977). The basal cover of the herbaceous layer is about 5%, the stoloniferous *Digitaria eriantha* ssp *pentzii* (hereafter referred to as *Digitaria eriantha*) and the tufted *Eragrostis pallens* predominating in the largely perennial sward (Van Rooyen and Theron, 1977).

The woody component of the scattered leptophyllous thorn savanna patches is dominated by *Acacia nilotica* and *Acacia tortilis*. *Eragrostis rigidior*, *Eragrostis lehmanniana* and, under trees, *Panicum maximum* are the dominant grass species. The dwarf shrub *Solanum panduraeforme* predominates in patches, often to the almost total exclusion of grasses. The important forage species *Cenchrus ciliaris* occurs in this community.

2.5 Biotic influences

During the 50 years prior to proclamation as a Provincial Nature Reserve in 1974, the study area was part of a cattle ranch (Grunow, 1974). Approximately 300 cattle were allowed to graze on the 750 ha forming the present study area, usually from January to April. This short grazing period was largely dictated by the presence of the toxic woody geophyte *Dichapetalum cymosum*, which usually exhibits first leaf flush early in the growing season, around September/October. At this time it would prove attractive to cattle as there is not much green grass. This toxic species would similarly be a problem after grass growth had all but ceased in about April. Cattle were excluded from the study area from April 1977, to the termination of this study in March 1980.

The most significant indigenous ungulate herbivore, in terms of the herbaceous layer, is the impala, *Aepyceros melampus*. The impala population is highly mobile throughout the reserve, and reliable estimates of impala numbers within the study area are not available for the period of this study.

Earlier, Monro (1979) reported considerable fluctuations in impala numbers within the study area with a mean of slightly more than 100 animals. Carr (1976) stated that impala were evenly distributed over the study area during the summer, but during the dry, colder months they moved out of *Burkea africana* savanna into other areas. Other grazing herbivores present in lesser numbers include zebra (*Equus burchellii*), blue gnu (*Connochaetes taurinus*), roan (*Hippotragus equinus*) and tsessebe (*Damaliscus lunatus*). Spring hares (*Pedetes capensis*) and warthog (*Phacocoerus aethiopicus*) are also present. Of the phytophagous insects, grasshoppers of several species are the most significant in terms of herbaceous layer folivory (Gandar, 1978).

The vegetation of the study area had been protected from fire for at least five years prior to the commencement of this study.

CHAPTER 3

THE INFLUENCE OF WOODY VEGETATION ON THE HERBACEOUS LAYER BIOMASS

3.1 Introduction

The herbaceous layer of tree savanna vegetation occurs in two distinct subhabitats - the open, between-tree subhabitat and the other one under tree and shrub canopies. The relationship between the two subhabitats has been described as '... an enigma of woodland savanna which demands continued research' (Grunow and Bosch 1978). From an animal production point of view, many deciduous savanna woody species, such as those at Nylsvley, provide browse throughout the year. Browse is provided both from living material and later from leaves on the ground, to those animals whose diet normally consists mainly of browse. It is particularly noteworthy too, that as grass quality deteriorates during the dry period, browse is normally taken by mixed feeders and even by animals whose diet normally consists mainly of grass. The provision of shade is an obvious benefit derived from trees, and localized, increased soil fertility, has been reported under trees relative to the surrounding open subhabitat (Bosch and van Wyk, 1970). Bate (1979) reported higher levels of total soil nitrogen, over a season, under Burkea africana trees when compared with the open subhabitat. The occurrence of palatable grasses has been found to be positively correlated with tree canopy cover (Bosch and van Wyk, 1970, Kennard and Walker, 1973).

Clearing of woody vegetation in several savanna types in Zimbabwe resulted in mean relative herbaceous dry matter yield increases of from 150% to 364% (Barnes, 1979). However, a concomitant change in the botanical composition was measured, with unpalatable species increasing and desirable palatable species decreasing in number.

The total amount of water entering the soil, and thereby becoming available to grasses, may be less under tree and shrub canopies than in the open, due to interception (Donaldson, 1969). On the other hand, reduced evapotranspiration under tree canopies may result in longer availability of soil water to grasses under trees than in the open, especially in semi-arid areas characterized by erratic rainfall distribution.

Woody vegetation is thought to play an as yet incompletely elucidated role in nutrient recycling in savanna. As the above-ground dry mass of the woody component of Burkea savanna at Nylsvley is of the order of 16 t ha^{-1} (Rutherford, 1978) it represents a large pool of unavailable nutrients, a portion of which is recycled to the soil annually.

However, in several savanna areas of southern Africa, there has been an increase in the woody component, at the expense of herbaceous plants (e.g. van der Schyff, 1964; West, 1965; Donaldson, 1969). Typically there appears to be an exponential decrease in herbaceous layer dry matter yield with increasing tree and shrub density,both in southern African savanna and other phytogeographical regions (Clary, 1969; Donaldson and Kelk, 1970; Walker, Moore and Robertson, 1972; Ford and Newbould, 1977).

Ideally there exists an optimal ratio, for each agro-ecological unit, of open: canopied surface area, in which the beneficial aspects of the woody vegetation exceed its suppressive effect on production of the herbaceous layer.

The objectives of the present study were to compare the amounts and quality of dry matter (DM) produced in open and canopied subhabitats. As the sward contains species not normally utilized by most ungulate herbivores, the herbaceous layer was divided into forage and non-forage categories in order to assess the relative significance of the different subhabitats in terms of utilizable herbaceous layer production. It is obvious that in certain cases, there will be a degree of overlap between the forage and non-forage categories. For example, Zimmerman (1978) reported that cattle at Nylsvley selected the generally unpalatable grass Urelytrum squarrosum to a large degree during September. For the rest of the year, this species was hardly grazed at all. In some parts of Africa, several species of the genus Aristida form a major part of herbivore diets (Grunow 1980), although such species are generally considered to be relatively unpalatable.

Ideally, maximum benefit would be gained by considering biomass trends of individual species, but this was not done in the present study for the following reason: -
there is a large number of species present, and the spatial distribution of many of these species is so variable as to exclude the possibility of using quadrats as sampling units for individual species when the harvest method is employed. Sampling individual tufts is both onerous and time consuming, and because of the variability in tuft size and vigour, large error limits attend data obtained by such a method (Grunow and Grossman, 1978).

3.1.1 Use of the harvest method

Various methods of determining herbaceous layer mass have been described, including non-destructive and destructive techniques. Included amongst the former, are techniques utilizing fairly sophisticated electronic devices, such as the radiometer and capacitance meter, mechanical devices such as the disc pasture meter (Bransby and Tainton, 1977) and subjective visual estimates (Haydock and Shaw, 1975). These techniques are relatively rapid compared with the destructive harvesting technique, but each suffer to a greater or lesser degree, from limiting drawbacks in natural rangeland. In all these methods, estimates obtained must be correlated to actual dry matter values obtained by destructive harvesting. The electronic instruments are not readily available and, as far as can be ascertained have not been satisfactorily tested in local natural rangeland. The disc pasture meter is not, it would appear, suitable for use in the Nylsvley sward, characterized as it is by a high degree of inter-specific morphological heterogeneity. In addition, the use of the disc pasture meter is further limited in a sward containing large moribund tufted perennials. The comparative yield method is suitable for rapidly assessing large areas (Kelly and McNeill, 1980) but if utilized sequentially over a season, would in any case require concomitant harvesting to establish regression relationships of visual estimate against yield.

3.2 Methods

For the purpose of this study, three major subhabitats were identified:

(i) under the dominant *Burkea africana* trees, (Fig 2)
(ii) under *Ochna pulchra* shrub clumps, (Fig 3) and
(iii) the between-tree, open subhabitat. (Fig 2).

Two height classes of *B.africana* were identified and sampled separately :-

(i) Between 1,5m and 3m high and
(ii) higher than 3m.

In order to assess the relative contribution of the different components of the grass layer it was divided into the following categories:

(i) Forage and intermediate (FI) species, including preferred and principal food species as well as other species of intermediate palatability to ungulates,
(ii) non-forage species (NF), including grasses and graminaceous species not usually grazed by ungulates,
(iii) non-forage non-grasses (NFNG), including non-graminaceous species (forbs) occurring in the herbaceous layer but not normally eaten by grazing ungulates.

The principal species in each group are listed in Appendix I.

Fig. 2. The 'under *Burkea africana*' and between tree, 'open' subhabitats.

Fig. 3. The 'under *Ochna pulchra* shrub clumps' subhabitat.

3.2.1 Quadrat sampling

As this particular study was confined to a relatively small study site, occupying some 6 ha, it was decided to use the destructive harvesting technique, employing quadrats as sampling units. Previous work at Nylsvley (Grunow, 1976; 1977) indicated that a sampling interval of four weeks during the growing season (October to May) extended to eight weeks during the dry dormant season (June to September) was suitable for determining biomass over a season. A sampling intensity of 30 to 40 0,5m^2 quadrats resulted in a standard error of ± 10% of the mean biomass value. Accordingly, in this study, at 4-weekly intervals between October 1978 and May 1979, and thereafter at 8-weekly intervals to September 1979, four sites were selected in each subhabitat and ten 1 m x 0,5m quadrats were harvested at each site.

3.2.2 Experimental layout and method of harvesting

At each harvest date, four sites were randomly selected in each of the four subhabitats previously described. They were regarded as being replicates in a random design layout. To ensure the random selection of trees and shrub clumps at each harvest date, the following method was adopted; prior to the commencement of the study, suitable trees and bush clumps were selected and numbered. At each harvest date, random numbers were drawn and the corresponding tree or bush clump sites were sampled. Quadrats were harvested in the open subhabitat between the randomly selected trees and bush clumps. In each replicate, at each harvest date, ten 1m x 0,5m quadrats were sited at randomly selected distances from each other in random directions. Species were clipped at a height above ground level that was considered to include all potentially grazeable material. A variable height stubble was thus left unharvested. Clipping height has been shown to be critical to the mass measured (Opperman, 1973) and care was taken to ensure a consistent height for each species. In practice, this height ranged from 1,2 cm above ground level for the smaller species to 5,5 cm for the larger, denser, harder tufted species. The three species groups previously defined were clipped and bagged separately in the field. In the laboratory, the harvested material was further sorted into biomass and necromass components, dried to constant mass in a forced draught oven at 70°C and subsequently weighed.

3.2.3 Chemical analyses

At each harvest date a representative, composite sample was kept from the live DM (biomass) harvested in each subhabitat. The samples were thoroughly ground through a 1 mm mesh sieve. Portions were analyzed for total nitrogen content, using the Kjeldahl technique, at the Citrus Exchange Leaf Laboratory, Verwoerdburg. Percentage crude protein (CP) content of each sample was calculated by multiplying percentage nitrogen by 6,25. This value was subsequently used to calculate the actual mass of CP per unit area.

Separate portions of each ground sample were analyzed for *in vitro* digestible organic matter (IVDOM) content at the Animal and Dairy Science Research Institute, Irene, using a modified two-stage Tilley and Terry (1963) technique. IVDOM, expressed as a percentage of total organic matter (OM) was used to calculate actual amounts of IVDOM per unit area.

3.2.4 Calculation of biomass accumulation rate

The following method, adapted from Singh, Lauenroth and Steinhorst (1975), was used to assess the mean rate of accumulation of biomass (BAR : g m^{-2} day^{-1})

$$BAR = \sum_{n=1}^{k} (B_n - B_{n-1})^* / t_k - t_o$$

Where B = grazeable above-ground biomass (g m^{-2})

t_o to t_k = times of harvest

* = only increments and their corresponding clipping intervals used

This method does not account for flow to necromass from biomass, nor for loss to insects, translocation of metabolites, leaching or exudation losses.

3.3 Results

3.3.1 Biomass and nutritional characteristics

The curves of the total biomass (sum of biomass of FI, NF and NFNG) under the two height classes of B.africana are similar (Fig. 4). The high value recorded in February under the smaller height class is largely due to a localized clump of the large tufted grass Trachypogon spicatus which was encountered at the site sampled on that particular date. Trachypogon spicatus is not generally found to any extent under more mature B. africana trees, and is probably a localized reflection of the less developed canopy of the saplings sampled on that date. However,

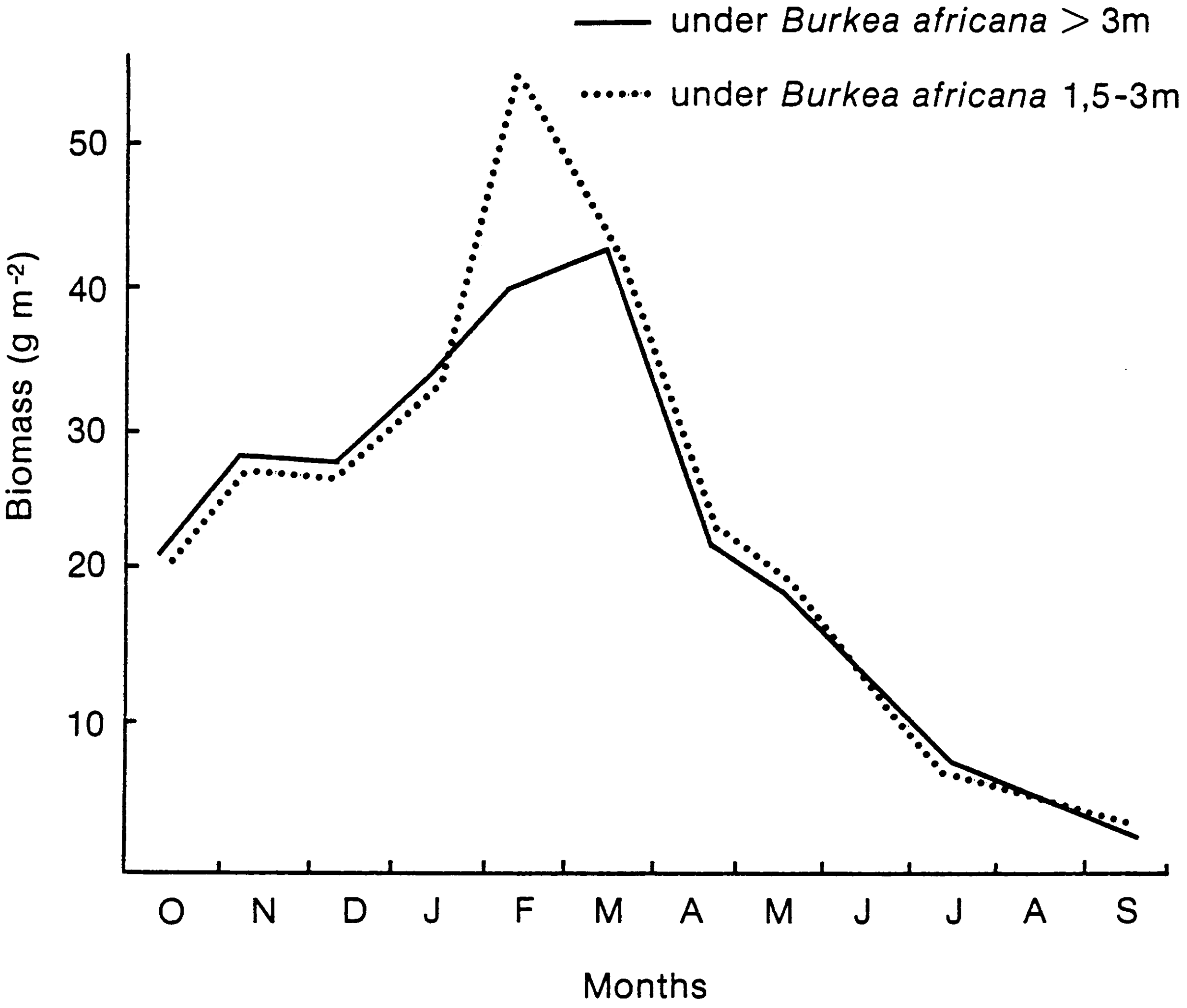

Fig.4. Biomass (g m^{-2}) of the sward as a whole (total biomass), under two height classes of Burkea africana, 1978/79.

an analysis of variance and comparison of means conducted on the areas under the total biomass curves revealed no statistically significant differences between the amount of biomass present, over the year, under the two height classes of _B. africana_ (Table 2). This would suggest that, generally, the smaller class of trees is exerting a similar influence on the herbaceous layer as the more mature trees. Accordingly, further treatment of data is limited to the general 'under _B. africana_' subhabitat and no distinction is made between height classes.

Table 2 : A comparison of the areas (cm^2) under the total biomass curves of the herbaceous layer under two height classes of _Burkea africana_, 1978/79

Replicate	_Burkea africana_	
	> 3 m	1,5 m - 3 m
I	49,0	49,6
II	56,7	46,3
III	44,2	43,6
IV	46,1	51,4
Mean	49,0	47,7

LSD means : F value NS

3.3.1.1 Biomass under *Burkea africana*, *Ochna pulchra* and in the open subhabitat

The total biomass curves (Fig. 5) show similar trends over the year, but differ in the actual amounts of biomass present in the three subhabitats. Biomass decreases from the open subhabitat to under *B. africana* trees, with the lowest amount of biomass over the year occurring under *O. pulchra* shrub clumps. An analysis of variance and comparison of the subhabitat means conducted on the areas under the three biomass curves revealed that these differences are statistically highly significant (Table 3).

Table 3 : A comparison of the areas (cm^2) under the total biomass curves for three subhabitats, 1978/79

Replicate	Subhabitat		
	Under *Burkea africana*	Under *Ochna pulchra*	Open
I	49,0	35,1	72,2
II	56,7	34,9	64,1
III	44,2	34,3	67,7
IV	46,1	39,9	73,3
Mean	49,0	36,1	69,1

LSD Means : 7,0 ($p = 0,05$); 10,4 ($p = 0,01$)

However, when the sward is divided into the three categories described, it is apparent that the differences between subhabitats are largely due to the greater biomass of the NF species group in the open subhabitat as compared to the two canopied subhabitats (Fig. 6). Statistical analysis revealed that this difference

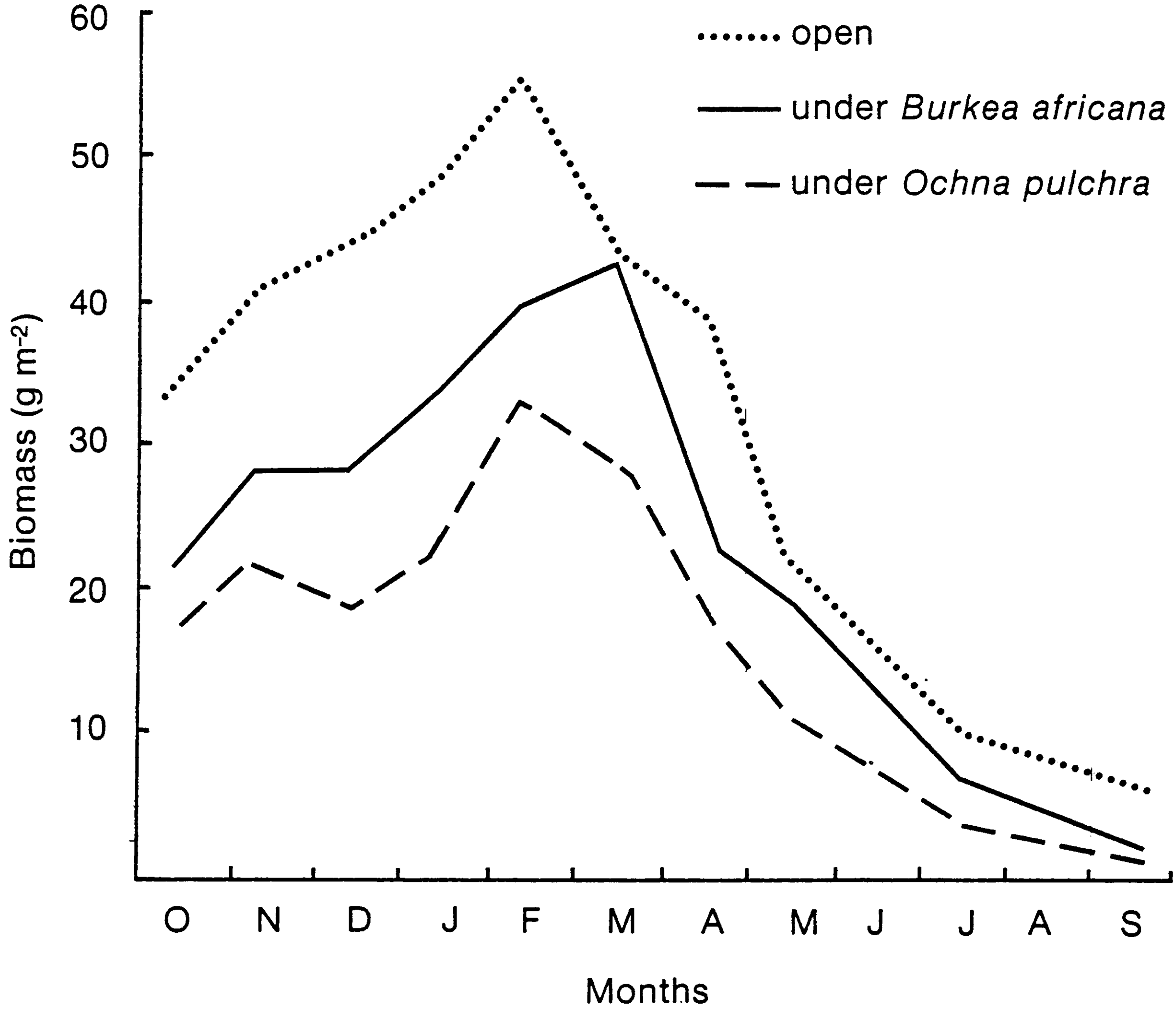

Fig. 5. Biomass (g m^{-2}) of the sward as a whole (total biomass), in three subhabitats, 1978/79.

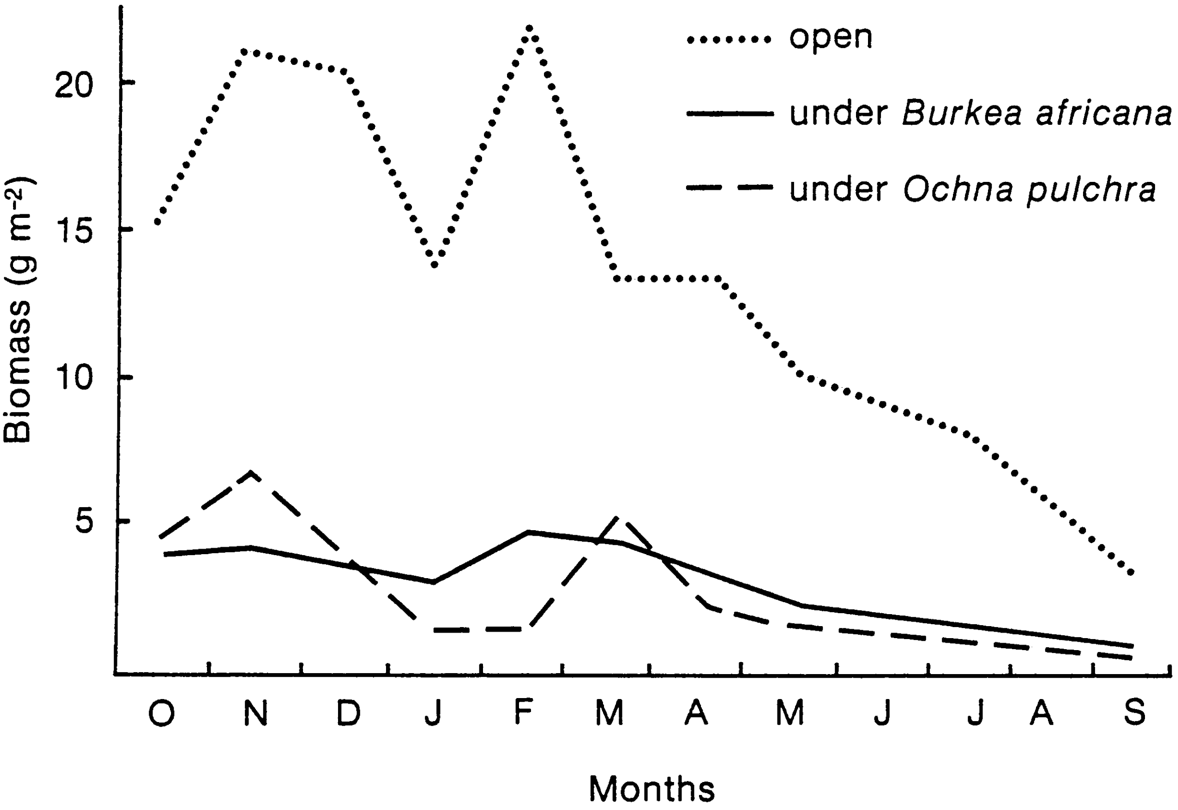

Fig. 6. Biomass (g m^{-2}) of non-forage species in three subhabitats, 1978/79.

is highly significant (Table 4).

<u>Table 4</u> : A comparison of the areas (cm^2) under the non-forage species biomass curves for three subhabitats, 1978/79.

Replicate	Subhabitat		
	Under *Burkea africana*	Under *Ochna pulchra*	Open
I	6,1	6,0	32,6
II	8,2	7,8	27,4
III	8,0	6,2	25,5
IV	6,8	6,6	29,5
Mean	7,3	6,7	28,8

LSD Means : 3,5 (p = 0,05); 4,4 (p = 0,01)

In fact, there is no significant difference between the amount of FI species biomass under *B. africana* and in the open (Fig. 7). The amount of FI biomass in these two subhabitats is however significantly higher than under *O. pulchra* shrub clumps (Table 5).

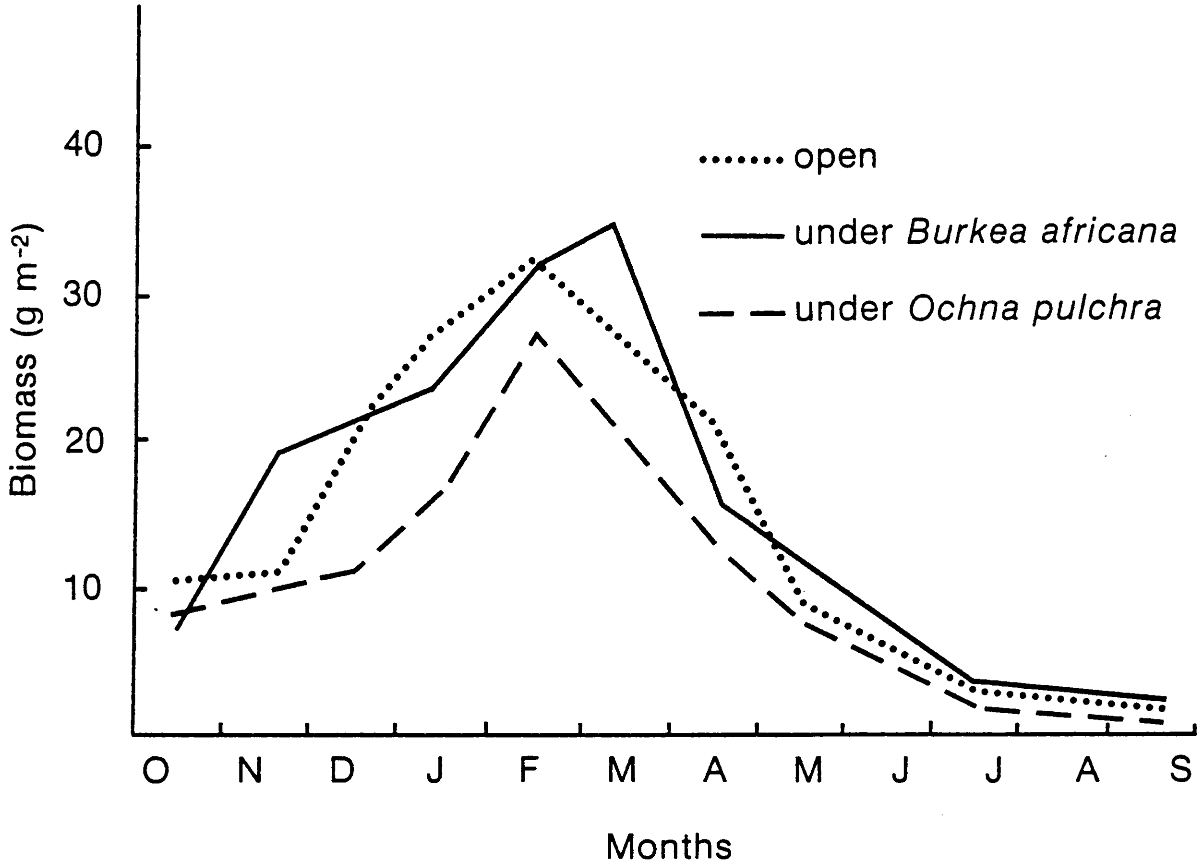

Fig. 7. Biomass (g m^{-2}) of forage and intermediate species in three subhabitats, 1978/79

Table 5 : A comparison of the areas (cm^2) under the forage and intermediate species biomass curves for three subhabitats, 1978/79.

Replicate	Subhabitat		
	Under *Burkea africana*	Under *Ochna pulchra*	Open
I	36,0	26,1	32,2
II	40,0	20,4	30,1
III	31,3	26,2	34,1
IV	34,7	27,4	37,0
Mean	35,5	25,0	33,4

LSD means : 5,2 (p = 0,05); 7,5 (p = 0,01)

Forage and intermediate species formed on average 72,4% of total biomass present under *B. africana*, 69,2% under *O. pulchra* and only 48,2% of the total herbaceous biomass in the open subhabitat (Table 6). Compared with this, non-forage species formed on average 41,5% of total biomass in the open subhabitat and only 14,9% and 18,6% under *B. africana* and *O. pulchra* respectively (Table 6).

Table 6 : Forage and intermediate species (FI), non-forage species (NF) and non-forage non-grasses (NFNG) average biomass as percentages of average total biomass in three subhabitats.

Grass layer category	Subhabitat		
	Under *Burkea africana*	Under *Ochna pulchra*	Open
FI species	72,4	69,2	48,2
NF species	14,9	18,6	41,5
NFNG	12,7	12,2	10,3

Rutherford (1978) observed that excluding non-grasses from estimates of herbaceous layer production would result in an underestimation of production. This component of the herbaceous layer formed on average 10,3% of the total biomass in the open subhabitat, 12,7% under *B. africana* and 12,2% under *O. pulchra*.

In order to achieve uniformity of precision within International Biological Programme production studies, an estimate with a standard error within 10% of the mean has been recommended (Milner and Hughes, 1968). In Table 7 it can be seen that the level of sampling in this study was generally sufficient to obtain this degree of accuracy, in the case of the herbaceous layer as a whole, at most sampling dates.

Table 7 : Standard error (SE) as a percentage of the mean biomass value of the herbaceous layer at each harvest date, 1978/79

Month	Subhabitat			Average per Harvest Date
	Under *Burkea africana*	Under *Ochna pulchra*	Open	
October	11,8	10,1	9,9	10,6
November	9,9	9,5	8,6	9,3
December	8,2	15,7	7,5	10,4
January	6,9	10,3	9,2	8,8
February	5,7	11,6	6,9	8,1
March	9,3	12,7	10,0	10,6
April	9,8	8,4	9,4	9,2
May	10,2	10,0	9,4	9,8
July	11,4	15,3	11,0	12,5
September	10,3	15,0	11,6	12,3
Average per Subhabitat	9,4	11,8	9,4	10,2

It is apparent that, using the same number of sampling units, a greater level of accuracy in sampling is obtained when a greater mass is harvested. Highest biomass values recorded around January and February resulted in standard errors expressed as percentages of the means of as low as *ca* 6%. Standard errors expressed as percentages of the means were generally higher in the under *O. pulchra* subhabitat, where biomass was lowest throughout the season, than in the other subhabitats. A similar observation was reported by Strugnell and Piggot (1978).

3.3.1.2 Nutritional characteristics

The IVDOM curves, reflecting the actual amounts of digestible organic matter available to herbivores over the year, largely exhibit the same tendencies as the biomass curves. The greatest amount of IVDOM in the herbaceous layer as a whole, is present in the open subhabitat (Fig. 8). As in the case of the biomass curves, this is largely due to the greater amount of IVDOM of the NF category in the open subhabitat, as compared to the two canopied subhabitats (Fig. 9). The amount of IVDOM in the FI species category is of the same order of magnitude under *B. africana* as in the open subhabitat, the lowest amount of IVDOM in this category occurring under *O. pulchra* shrub clumps (Fig. 10).

In the case of the CP curves, reflecting the actual amounts of CP available to herbivores, a noteworthy difference is apparent :- unlike both biomass and IVDOM which were greater in the open in the case of the herbaceous layer as a whole, the amount of CP (total biomass) is of the same order under *B. africana* and in the open subhabitat (Fig. 11). The least amount of CP over the season is, as in the case of biomass and IVDOM, found under *O. pulchra* shrub clumps.

From Fig. 12 it is apparent that the above phenomenon is due to the greater amount of CP in the FI species under *B. africana*, particularly between October and March, as compared to the other two subhabitats. The greater amount of CP in the FI species under *B. africana* is due to the fact that in this particular subhabitat the FI species group has a higher percentage CP content than do the FI species in the open and under *O. pulchra* (Table 8).

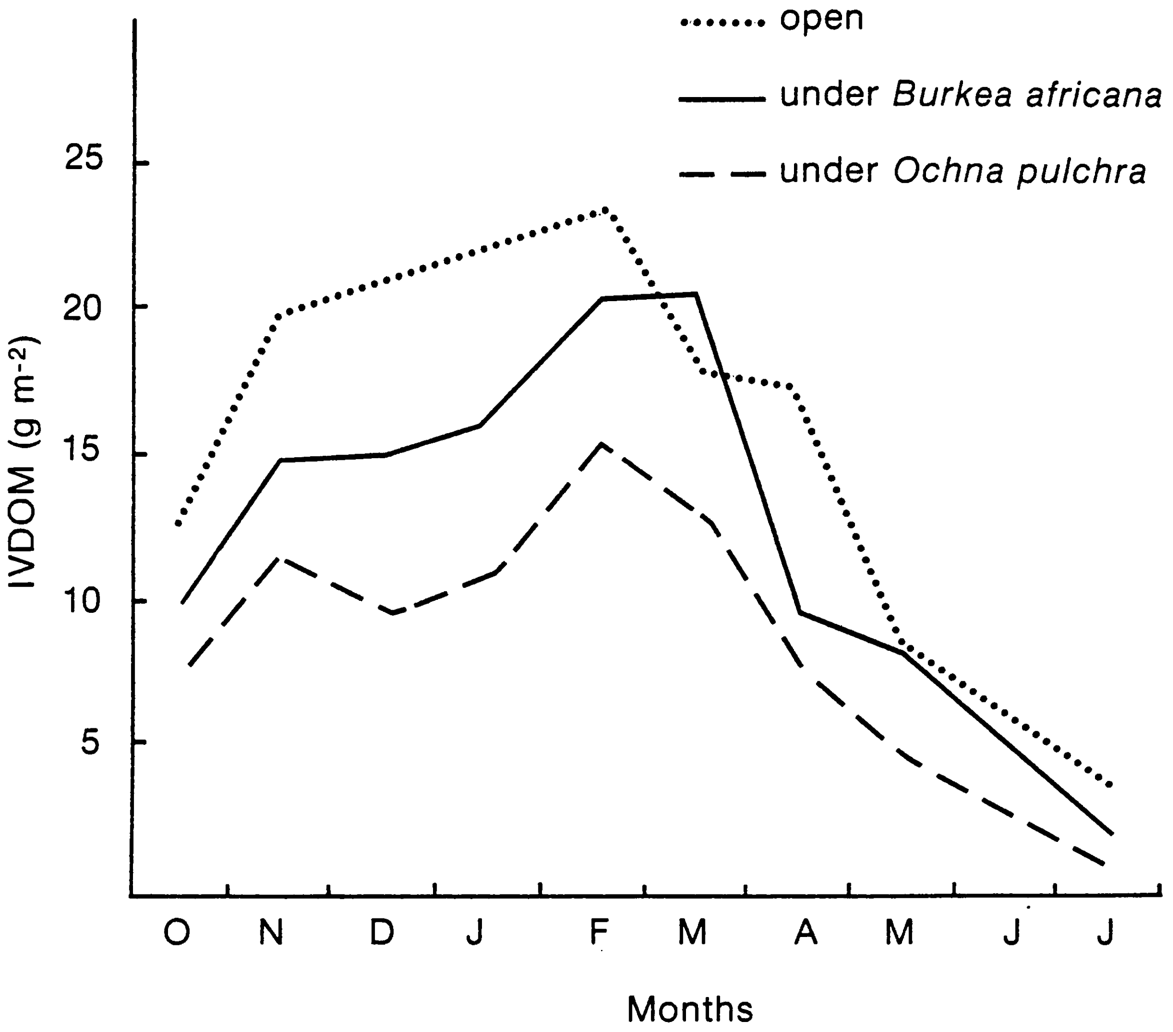

Fig. 8. In-vitro digestible organic matter (g m^{-2}) in the herbaceous layer as a whole, in three subhabitats, 1978/79.

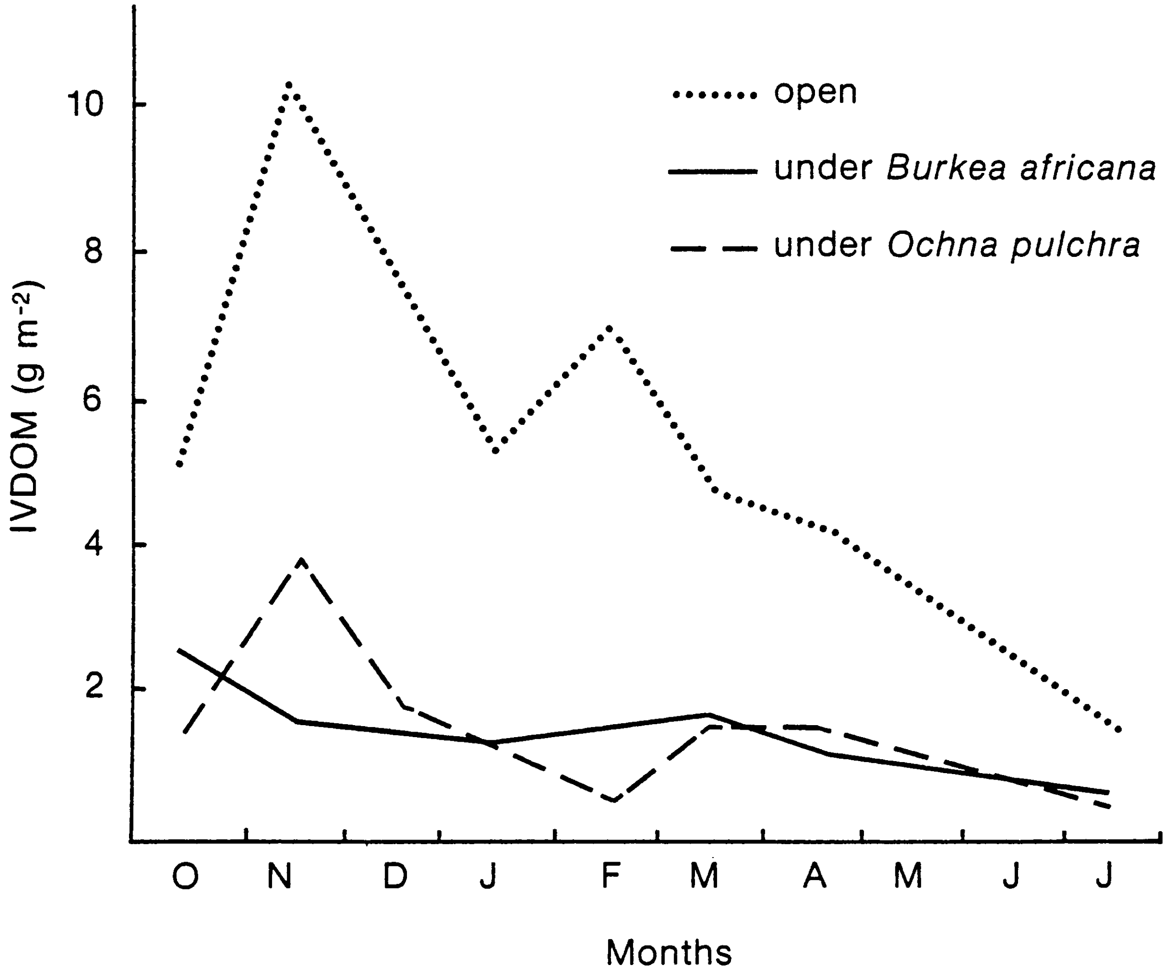

Fig. 9. In-vitro digestible organic matter (g m^{-2}) in non-forage species, in three subhabitats, 1978/79.

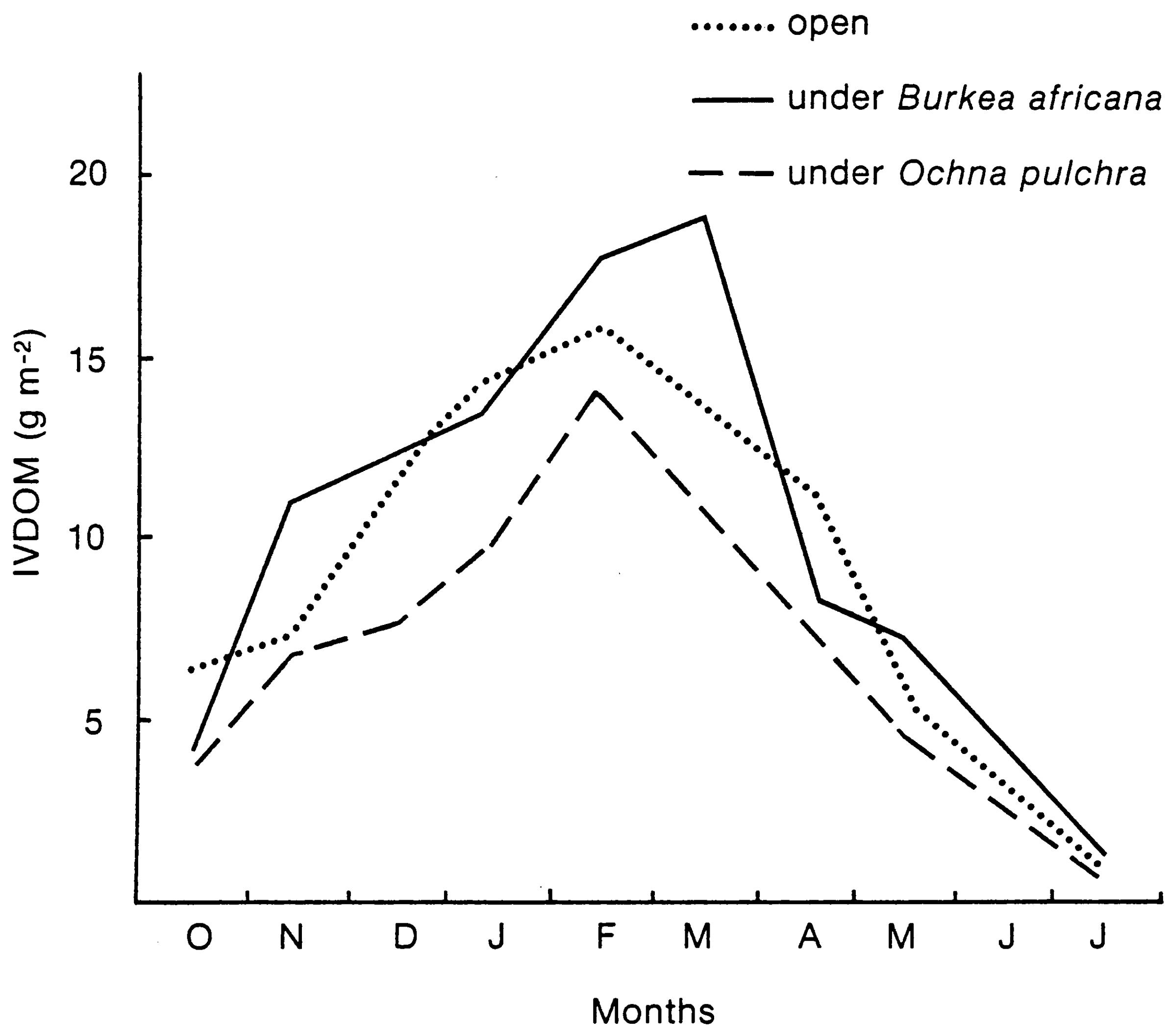

Fig. 10. In-vitro digestible organic matter (g m^{-2}) in forage and intermediate species, in three subhabitats, 1978/79.

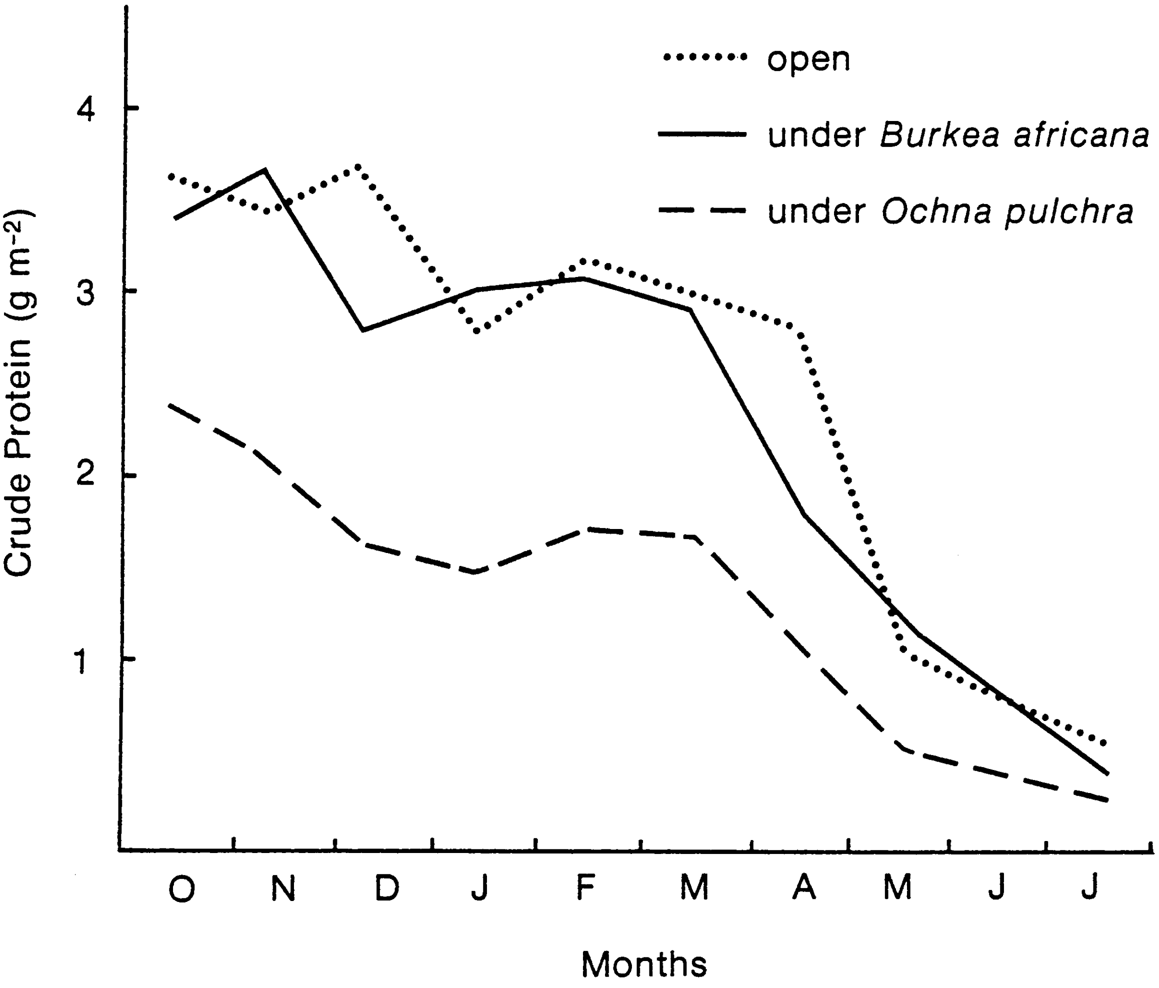

Fig. 11. Crude protein (g m^{-2}) in the sward as a whole, in three subhabitats, 1978/79.

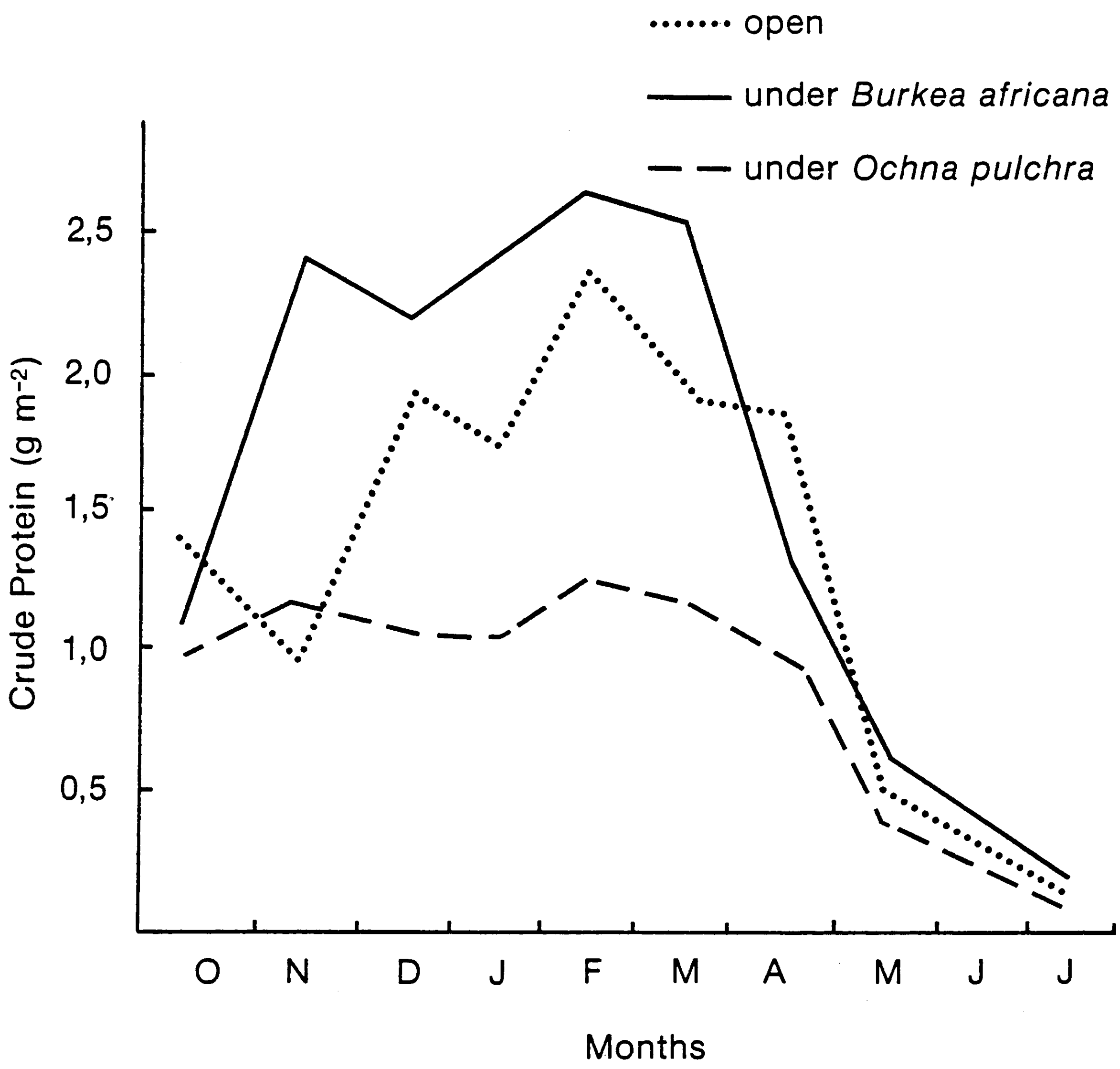

Fig. 12. Crude protein (g m^{-2}) in forage and intermediate species, in three subhabitats, 1978/79.

In the same table (Table 8) it can be seen that FI species generally have higher percentage CP contents than do the NF species, in each particular subhabitat. The greatest amount of CP in NF species was present in the open subhabitat (Fig. 13). In Fig. 14 it can be seen that FI species IVDOM, expressed as percentages of OM, were similar in all three subhabitats over the season, ranging from an early season high of nearly 65% to about 50% in July. Percentage IVDOM values of NF species were consistently lower than those of FI species, although more or less similar in the three subhabitats (Fig. 15).

Table 8 : Crude protein (CP) contents (expressed as percentages of dry matter) of forage and intermediate species (FI) and non-forage species (NF) in three subhabitats, 1978/79

Month	FI			NF		
	Under *Burkea africana*	Under *Ochna pulchra*	Open	Under *Burkea africana*	Under *Ochna pulchra*	Open
October	14,50	11,50	14,00	13,00	11,25	15,50
November	12,50	10,50	8,50	7,00	7,25	7,50
December	10,25	8,25	9,50	7,25	7,50	6,25
January	9,25	6,00	6,50	5,00	5,75	4,25
February	8,00	4,50	7,25	5,00	5,50	4,50
March	6,50	5,25	6,25	6,25	5,25	4,75
April	7,50	5,50	7,50	5,75	4,75	3,00
May	5,00	4,50	5,00	6,00	4,50	3,50
June	5,00	4,50	4,87	5,25	4,25	3,50
July	5,00	4,50	4,75	4,50	4,00	3,50
Average	8,40	6,50	7,40	6,50	6,00	5,60

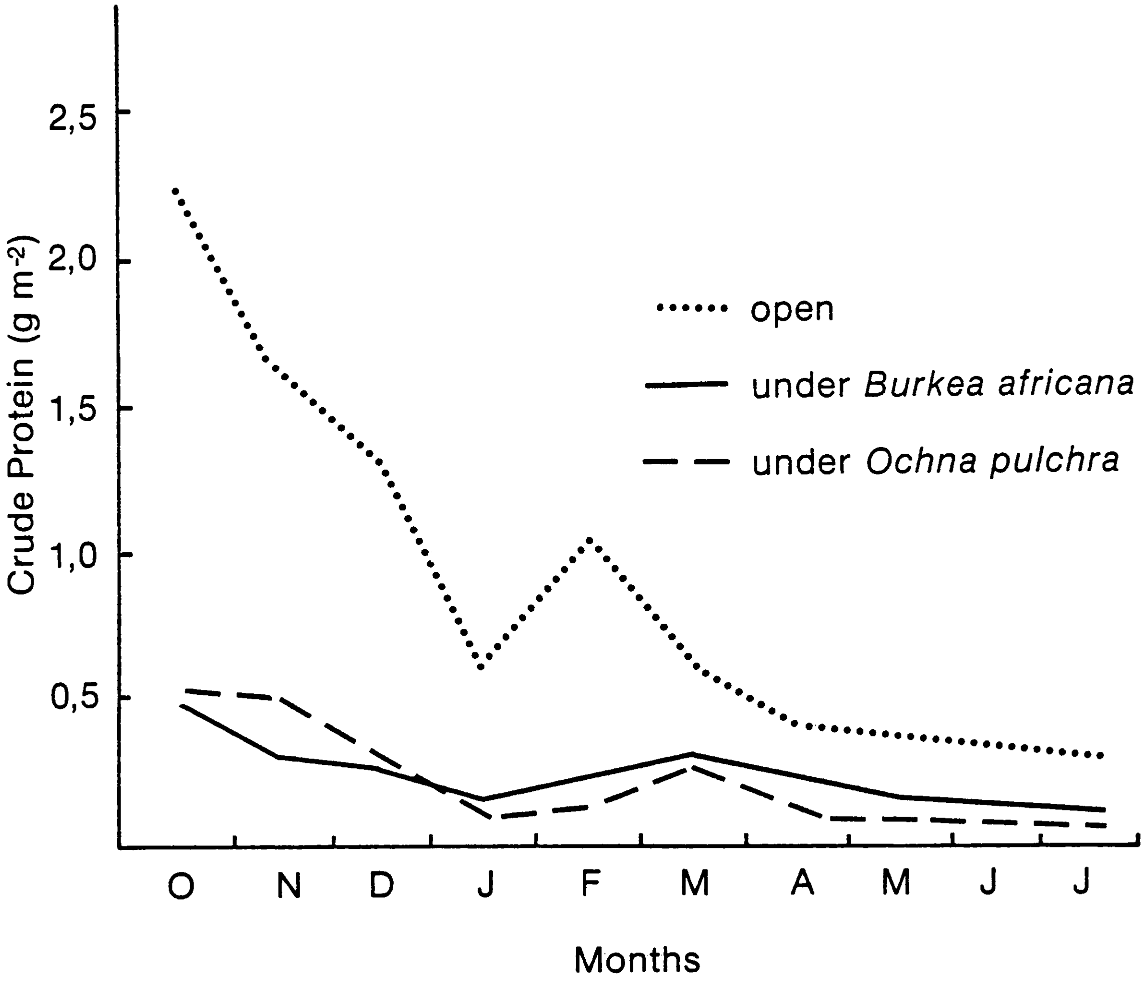

Fig. 13. Crude protein (g m^{-2}) in non-forage species, in three subhabitats, 1978/79.

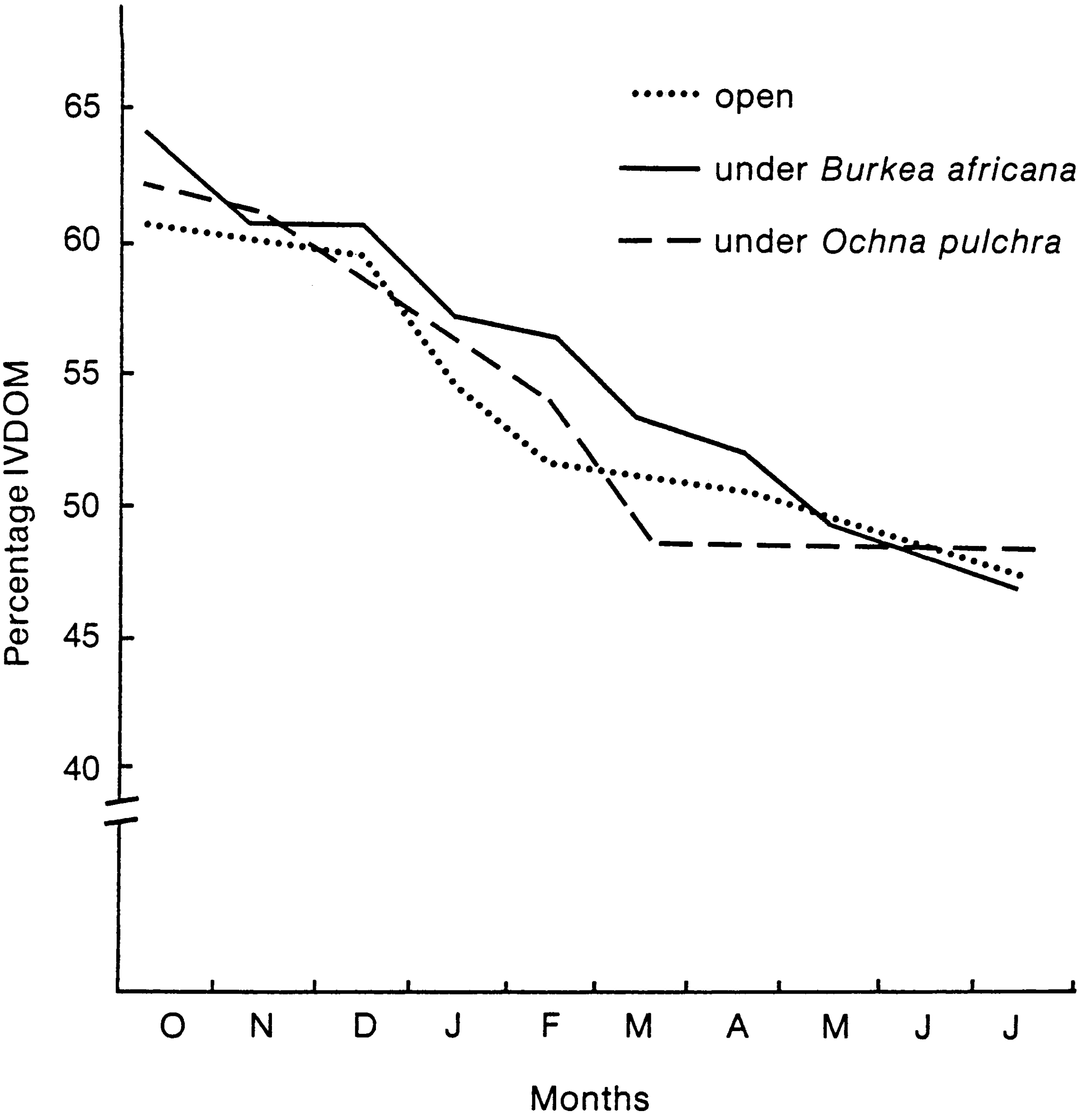

Fig. 14. Percentage in-vitro digestible organic matter content of forage and intermediate species, in three subhabitats, 1978/79.

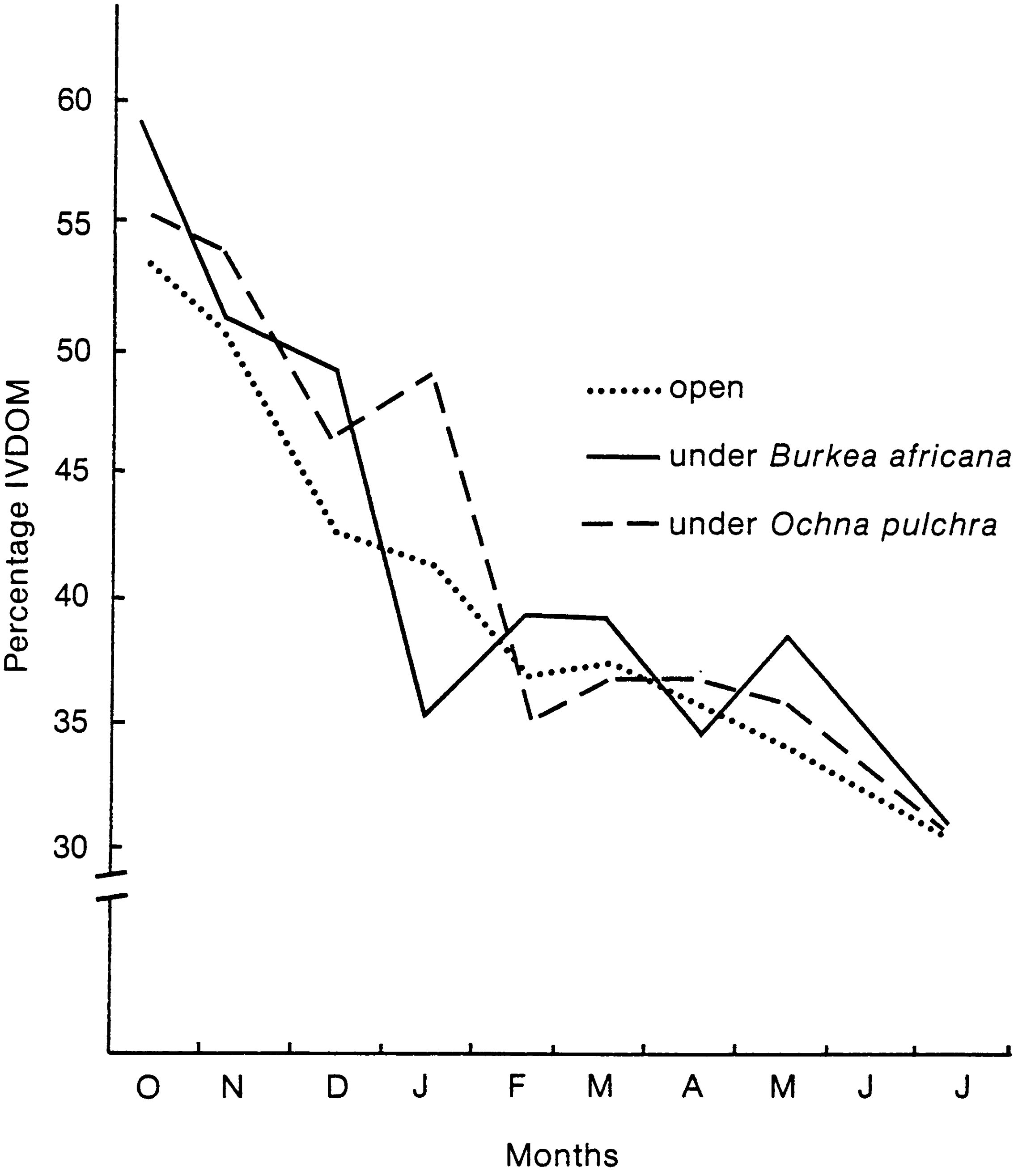

Fig. 15. Percentage in-vitro digestible organic matter content of non-forage species, in three sub-habitats, 1978/79.

As it was only possible to analyze single, composite samples for each category at each harvest date, no estimate of error or variation can be calculated. However, in collecting the composite sample for analysis, care was taken to ensure that such samples were representative of each category at each sampling date. Thorough milling and mixing should also have ensured that the values quoted are acceptable.

3.3.2 Necromass of different species groups

It is evident that there has, in the absence of fire and grazing, been a marked accumulation of necromass: - values in October, for total necromass, range from 34 g m^{-2} under *B. africana* to 77 g m^{-2} in the open subhabitat (Fig. 16). In all three subhabitats, there is, in general, a decline in necromass from early in the growing season, followed by an increase towards the end of the year. This corresponds to an initial flow of previous season's necromass to litter, followed by flow of current season's biomass to necromass towards the end of the current season.

The trend is further demonstrated when considering necromass as a percentage of standing crop (biomass + necromass). In Table 9 it is apparent that the percentage of necromass gradually decreases from October to a low around December to February and then increases to the end of the year, in all subhabitats.

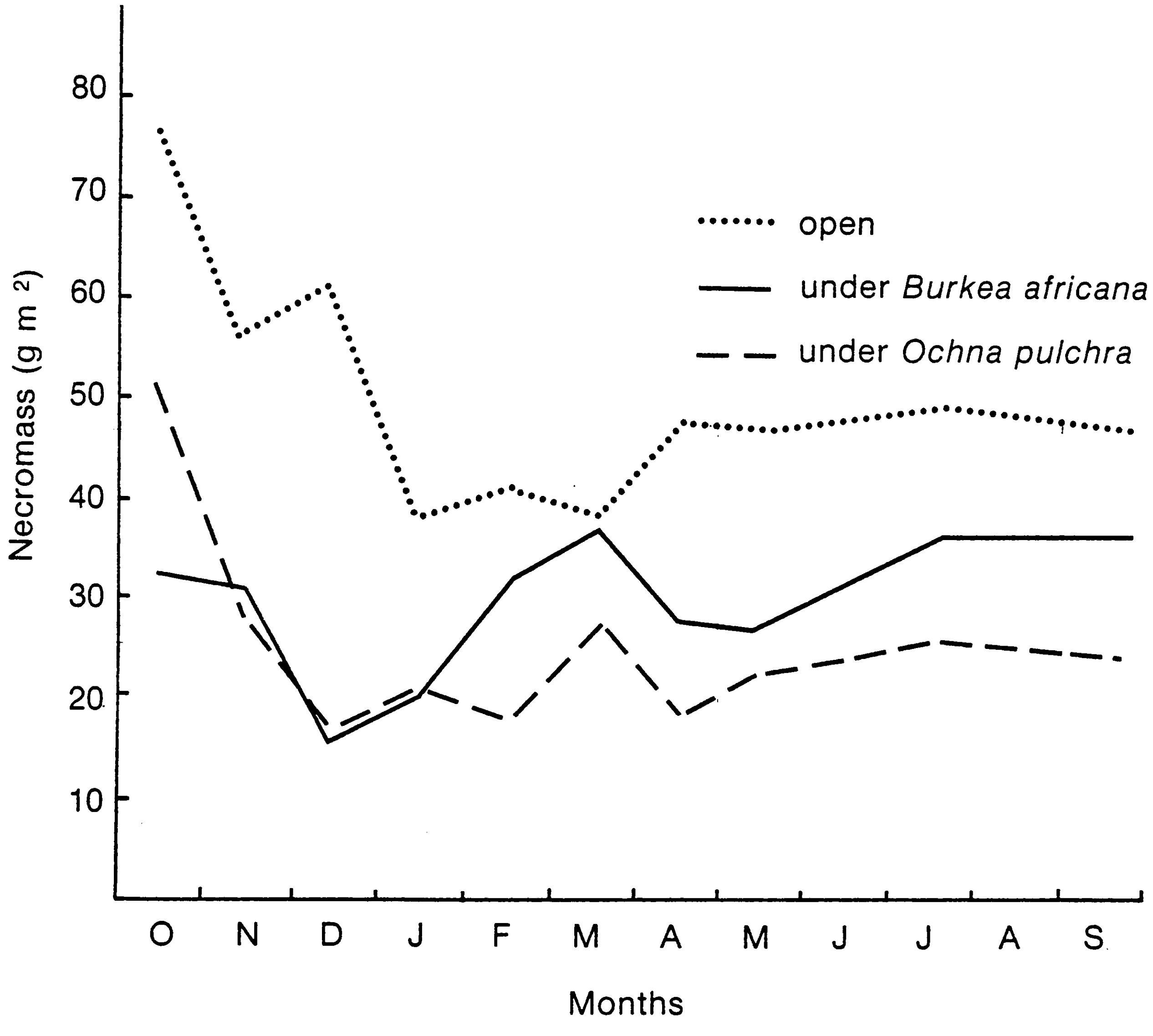

Fig. 16. Necromass (g m^{-2}) of the sward as a whole, in three subhabitats, 1978/79.

Table 9 : Necromass as a percentage of standing crop, in three subhabitats, 1978/79

Month	Under *Burkea africana*	Under *Ochna pulchra*	Open
October	61,3	74,7	70,1
November	52,8	56,1	58,3
December	32,1	44,5	42,1
January	33,0	47,5	42,2
February	37,0	34,5	42,1
March	47,3	47,6	45,3
April	55,4	49,7	54,3
May	58,0	64,9	67,8
July	85,9	86,1	83,3
September	87,5	93,0	83,6

3.3.3 Biomass accumulation rates

3.3.3.1 Total biomass (all species)

Mean monthly BAR's, over the periods of biomass increment, are shown in Table 10.

Table 10 : Rainfall and mean monthly biomass accumulation rates ($g\ m^{-2}\ day^{-1}$) for total biomass in three subhabitats (increments only, ranks in parentheses), 1978/79.

Period	Rainfall (mm)	Under *Burkea africana*	Under *Ochna pulchra*	Open
October to November	96,7 (1)	0,289 (1)	0,185 (2)	0,270 (1)
November to December	49,5 (4)	0 (4)	- (4)	0,131 (4)
December to January	56,5 (3)	0,152 (3)	0,129 (3)	0,141 (3)
January to February	71,9 (2)	0,245 (2)	0,400 (1)	0,269 (2)
February to March		0,093	-	-
Mean (increments)		0,156	0,179	0,203

Biomass accumulation rates of the herbaceous layer under *B. africana* and in the open, showed the same tendencies between October and February, as is evident from the ranking values in parentheses (Table 10). The rate of 0,400 $g\ m^{-2}\ day^{-1}$ under *O. pulchra* during January is not easily explained and is probably a reflection of the higher sampling error in this subhabitat, referred to earlier. Furthermore, BAR is subject to a double sampling error when calculated by the subtractive technique. (Actual field data ± S.E. used to calculate BAR under *O. pulchra* between January and February were : January 21,7 ± 2,25 $g\ m^{-2}$; February 33,3± 3,89 $g\ m^{-2}$.

No statistical analyses of BARs per se were undertaken, in view of the reasons described in Appendix 2.

Recognizing this possible limitation it is nevertheless apparent that the greatest mean BAR over the period of biomass increment occurred in the open subhabitat. The trends apparent in the open and under *B. africana* subhabitats follow the trends in rainfall (*vide* rankings) in the month during which the rate was calculated:- in both subhabitats, BAR's exhibited the same ranks as rainfall i.e. greatest rainfall resulted in greatest BAR and BAR decreasing as rainfall decreased. A correlation coefficient (r^2) of 0,77 was obtained using linear regression of BAR against rainfall in the case of the under *B. africana* subhabitat, and r^2 = 0,76 for the open subhabitat.

3.3.3.2 Forage and intermediate, and non-forage categories

Mean BAR's of the FI and NF categories are shown in Table 11.

Table 11 : Mean biomass accumulation rates (g m^{-2} day^{-1}) of forage and intermediate (FI) and non-forage (NF) species groups in three subhabitats over the period of biomass increments, 1978/79

Category	Under *Burkea africana*	Under *Ochna pulchra*	Open
FI	0,204	0,174	0,192
NF	0,012	0,036	0,120

The sum of the BAR's of the categories in any subhabitat does not equal the BAR of the sward as a whole (total BAR) because categories, comprised as they are of different species with differing phenological cycles, exhibit different rates of accumulation.

The mean BARsof the FI species under B. africana and in the open, are greater than the BAR of FI species under O. pulchra. BAR's of the NF group are consistently lower than those of the FI group, in all subhabitats.

3.4 Discussion

The results presented generally emphasize the significance of the canopied subhabitat in terms of amount and quality of the herbaceous component. Whereas there is a greater quantity of herbaceous vegetation *per se* in the open subhabitat than under trees and shrubs, the quantity and nutritional value of FI species under the dominant tree species of this savanna vegetation type is of the same order, or as in the case of crude protein, greater than that in the open subhabitat. Lowest amounts of biomass, IVDOM and CP, over the season, were recorded under O. pulchra shrub clumps, which, by their physical nature, exclude many grazers. Whereas the leaves of O. pulchra are browsed by cattle it would appear that this phenomenon is confined to a short period before the onset of the rainy season and the initiation of herbaceous layer early season 'flush' (Zimmerman, 1978). It is obvious that any marked increase in this woody species, which at present comprises *ca* 21% of the total woody species canopy spread cover (Van Rooyen and Theron, 1977) would be undesirable from a range utilization point of view.

3.4.1 Accuracy of biomass results

Confidence intervals were not included on the graphical representations of biomass over the year (Fig. 4 to 7). With there being three curves in each figure, and with several points lying close together, it is felt that it would become difficult to visually interpret the resulting clumsy and cluttered figures.

The fact that in all cases the observed differences in amount of biomass present over the season were statistically significant, is an indication that:

(1) such differences were greater than could be accounted for by chance,

and

(2) such differences were greater than the variation between replicates used in the calculation of the mean values plotted in each curve.

3.4.2. Seasonal trends

Sampling of biomass commenced in October 1978, at which stage a noticeable amount of biomass was recorded in each subhabitat. This would have included, in addition to early 'current' years growth, a certain amount of biomass 'carried over' from the previous growth year. This phenomenon is of critical significance in any attempt to quantify herbaceous layer production and is elaborated on in Chapter 6.

Peak total biomass of 55,4 g m^{-2} was recorded in the open subhabitat in February. This value is lower than the average peak biomass of 81 g m^{-2} recorded in the open subhabitat over the previous four years (Grunow and Grossman, 1978) and is probably largely a reflection of

(1) the lower amount of rainfall during the current year (Fig. 1), and

(2) the increasing moribundity of the sward after several years of protection from fire, and only light utilization by herbivores.

Peak total biomass of 42,6 g m^{-2} was recorded in the under *B. africana* subhabitat in March. A possible cause of the later 'peak' in this subhabitat compared to the open subhabitat is that the canopies of this tree species would reduce direct insolation on the herbaceous layer below. Evapotranspiration may be expected to be lower under these canopies than in the open, and it is conceivable that the soil moisture content in the root zone of the herbaceous layer may remain at a higher level than the surrounding, open areas for a longer period, thereby prolonging the period of biomass accumulation in the under *B. africana* subhabitats.

O. pulchra shrubs have a fairly extensive shallow, lateral root system (Rutherford, 1979) and would in all probability compete directly with herbaceous plant roots for available moisture, both in the immediate vicinity of the shrub clumps as well as some distance into the open subhabitat. This competition would be most crucial at times when soil moisture content was low. From the onset of growth around September through February, 347 mm of rain was recorded (Table 1). Evaporation from a USA Class A pan over the same period was 1 505 mm. Using a theoretical pan factor of 0,6 (Huntley and Morris, 1979), ca 900 mm of water could be lost from the ecosystem through evapotranspiration over this period. This is equivalent to ca 255% of the actual rainfall over this period and it is apparent that soil moisture content would in fact be low in the sandy soils of the study area during the period under review.

Biomass in all subhabitats declined after attaining peak values, to the low levels recorded in September. In previous studies of herbaceous biomass at Nylsvley (Grunow and Bosch, 1978) biomass in the open had never been less than 20 g m^{-2} at the end of the year. The low value of less than 10 g m^{-2} recorded in the open subhabitat in September is a further reflection of the relatively low production during the period of study.

3.4.3 Categories

Whereas FI species biomass curves largely exhibit the same tendencies as the sward as a whole (total biomass) the trends of the NF species are noteworthy. In the open subhabitat, apart from a peak during February, at which time *Eragrostis pallens* produced numerous flowering culms, there is a gradual decline in the biomass of NF species over the year. This component of the sward seems, in particular, to be becoming increasingly moribund. The FI species group is lightly utilized but apart from insect herbivory, there is no significant defoliation of the NF species, nor has there been for several years. Gandar (1980) demonstrated a greater degree of vigour in Eragrostis pallens tufts subject to insect herbivory compared to tufts of the same species treated with insecticide. It is however doubtful whether insect herbivory, estimated as being responsible for the removal of only ca 10% of herbaceous layer production (Gandar, 1978) would be of a sufficient order to prevent increasing moribundity of the NF grasses in the absence of fire and other herbivory.

3.4.4 Necromass

An estimate of flow from biomass to necromass is essential for any calculation of net aerial production. However, in this perennial sward with varying carry-over from year to year, field data on necromass are inadequate to calculate such flow rates:- it was found by trial to be impracticable to distinguish newly formed, or current year's, necromass, from that formed during the immediate past year. The criteria used to make such a distinction must in the absence of any direct estimate, be largely subjective and indirect and are as a result, open to severe criticism. Rutherford (1976) working in a similar savanna vegetation type in South West Africa, found it possible to distinguish current year's biomass (defined as attached plant material) from that formed in the previous year only until about the middle of the growing season. The vegetation in which Rutherford worked had been recently burnt prior to the commencement of his study, and thus, unlike Nylsvley, there was not a further confounding influence of several years' accumulated necromass.

In Chapter 6 flow to necromass has been calculated in a burnt sward, but in view of the foregoing considerations such calculations were considered impracticable in the present study.

3.4.5 Nutritional characteristics

The digestibility values presented are mean values of each composite sample, at each harvest date, and represent the mean of a range of species which probably have varying degrees of *in vitro* digestibility. Different herbivores, exhibiting varying degrees of diet selection will be able to select diets containing higher percentage IVDOM than the mean of the FI species category if the stocking pressure is light, but the results presented do reflect the range and order of IVDOM available to herbivores over the year.

The diets of less selective, bulk-roughage feeders, may be expected to exhibit IVDOM levels similar to those of the FI species category.

In vitro digestible organic matter did not correlate with any climatic variables tested. This would suggest that this variable is more a function of phenology and growth. Furthermore, the similarity of percentage IVDOM levels in all three subhabitats in both FI species and NF species suggests that percentage IVDOM content is, within limits, more of an inherent characteristic than it is dependent on such environmental factors as may differ between subhabitats.

A noteworthy feature of the percentage CP levels is that in October, NF species showed relatively high CP contents (Table 8). Zimmerman (1978) found that cattle at Nylsvley showed selection for such generally unpalatable species as *Eragrostis pallens* and *Urelytrum squarrosum* only during the early stages of the growing season. *E. pallens* is one of the first species to exhibit new leaf flush at the onset of the growing season. *E. pallens* is furthermore one of the dominant species within the NF category and it is possible that cattle selection for such species early in the growing season is related to the relatively higher amount of CP in these species at this stage of the seasonal cycle.

Crude protein content also declined after the initial high values in all categories and subhabitats, but was not correlated to any climatic variables tested. Dradu and Harrington (1972) showed that a decline in CP content coincided with a reduced amount of rainfall but that onset of maturity and flowering coupled with depletion of accumulated nitrogen reserves also contributed to CP decline.

3.4.6 Biomass accumulation rates

It is probable that the greater BAR of the sward as a whole in the open subhabitat is largely due to the greater amount of biomass in this subhabitat. Uresk, Sims and Jameson (1975) established that 54% of the variation in rates of change of live herbage in a shortgrass ecosystem was accounted for by the amount of biomass present. However, the mean BAR of FI species is greater under *B. africana* than in the open although the amount of FI species biomass in both these subhabitats was of the same order over the season. Bosch and van Wyk (1970) demonstrated that there is a localized higher soil fertility under trees than in the open on poor soils in the western Transvaal. Bate (1979) has shown that soil total nitrogen content is higher in the canopied subhabitat than in the open, at Nylsvley. Furthermore, herbivore selection of the canopied subhabitat may, in the long-term, stimulate forage species through defoliation. These factors may, in combination, favour the FI species group and account for the greater BAR and the higher CP content of this group under *B. africana* trees.

As stated, lowest levels of nearly all plant variables measured were recorded under *O. pulchra* shrub clumps. The desirability of trees in this (and other) savanna vegetation types is confirmed by this and other studies referred to, and the undesirability of complete woody vegetation removal has been alluded to. However, in the interests of increased production from cattle ranching, the major form of land-use, there is conceivably a sound argument in favour of selective removal of less desirable woody species, such as, in this vegetation type, *Ochna pulchra*. The absence of completely satisfactory methods of selective thinning coupled with the often high costs involved are factors to be considered when contemplating such environmental manipulation.

CHAPTER 4

THE EFFECT OF FIRE, WITH AND WITHOUT SUBSEQUENT DEFOLIATION, ON THE HERBACEOUS LAYER

4.1 Introduction

Fire is a phenomenon which occurs in savanna both naturally and as a management aid. Natural fires are probably not as influential on South African savanna dynamics now as they were historically, due to such factors as form of land-use and management, artificial fire-breaks and fire control methods. In the major savanna land-use enterprise, namely cattle ranching, and in the field of conservation, fire is generally used to attempt to control woody vegetation and to remove moribund herbaceous vegetation (Trollope, 1979).

Historically, research into the ecological effects of fire in South Africa has enjoyed greater attention in grassland areas than in savanna areas. Several long-term burning trials have been maintained in grasslands, such as those at Frankenwald, Estcourt, Ukulinga, Cathedral Peak and Giants Castle (Anon, 1978 (b)). The effect of fire on herbage production in grassland has been reviewed by Tainton, Booysen, Bransby and Nash (1978).

Within the savanna biome, quantitative data on the effect of fire on herbaceous production appear to be limited. Fire has been studied more in relation to such factors as basal cover, species composition and effect on grass/woody balance (e.g. Donaldson, 1969; van Wyk, 1971; Gertenbach and Potgieter, 1979).

Elsewhere in southern Africa, research has shown that regular burning increases production in relatively moist areas where dead, self-smothering unpalatable material accumulates, but is generally detrimental in areas where rainfall is less than *ca* 650 mm per annum (West, 1965; Daubenmire, 1968).

As stated, one of the most abundant grasses is the large tussock species *Eragrostis pallens* (Van Rooyen and Theron, 1977). This species, together with other larger unpalatable species such as *Trachypogon spicatus* and *Urelytrum squarrosum* generally exhibit new leaf flush before the palatable, leafier species such as *Digitaria eriantha* and *Brachiaria nigropedata* (Zimmerman, 1978; Gandar, (i) 1978: *pers. comm.*; and, personal observation). With a view to improving the species composition of the sward, it was decided to apply an intense, hot fire against the prevailing wind (backfire). It was postulated that the larger non-forage species, exhibiting a marked accumulation of necromass (Fig. 17), would generate high temperatures within the tussocks and possibly burn into the stem bases, thereby severely damaging or destroying the growing points. Correctly timed to coincide with new leaf flush of the unpalatables such a fire would be detrimental to such species whereas the leafier, smaller forage species (Fig. 18), still dormant, would not generate sufficient temperature to destroy their protected growing points.

A headfire does not generate the same intense heat closer to the ground as it sweeps through the sward at a faster rate than a backfire (Trollope, 1979).

(i) M. Gandar, Institute for Natural Resources, University of Natal, Pietermaritzburg.

Fig. 17. An illustration of a largely moribund area of the Nylsvley sward, taken during January 1979. The main grass species illustrated is Eragrostis pallens. Ochna pulchra seedlings are evident.

Fig. 18. An illustration of the difference in size between the leafier, palatable Digitaria eriantha ssp pentzii (right, foreground) and the larger, densely tufted unpalatable Eragrostis pallens (left, back).

The objectives of the series of experiments reported on in this section, were to quantify the effects of fire and subsequent treatments on the herbaceous layer, in the short-term. As the effects of fire per se may be modified by subsequent treatment of the vegetation, the response of the herbaceous layer was monitored under conditions of unchecked growth, mechanical defoliation and grazing by the indigenous herbivores. In this, and the following section (Chapter 5), the term 'clipping' is used inter-changeably with the term 'defoliation' where mechanical removal of herbaceous material (using scissors or shears) is implied.

4.2 Methods

4.2.1 Experimental layout

Six plots, each measuring 16 m x 16 m, were selected (using random numbers) out of nine plots in an area enclosed by a 2,5m high game-proof fence. Each plot was similarly randomly assigned to one of two treatments viz:burn or no burn, resulting in three replicates for each treatment.The area is shown in Appendix 3, as 'site 3'.

At 16h00 on 18-9-78, the three plots assigned to the burn treatment were ignited. In Table 12, meteorological data recorded at the station adjacent to 'site 3', are shown.

Table 12 : Meteorological data recorded at Station 2, at the time of the backfire on 18-9-78.

Temperature		Relative humidity	Wind speed
Dry bulb °C	Wet bulb °C	%	m sec^{-1}
28,7	15,7	34,0	2,0

The fuel loads (total amount of herbaceous standing crop) recorded in each replicate were:

Replicate I	93,7 g m^{-2}	11,0% moisture*
II	88,6 g m^{-2}	12,3% moisture
III	95,1 g m^{-2}	11,7% moisture

*Moisture expressed as a percentage of undried mass.

4.2.2 Post-fire treatment and sampling procedure

Each plot was divided into twelve sub-plots for sequential sampling through the year. Between October 1978 and May 1979, twenty 0,5 x 1 m quadrats were harvested at 4-weekly intervals on each burnt and unburnt plot. Thereafter the same number of quadrats were harvested at 8-weekly intervals, to September 1979. In order to quantify biomass accumulation under a post-fire defoliation regime, quadrats clipped for determining unchecked growth in October, December, February and April were marked with wire pins to facilitate relocation, and the herbaceous regrowth was harvested eight weeks after each initial clip e.g. a quadrat harvested and marked in December 1978 would be reharvested in February 1979, and the amount of regrowth determined. Biomass accumulation was thus determined under conditions of unchecked growth and 8-weekly clipping. This treatment was applied on burnt and unburnt plots. Groups of species were clipped in the same way and sorted into the same categories as described in paragraph 3.2, dried and weighed.

4.2.3 Calculation of biomass accumulation rates

BAR may be calculated in the same manner as described earlier (para. 3.2.4). However, in the case of the burnt plots, the following considerations apply: all necromass accumulated and carried over from previous seasons had been burnt therefore all necromass must have come from current biomass and thus a direct measurement of necromass accumulation is possible. If this is then added to biomass accumulation, the resultant will more closely approximate net annual above-ground production (*sensu lato*).

The equation, hereafter referred to as Method 2, may be expressed as follows :

$$BAR = \sum_{n=1}^{k} (B_n - B_{n-1}) + (N_n - N_{n-1})^* / t_k - t_o$$

where:- BAR = mean biomass accumulation rate, including losses due to flow from biomass to necromass (g m^{-2} day^{-1})

B = grazeable above-ground biomass (g m^{-2})

N = grazeable above-ground necromass (g m^{-2})

t_o to t_k = times of harvest

* = only concurrent increments and their corresponding clipping intervals used.

4.2.4 Botanical surveys

Sharp point surveys were conducted six months before the fire, during March 1978, and eighteen months after the fire during March 1980 to determine any changes in basal cover of ecologically important species. At both dates 2000 points were taken in fire treatment as well as unburnt plots, using a bridge point apparatus with sharp points 15 cm apart. Points were taken along randomly placed guidelines. During the post-fire survey, the *E. pallens* tuft nearest to every tenth point was examined and classed as live or dead.

4.2.5. The effect of the exclusion of large herbivores on post-fire recovery of the herbaceous layer

On 5-9-78, a headfire was applied to 'Camp-2' of the study area (Appendix 3). In order to determine whether different periods of excluding large herbivores had any effect on post-fire recovery of the herbaceous layer as indicated by peak standing crop, the following experimental procedure was adopted: twenty sites were chosen randomly in canopied areas of *Burkea africana* savanna. Canopied areas were sampled as these areas were generally preferred by the indigenous ungulates. A further 20 sites were randomly selected in patches of *Acacia* spp savanna. Four treatments, each replicated five times were assigned randomly to sites in both vegetation types, viz:

(1) Protection from large herbivores for 29 days after the fire,
(2) Protection from large herbivores for 67 days after the fire,
(3) Protection from large herbivores for 101 days after the fire,
(4) Completely unprotected.

In addition 5 "permanent" exclosures were erected to exclude herbivores for the entire post-fire period.

Exclosures, each measuring 3 m x 3 m were erected at each site. The exclosures consisted of black polythene sheeting wound around four corner posts. Each exclosure was removed after the elapse of the appropriate post-fire exclusion period (i.e. 29, 67 or 101 days after the fire, depending on the particular period each plot was initially assigned). The herbaceous material formerly protected from grazing thus became accessible to herbivores at the different intervals after the fire. As each exclosure was removed, its site was unobtrusively marked and its position indicated on a map. This facilitated accurate relocation for the purpose of determining the peak standing crop.

On 16-2-1979, around the time of peak standing crop, all sites were relocated. In each site, a 1 x 2 m quadrat was harvested. A sickle bar mower powered by a petrol-driven tractor was used to hasten the process. The harvested material was sorted into grasses and forbs, oven-dried at 70°C to constant mass, and weighed.

Quadrats were also harvested from the 5 exclosures maintained for the entire post-fire period.

4.3 Results

4.3.1 Biomass curves

Biomass curves for the sward as a whole (total biomass) on the burnt and unburnt plots are shown in Fig. 19. Peak biomass on the unburnt plot of 44,9 g m^{-2} was recorded in January. Peak biomass of 45,6 g m^{-2} was recorded in March on the burnt plots. After the initial depression of biomass on the burnt plot as a result of the fire, the peak values recorded were thus of the same order. After reaching a peak value, amount of biomass decreased somewhat faster in the burnt plots compared to the unburnt plots. An analysis of variance and comparison of the treatment means conducted on the areas under the biomass curves revealed that there was a significantly greater amount of biomass present on the unburnt plots over the season (Table 13). Percentage-wise, this amounted to 29,4%.

Table 13 : A comparison of the areas (cm^2) under the total biomass curves on burnt and unburnt plots, 1978/79

Replicate	Burnt plots	Unburnt plots
1	55,5	79,5
2	61,0	78,0
3	58,0	68,5
Mean	58,2	75,3

LSD means : 10,5 (p = 0,05)

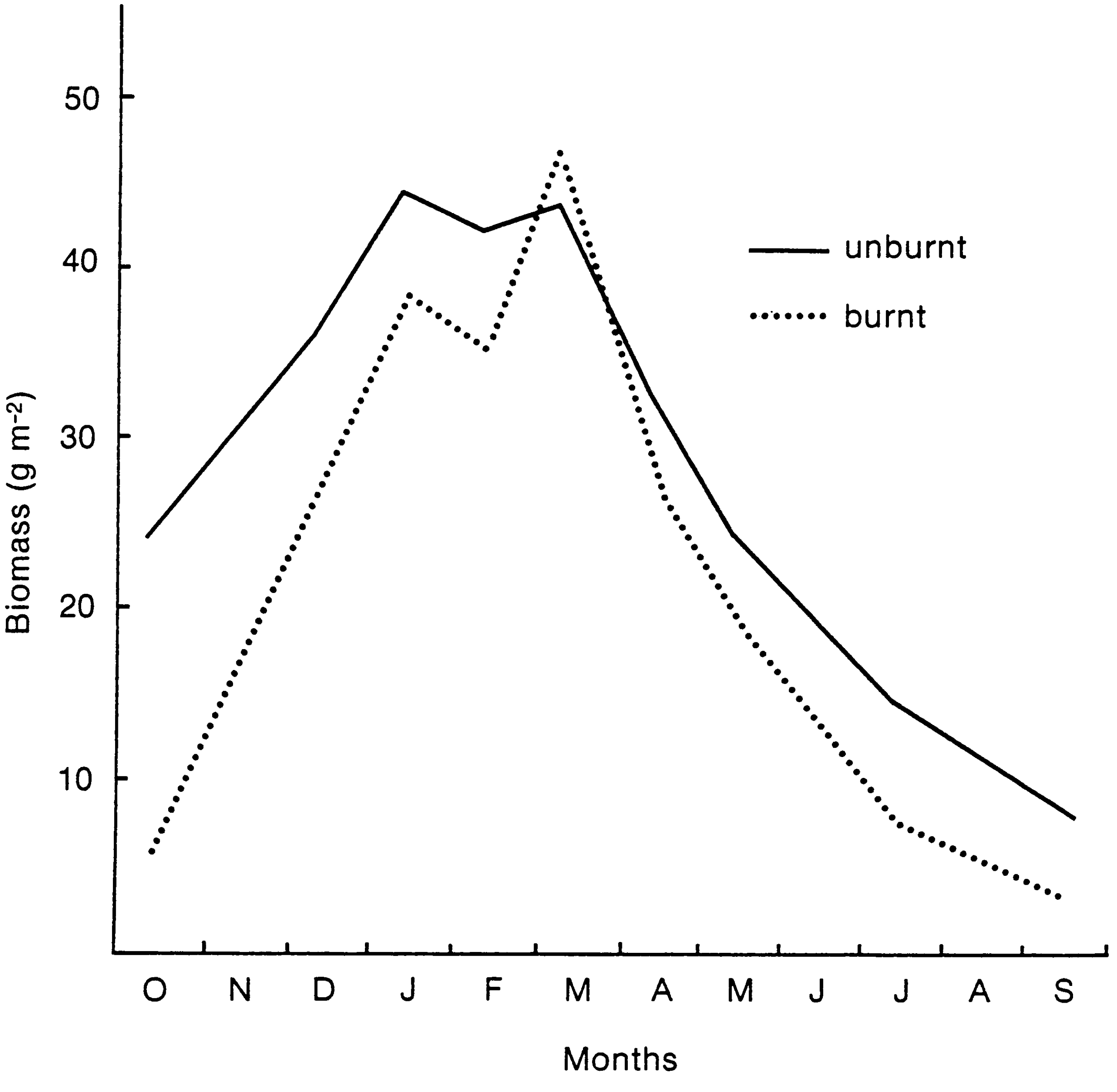

Fig. 19. Biomass (g m^{-2}) of the sward as a whole (total biomass), on burnt and unburnt plots, 1978/79.

Examination of the biomass curves of the FI species group (Fig. 20) reveals that the amount of biomass over the season was similar on burnt and unburnt plots. An analysis of variance conducted on the areas under the FI species biomass curves revealed no statistically significant difference between the amounts of biomass in the two treatments (Table 14).

Table 14 : A comparison of the areas (cm^2) under the forage and intermediate species biomass curves on burnt and unburnt plots, 1978/79

Replicate	Burnt plots	Unburnt plots
1	44,1	49,2
2	48,7	50,1
3	49,3	46,2
Mean	47,4	48,3

LSD means : F value NS

However, Fig. 21 shows that there was a marked reduction in the amount of NF species biomass on the burnt plots compared to the unburnt plots. In Table 15 it is shown that this difference is statistically significant.

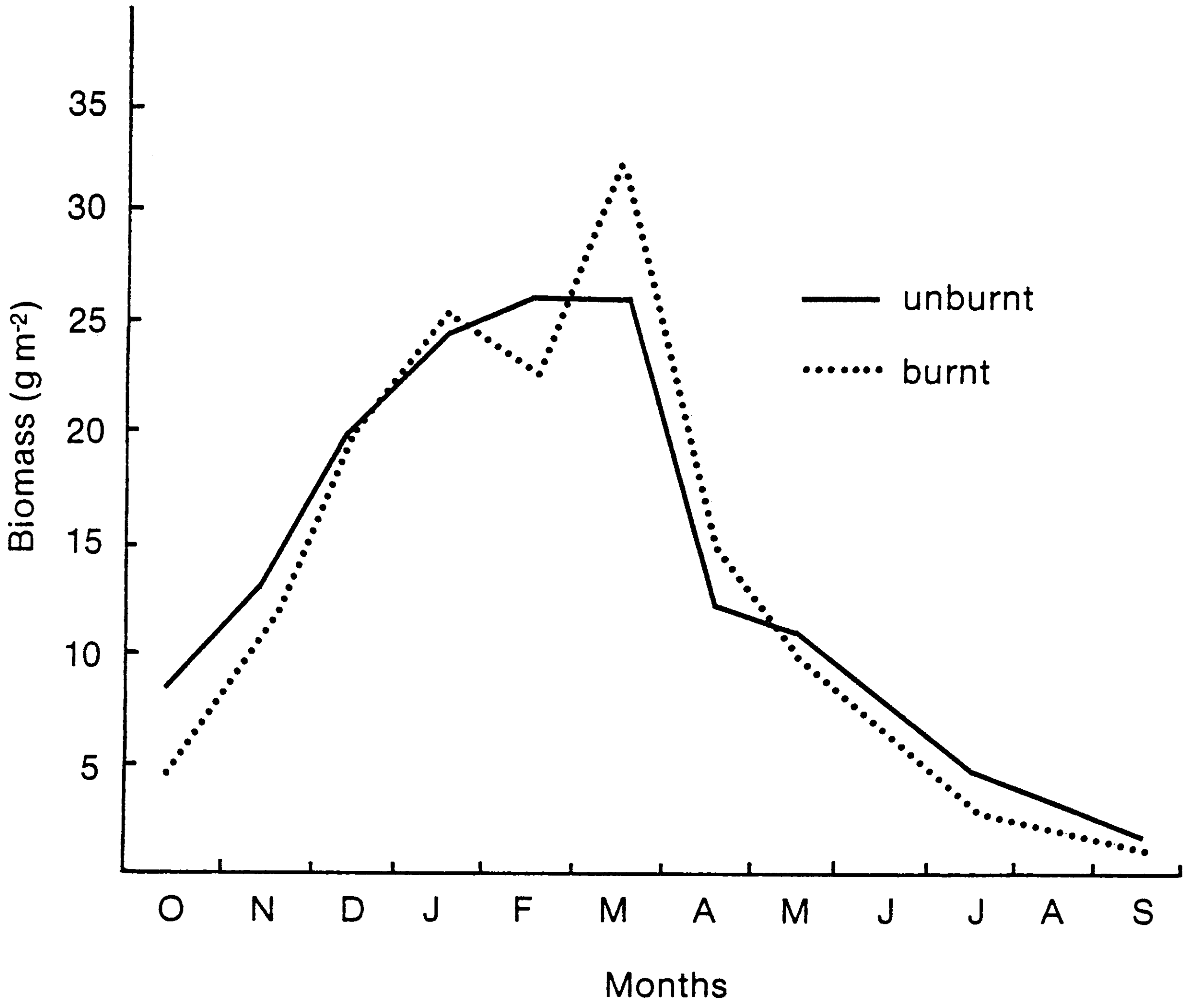

Fig. 20. Biomass (g m^{-2}) of forage and intermediate species, on burnt and unburnt plots, 1978/79.

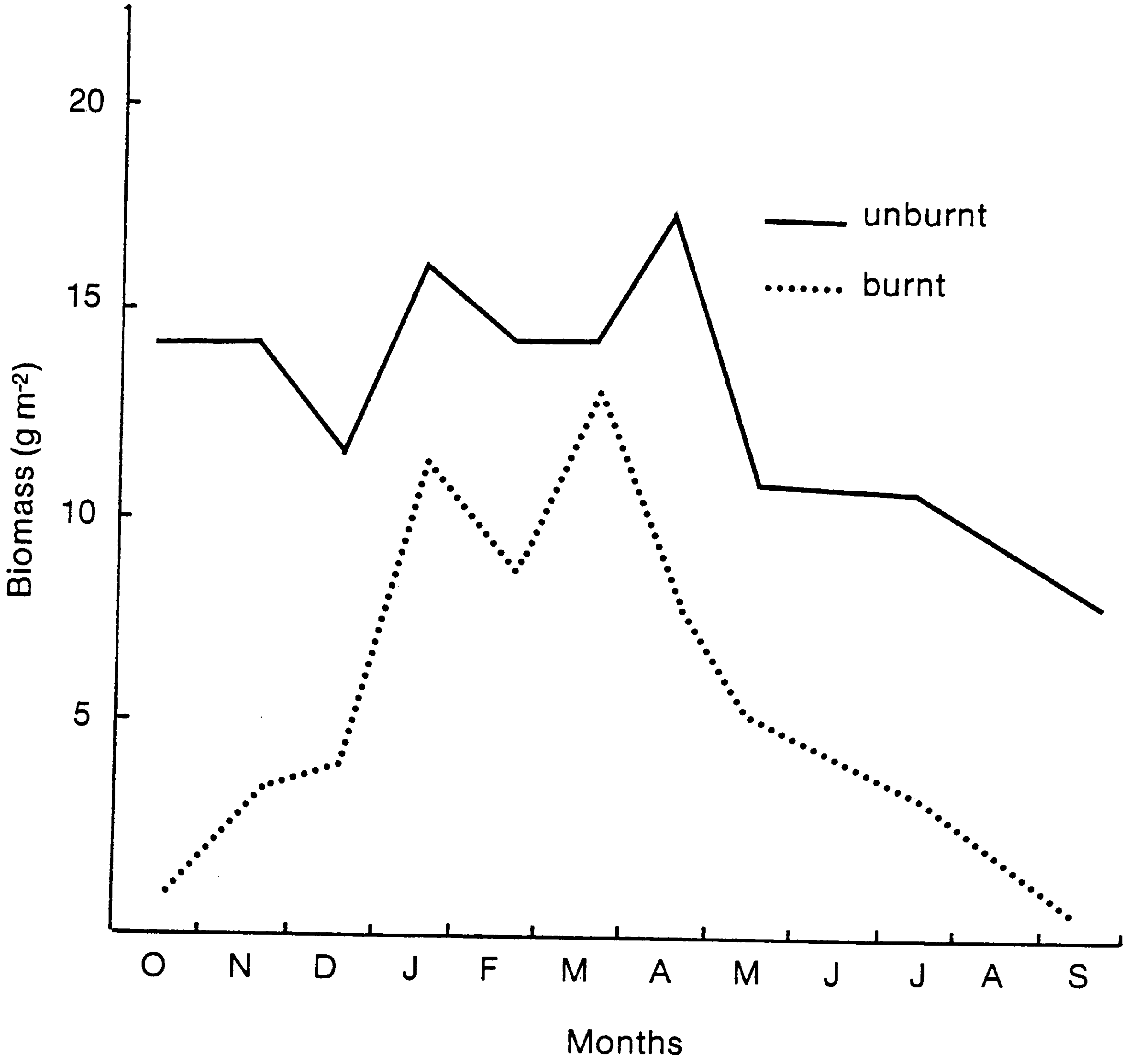

Fig. 21. Biomass (g m^{-2}) of non-forage species, on burnt and unburnt plots, 1978/79.

Table 15 : A comparison of the areas (cm^2) under the non-forage species biomass curves on burnt and unburnt plots, 1978/79

Replicate	Burnt plots	Unburnt plots
1	21,3	32,2
2	27,1	36,1
3	24,6	35,3
Mean	24,3	34,5

LSD means : 5,7 (p = 0,05) , 8,4 (p = 0,01)

FI species formed, on average, 40,0% of total biomass on the unburnt plots, compared with an average of 60,0% of total biomass on the burnt plots (Table 16). NF species formed on average, 54,0 of total biomass on unburnt plots and only 32,1% on burnt plots (Table 16).

Table 16 : Forage and intermediate (FI) and non-forage species (NF) biomass as percentages of total biomass on burnt and unburnt plots, 1978/79.

Harvest date		FI species		NF species	
		Burnt plots	Unburnt plots	Burnt plots	Unburnt plots
1978	October	81,5	35,4	16,7	57,8
	November	71,9	42,1	19,2	48,2
	December	77,5	58,4	14,6	32,6
1979	January	68,5	53,7	26,1	37,2
	February	64,8	58,7	25,2	33,7
	March	69,7	58,9	28,1	33,3
	April	57,9	36,0	30,4	56,5
	May	55,8	42,2	37,8	44,6
	June	47,5	36,5	42,9	59,2
	July	40,0	30,7	48,0	73,8
	August	39,5	19,3	40,1	80,4
	September	39,0	7,9	52,0	87,0
	Mean	60,0	40,0	32,1	54,0

In Table 16 it can be seen that FI species as a percentage of total biomass decreased from an initial high of 81,5% to 39,0% at the end of the period, on burnt plots. NF species biomass expressed as a percentage of total biomass increased from an initial low of 16,7% to 52% in September on burnt plots (Table 16). This is largely due to the persistent green stems and flowering culms of the unpalatable species Eragrostis pallens, giving a bias towards the biomass component of the NF species. During September, stems and leaves of this species were separated. Stems and flowering culms formed 92% of total biomass of this species. In comparison, leaf material formed 84% of biomass of the FI species harvested during September. On the unburnt plots, the leafier FI species formed more than 50% of total biomass during the period December through March. Towards the end of the period, from April to September, the NF species constituted the major portion of total biomass. This was again largely due to the persistent green stems and flowering culms of E. pallens.

4.3.2 Necromass

In Fig. 22, necromass curves for the sward as a whole, on burnt and unburnt plots are shown. The extent to which accumulated necromass is 'carried over' from previous to the current year is well illustrated: on the unburnt plots, 59,8 g m^{-2} of necromass was harvested during October, compared with a mere 3,2 g m^{-2} of necromass on the burnt plots at the same time. Necromass on the burnt plots increased from 0 immediately after the burn, to high values around July and thereafter decreased as necromass became detached and transferred to the litter compartment. In the unburnt sward, the trend is for necromass to decrease initially to a low around November/December (corresponding to the period of most active growth). Between January and March/April, necromass increases as current year's biomass dies, and thereafter necromass gradually decreases as flow to litter exceeds flow of current year's biomass to necromass.

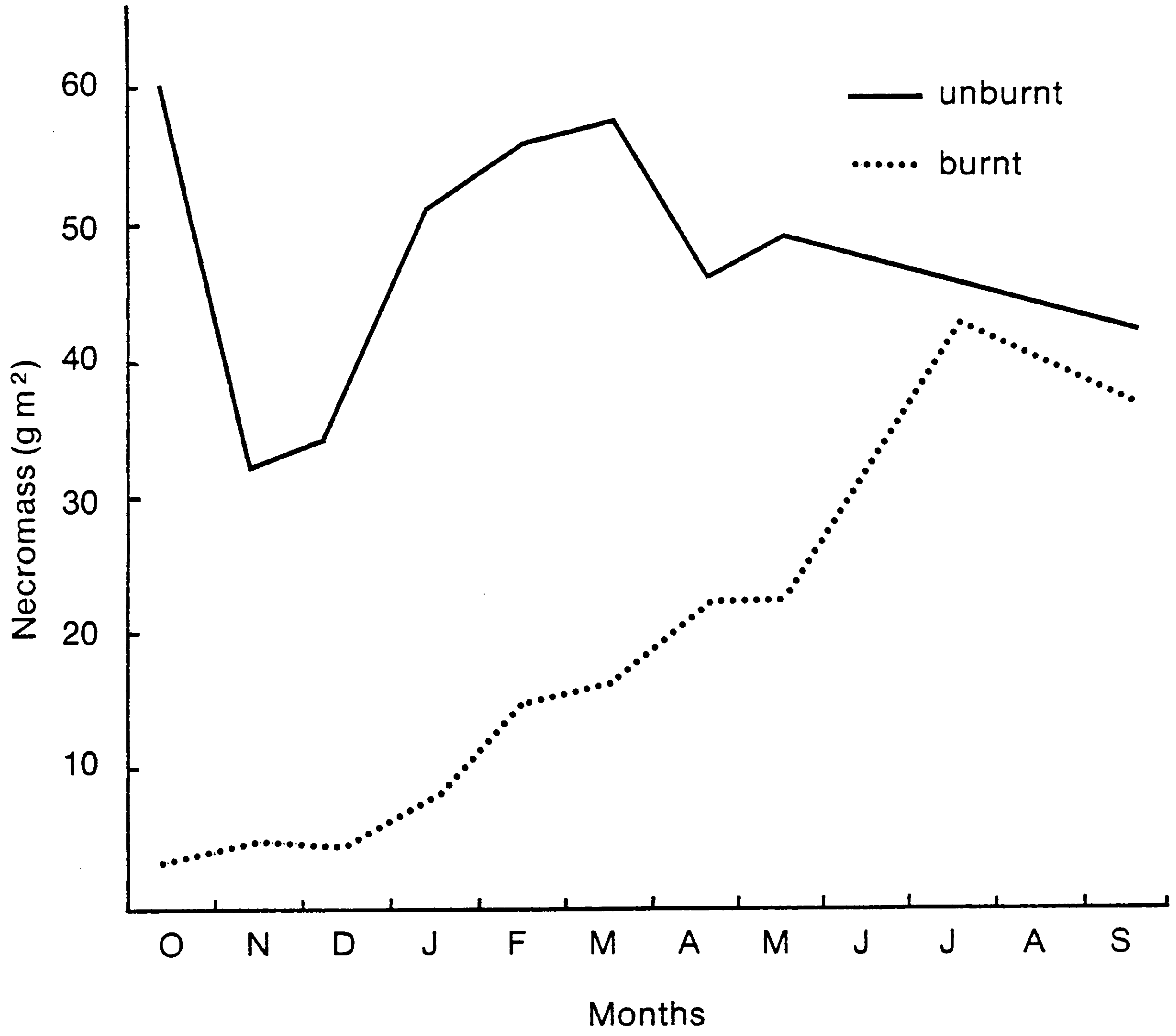

Fig. 22. Necromass (g m^{-2}) of the sward as a whole, on burnt and unburnt plots, 1978/79.

At the time of peak biomass of unburnt plots, necromass formed 62,4% of standing crop of NF species, compared with FI species necromass forming only 45,6% of FI standing crop, illustrating the relatively moribund nature of the NF species.

4.3.3 Biomass accumulation rates

In order to compare the BARs of the sward as a whole on burnt and unburnt plots, use will be made of Method I, (para. 3.2.4) as necromass increment cannot be determined accurately from field data on unburnt plots, due to the accumulated previous year's necromass. The mean BARs over the periods of biomass increment are shown in Table 17.

Table 17 : Mean biomass accumulation rates (g m^{-2} day^{-1}) over monthly periods, for burnt and unburnt plots (for total biomass) 1978/79

Period	Burnt plots	Unburnt plots
October to November	0,329	0,189
November to December	0,382	0,157
December to January	0,421	0,386
January to February	-0,118	-0,110
February to March	0,441	0,028
Mean (increments only added)	0,315	0,152

Mean BAR on burnt plots was consistently greater than on unburnt plots. It is noticeable that there was a decrease in biomass in both treatments between the January and February harvest dates. During this period, only 45 mm of rain was recorded at the adjacent weather station.

Using Method 2 (para. 4.2.3) to calculate BAR on the burnt plots, the mean BAR over the periods of concurrent biomass and necromass increments is 0,409 g m^{-2} day^{-1}. This finding is elaborated on in a later section (Chapter 6). Mean BARs for the FI and NF groups are shown in Table 18.

Table 18 : Mean biomass accumulation rates (g m^{-2} day^{-1}) of forage and intermediate species (FI) and non-forage species (NF) on burnt and unburnt plots, over the period of biomass increment

Category	Burnt plots	Unburnt plots
FI	0,224	0,117
NF	0,095	0,057

The BAR of the FI species on the burnt plots is 91,5% greater than that of the FI species on unburnt plots. In contrast, the BAR of NF species on burnt plots is only 66% higher than that of the largely moribund NF species on the unburnt plot.

4.3.4 Cumulative biomass production after eight-weekly clipping on burnt and unburnt plots

The cumulative biomass production curves, obtained by summation of regrowth measured over each eight-week period, are shown in Fig. 23, for the sward as a whole.

The different initial values (24 vs 5 g m^{-2}) reflect the difference in biomass on burnt and unburnt plots caused by the fire. The actual amount of regrowth on burnt and unburnt plots over each eight-week period was, in the case of the sward as a whole, very similar, as is shown in Table 19.

Table 19 : Mean biomass increments of the sward as a whole (regrowth) (g m^{-2}) on burnt and unburnt plots subjected to eight-weekly clipping , over each eight-weekly period, 1978/79

Regrowth period	Burnt plots	Unburnt plots	LSD p=0,05
October to December	24,2	23,4	NS
December to February	10,4	10,4	NS
February to April	7,2	6,2	NS
April to June	0,0	0,0	
Total	41,8	40,0	NS

4.3.5 Cumulative biomass production of the FI and NF categories

The cumulative biomass production curves of the FI species category subjected to eight-weekly clipping on burnt and unburnt plots are shown in Fig. 24. An analysis of variance conducted on the areas

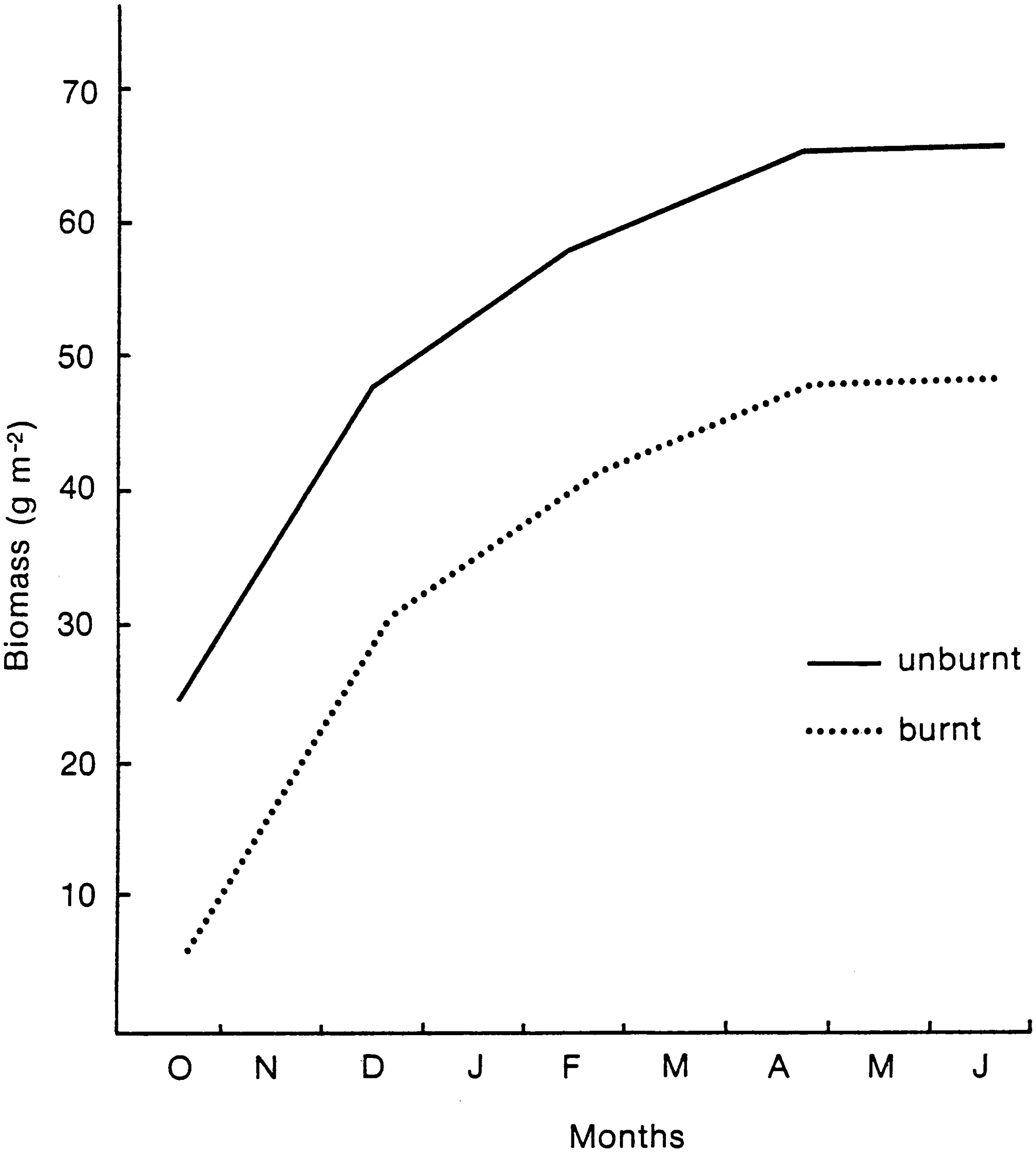

Fig. 23. Cumulative biomass production (g m^{-2}) of the sward as a whole, on burnt and unburnt plots subjected to eight-weekly clipping, 1978/79.

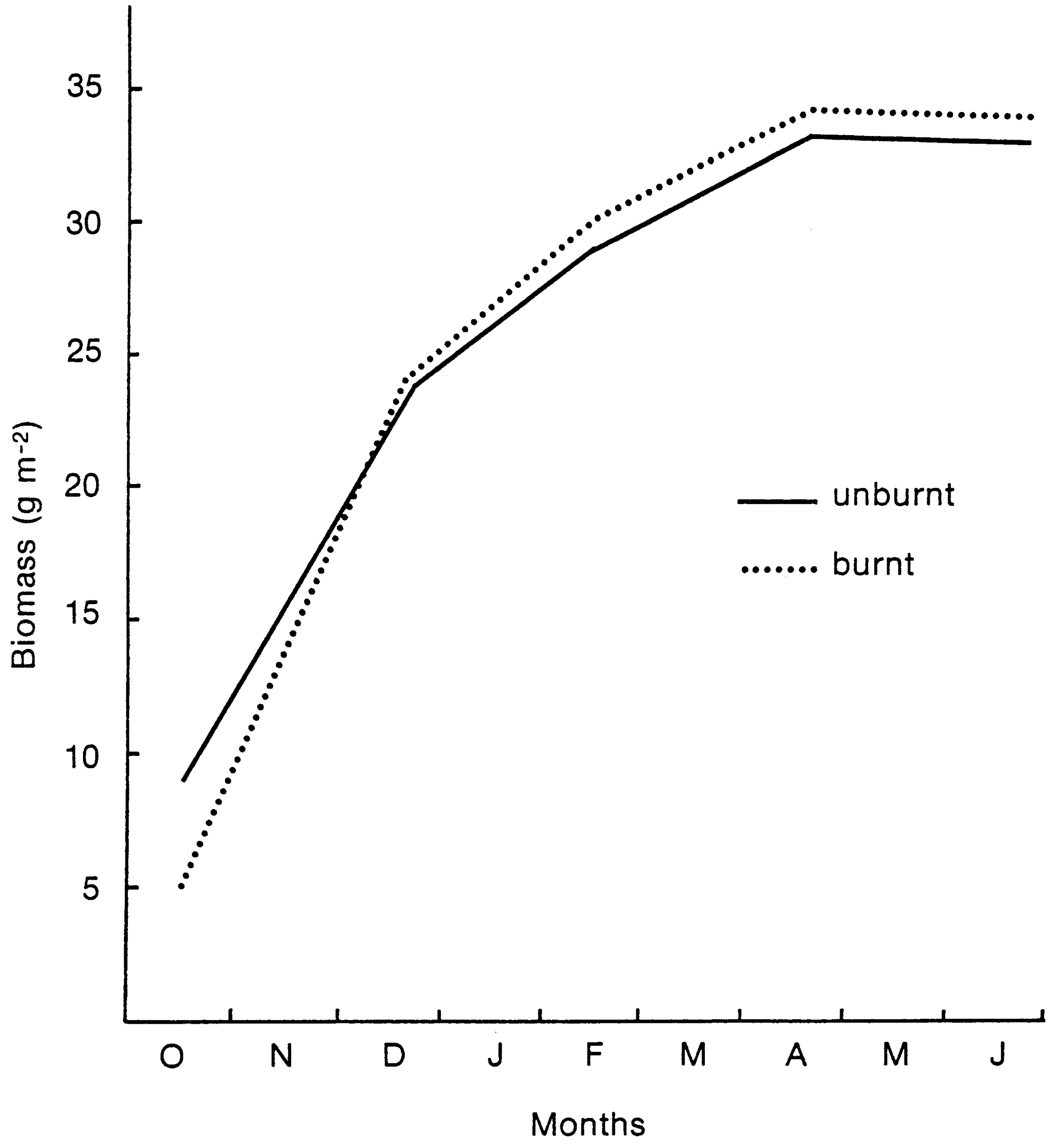

Fig. 24. Cumulative biomass production (g m^{-2}) of forage and intermediate species, on burnt and unburnt plots subjected to eight-weekly clipping, 1978/79.

under these two curves revealed no significant difference between the amounts of biomass present. Actual amounts of regrowth are shown in Table 20.

Table 20 : Mean biomass increments (regrowth) of forage and intermediate species (g m^{-2}) on burnt and unburnt plots subjected to eight-weekly clipping, over each eight-week period, 1978/79

Regrowth period	Burnt plots	Unburnt plots	LSD p=0,05
October to December	17,4	13,2	NS
December to February	7,5	6,9	NS
February to April	4,7	4,7	NS
April to June	0,0	0,0	
Total	29,6	24,8	NS

NF species cumulative biomass production is shown in Fig. 25 and Table 21.

Table 21 : Mean biomass increments (regrowth) of non-forage species (g m^{-2}) on burnt and unburnt plots subjected to eight-weekly clipping, over each eight-week period, 1978/79.

Regrowth period	Burnt plots	Unburnt plots	LSD p=0,05
October to December	5,1	7,9	2,3
December to February	1,7	2,6	NS
February to April	2,2	1,0	NS
April to June	0,0	0,0	
Total	9,0	11,5	NS

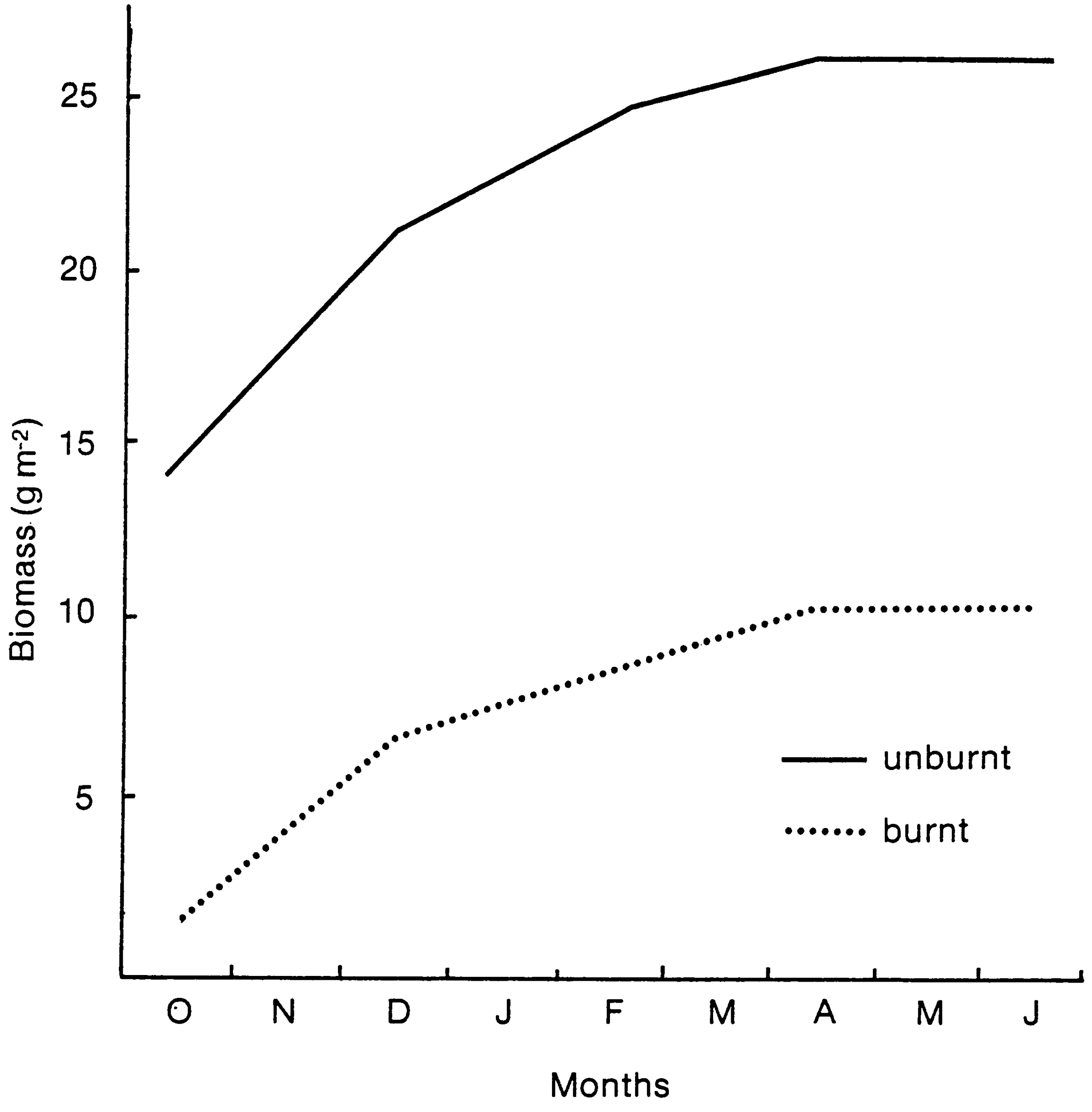

Fig. 25. Cumulative biomass production (g m^{-2}) of non-forage species, on burnt and unburnt plots subjected to eight-weekly clipping, 1978/79.

The amount of NF biomass produced on burnt plots between October and December was significantly lower than that produced on unburnt plots. It is noticeable that most regrowth occurred early in the year and declined over the year. Although quadrats were clipped in April, regrowth was infinitesimal and upon re-examination in June, no harvestable regrowth was noticed.

4.3.6 Necromass production under an eight-weekly clipping regime

As all necromass was removed during each clipping treatment, it was possible to calculate flow from newly-grown biomass to necromass during each eight-week regrowth period. This gives an indication of death rates, at least under the applied clipping regime. Amounts of necromass formed over each eight-week period are shown in Table 22.

Table 22 : Necromass formation (g m^{-2}) of the sward as a whole subjected to eight-weekly clipping, on burnt and unburnt plots, 1978/79.

Period	Burnt plots	Unburnt plots	LSD p=0,05
October to December	2,7	3,6	NS
December to February	2,3	2,8	NS
February to April	1,8	1,8	NS
Total	6,8	8,2	NS

On average, necromass production was 16,3% of biomass production on burnt plots, and 20,4% of biomass production on unburnt plots, subjected to eight-weekly clipping (c f Tables 19 and 22). As biomass regrowth over each 8 week period decreased from the October/December to the February/April regrowth period (Table 19), so too did the amount of necromass (Table 22). It is unlikely that significant quantities of newly-formed necromass would become detached from the plant in the short period. The data presented are thus felt to accurately reflect the actual amounts of necromass formed.

4.3.7 Comparison of the biomass accumulation rates on burnt and unburnt plots, with and without subsequent eight-weekly clipping

In order to facilitate comparison of the BARs pertaining to each treatment, BARs of the sward as a whole and of FI species and NF species are presented in Table 23.

Table 23 : Mean biomass accumulation rates of total biomass, forage and intermediate (FI) species and non-forage species (NF), subjected to different treatments, 1978/79

	Treatment			
	Unburnt		Burnt	
	Unchecked growth	Eight-weekly clipping	Unchecked growth	Eight-weekly clipping
Total biomass	0,152	0,240	0,315	0,251
FI species	0,117	0,148	0,224	0,177
NF species	0,057	0,069	0,095	0,053

It is noteworthy that although the clipping regime imposed was considered to be more severe than grazing would have been, both burning (column 3) and clipping (columns 2 and 4) apparently stimulated the rates of biomass accumulation relative to the sward allowed unchecked growth (column 1,Table 23), in most cases.

4.3.8 Botanical surveys

The results of the botanical surveys conducted using a sharp-pin, bridge-point apparatus are shown in Table 24.

Table 24 : Percentage basal cover of herbaceous layer species on plots before and after a burn during 1978. (2000 points per treatment per survey)

Species	Pre-fire survey (March 1978)		Post-fire survey (March 1980)	
	No Burn	Burn	Unburnt	Burnt
* *Digitaria eriantha*	1,92	2,45	1,62	2,12
Eragrostis pallens	1,66	1,47	1,52	0,69
* *Schizachyrium jeffreysii*	0,29	0,32	0,29	0,10
Perotis patens	0,07	0,24	0,24	0,17
Aristida argentea	0,04	0,25	0,20	-
* *Rhynchelytrum villosum*	0,01	0,19	0,04	0,17
* *Rhynchelytrum* sp.	-	0,07	-	-
Cyperus margaritaceus	0,17	-	-	-
Fimbristylis sp.	0,02	0,04	-	0,17
* *Themeda triandra*	-	0,17	-	0,10
* *Justicia minima*	0,17	-	0,04	0,17
* *Heteropogon contortus*	0,01	0,12	-	0,10
Aristida diffusa	0,04	0,07	0,12	0,10
Aristida stipitata	0,09	0,01	0,10	0,04
Lippia sp.	0,04	0,05	-	-
Forb (unidentified)	0,03	0,06	0,06	0,06
Eragrostis rigidior	0,05	-	-	-
* *Panicum maximum*	0,03	0,02	-	0,12
* *Diheteropogon amplectens*	0,04	-	0,04	0,09
Aristida congesta	0,04	-	0,04	0,04
Eragrostis gummiflua	0,03	-	-	-
* *Brachiaria nigropedata*	0,01	0,02	-	0,17
* *Brachiaria serrata*	-	0,02	-	-
Pogonarthria squarrosa	-	0,02	-	-
* *Hyperthelia dissoluta*	-	0,01	0,06	0,12
Unidentifiable	0,13	-		
Total	4,89	5,60	4,37	4,53

* Forage and Intermediate species

It is apparent that the percentage basal cover of *Eragrostis pallens* tufts is lower on plots subjected to the fire than on unburnt plots (0,69% vs. 1,52% Table 24 : significant at p = 0,05). Notably, *Digitaria eriantha* tufts have not significantly changed on burnt plots compared with unburnt plots (Table 24). On the "burn" plots, the basal cover of *E. pallens* has decreased from 1,47% recorded during the pre-fire survey to 0,69% recorded eighteen months after the fire (significant, p = 0,05). In contrast, there is no significant difference between the basal cover of *E. pallens* of 1,66% recorded on "no burn" plots before the fire and 1,52% recorded on unburnt plots during the post-fire survey. The combined basal cover percentage of FI species on "burn" plots does not differ significantly between the two surveys (3,39 before burning vs. 3,26% eighteen months after the fire). In Table 25 the percentage basal covers of FI and NF species are expressed as percentages of total basal cover for each date, and the change between surveys is indicated.

Table 25 : Relative percentage basal covers of forage and intermediate (FI) and non-forage (NF) species on burnt and unburnt plots before and after the September 1978 burn

	FI species		NF species	
	Burn	No burn	Burn	No burn
March 1978 (pre-fire)	60,2	50,7	37,8	47,8
March 1980 (post-fire)	72,0	47,8	26,8	50,8
Change (pre-fire to post-fire)	+ 11,8	- 2,9	- 11,0	+ 3,0

It is apparent that the burn favours the FI species to the detriment of the NF species. There were indications of the opposite effect where no burning took place.

Of the Eragrostis pallens tufts examined during the post-fire survey in March 1980, 59% were dead on the burnt plots, compared with only 7% on the unburnt plots.

4.3.9 Exclusion of herbivores for differing periods after a fire

The February standing crops recorded in the different plots enclosed for varying periods after the burn in Camp 2, in the two vegetation types are shown in Table 26.

Table 26 : February standing crop (biomass and necromass) of grass and forbs in two vegetation types subjected to different periods of post-fire protection from large herbivores (g m^{-2})

	Period of protection from herbivores (days)			Unprotected	Level of* Significance	LSD p=0,05
	29	67	101			
Acacia spp savanna						
grass	11,0	15,8	23,3	7,2	NS	-
forbs	16,7	8,4	11,3	12,2	NS	-
Total	27,7	24,2	34,6	19,4	NS	-
Burkea africana savanna						
grass	5,0	5,8	25,2	8,3	++	9,8
forbs	0,5	2,6	0,5	0,6	NS	-
Total	5,5	8,4	25,7	8,9	++	9,6

* NS = non-significant, ++ = significant at p = 0,01

Within Burkea africana areas, the sites protected from herbivores for the longest period (101 days after the fire) exhibited the greatest February standing crop of 25,7 g m^{-2}. This was highly significantly greater ($p = 0,01$) than the February standing crop measured in the plots protected for 29 or 67 days after the fire and than the completely unprotected control plots. In the nearby "permanent" exclosures in which no herbivores had grazed, a February standing crop of 64 g m^{-2} was harvested, illustrating the degree of herbivore utilization of the burnt sward, especially the sites left unprotected or protected for shorter periods after the fire.

The apparent trend in the Acacia spp. areas viz. an increase in the standing crop harvested in February from the completely unprotected plots (19,4 g m^{-2}) to the highest standing crop of 34,6 g m^{-2} recorded in the plots protected for the longest period after the fire (101 days) did not achieve statistical significance.

The generally high forb phytomass in Acacia spp areas is evident, and in Table 27, forb phytomass is expressed as a percentage of total phytomass, for each treatment.

Table 27 : Forb species standing crop as percentages of total standing crop in two vegetation types subjected to different periods of post-fire protection from large herbivores

	Period of protection from herbivores (days)			unprotected
	29	67	101	
Acacia spp savanna	60,3	34,7	32,7	62,9
Burkea africana savanna	9,1	30,9	2,0	6,7

4.4 Discussion

The use of fire in range management has been justified in situations where accumulated necromass reduces the vigour of the sward (Trollope, 1979). As is evident from the data presented here, the herbaceous layer is rather moribund after several years of protection from fire and only light grazing. The fire removed the accumulated necromass, preventing shading and other negative effects of this standing dead material. From the onset of growth, up to the January 1979 harvest, only 260 mm of rain had fallen (Table 1). From then to March, a further 92 mm of rain fell, and it is possible that the 'rejuvenated' sward on the burnt plots responded better to this moisture availability than did the unburnt sward, accounting in part for the differing times of peak biomass in the two treatments.

The mean biomass accumulation rates of the sward as a whole were similar on burnt and unburnt plots subjected to eight-weekly clipping (0,251 vs. 0,240 g m^{-2} day^{-1}, Table 23). In contrast, the mean BAR of the unburnt sward, allowed unchecked growth, was only 0,152 g m^{-2} day^{-1}, as compared to 0,315 g m^{-2} day^{-1} for the burnt plots. If BAR is considered to be an indication of the vigour of the sward, several inferences may be drawn from the BARs pertaining to each treatment: (1) fire followed by conditions of unchecked growth, although depressing the actual amount of biomass present over the season (para. 4.3.1) stimulated the sward to a greater rate of biomass accumulation when compared to the unburnt sward; (2) fire followed by clipping, resulted in lower BARs than were measured in a sward burnt and then protected from defoliation. A similar observation is reported by Huntley (1972) for a northern Transvaal savanna region whilst Tainton, Groves and Nash (1977) reported that harvesting of recovery growth in burnt tall grassveld in Natal considerably reduced yield in the short term.

An eight-weekly defoliation regime imposed on the unburnt sward resulted in a greater mean BAR than was measured on the undefoliated, unburnt sward allowed unchecked growth (0,240 vs. 0,125 g m^{-2} day^{-1}). The defoliation treatment removed much of the inhibitory necromass. Furthermore, complete protection from defoliation is a somewhat harsh treatment of grass plants, which have been described as 'obligate grazophils' (MacNaughton, 1979).

The above discussion has referred to the sward as a whole. The BARs of the FI species generally substantiate the above inferences. It is noteworthy, however, that whereas the mean BAR of FI species allowed unchecked growth is 91,5% greater on burnt plots as compared to unburnt plots, FI species subjected to eight-weekly defoliation exhibited BARs only 19,5% greater on burnt than unburnt plots. Thus, although the 'double' defoliation of fire and subsequent clipping did not result in a lower BAR than the 'single' defoliation of clipping alone, the eight-weekly clipping treatment decreased the magnitude of stimulation of FI species on burnt versus unburnt plots.

In the case of the NF species, the 'double' defoliation actually resulted in the lowest BAR measured. The severe backfire proved to be deleterious to the NF species in general, whilst in fact stimulating the FI species (Fig. 26 and 27). Percentage basal cover of the NF species in general, and of the predominant _Eragrostis pallens_ in particular, was significantly lower on the burnt plots compared to the unburnt plots. A high proportion of _E. pallens_ tufts were killed by the fire, and the amount of biomass of the NF species was lower on burnt plots compared to unburnt plots. It is possible that a 'double' defoliation exhausted root reserves of tufts already largely moribund.

These findings are of significance in terms of range management in this vegetation type. The practice of controlled selective grazing is currently gaining favour amongst pasture scientists. In summary, the theory postulates that utilization of only forage species will maintain the vigour of this category, whilst non-defoliation of unpalatable species will result in this category becoming moribund and senescing. Fire is used only sparingly

Fig. 26. A view of a burnt plot taken during March 1980. The predominantly visible species is Digitaria eriantha ssp pentzii.

Fig. 27. A view of an unburnt plot taken during March 1980. The predominantly visible species in this case is the unpalatable Eragrostis pallens.

in this system, as it is considered that fire will maintain the vigour of the unpalatable species.

In the light of the findings on the effect of the intense backfire, it would appear that such a fire, particularly if followed by judicious utilization of the sward, may hasten the demise of undesirable unpalatable species where such species are allowed to become moribund.

The findings of the experiment which excluded herbivores for different periods after the fire on camp 2, have significance in terms of range management in the Nylsvley Nature Reserve. Although the standing crop of grass harvested in February in the different treatments in *Acacia spp* savanna did not differ significantly, due to high variability, an apparent trend is discernable. There is an increase in standing crop of grass with increasing length of protection from large herbivores, the lowest standing crop being recorded in completely unprotected sites. Highest February grass standing crop in *Acacia spp* areas was recorded in the sites protected for 101 days after the fire. Forbs constituted a large percentage of total standing crop in *Acacia spp* savanna, largely due to the proliferation of *Solanum panduraeforme* after the fire.

In *Burkea africana* savanna, the February grass standing crop harvested on sites protected for 101 days after the fire was significantly ($p = 0,01$) greater than the February standing crop harvested in the other sites protected for shorter periods. In general, visual observation revealed that grasses in *Burkea africana* savanna were well utilized while still young i.e. shortly after the fire, but utilization of these areas decreased as the grasses matured. Monro (1978) reported that impala concentrated in *Burkea* *africana* areas after the fire and appeared to select for this vegetation type, in contrast to the situation before the fire when impala showed a distinct preference for *Acacia* *spp* areas. With increasing time after the fire, impala reverted to the more usual distribution through the vegetation mosaic.

The exceptionally low standing crop values recorded in February reflect the over-utilization which occurred in camp 2 after the fire and emphasizes the notion that a sufficiently large surface area should be burnt in such circumstances, in order to avoid overgrazing which results from immigration of herbivores onto newly-burnt areas.

CHAPTER 5

EFFECTS OF FREQUENCY AND INTENSITY OF DEFOLIATION ON DRY MATTER PRODUCTION OF DIGITARIA ERIANTHA AND BRACHIARIA NIGROPEDATA

5.1 Introduction

A prerequisite for any progressive livestock production system is an estimate of the effects of defoliation on dry matter production of perennial grasses (Barnes, 1979). Although the herbaceous layer at Nylsvley consists of numerous species, a relatively small number of species dominate or are of value to stock. This fact is in accordance with findings in other areas (e.g. Foran, Tainton and Booysen, 1978). In this light, Tainton (1979) stated that an understanding of the response of a relatively small number of species to defoliation should 'assist materially in the interpretation of the response of the veld as a whole to management'.

5.1.1 Effect of defoliation on the individual plant

Defoliation will, as an initial effect, reduce the photosynthetic leaf area of the plant. Regrowth of new leaf material is dependent on the intensity of defoliation in the following manner:- if defoliation is of a moderate nature such that a large percentage of intercalary meristematic regions in the leaf sheaths and blades are not removed, then regrowth of leaf tissue will continue via these meristematic regions, dependent on mobilisation of reserves in the storage organs. If grazing is of such severity that the apical meristem is removed, then such tillers will die back to the base (Branson, 1953). However, removal of apices and the inhibitory effect of apical dominance does appear to allow for development of lateral 'daughter' tillers which would otherwise have been suppressed (Tainton, 1979). Apical meristems of grasses are generally well protected from grazing due to their compact nature and proximity to the soil surface during the vegetative stage, and are only subject to possible removal after elevation. Rabie (1964) observed that in the majority of grasses studied the reproductive stage was entered before stem apex elevation so that it is unlikely that many vegetative apices are subject to removal under any but the most severe defoliation regime. Branson (1953) states that elevation of apices to a height of 2,5 cm renders them available to removal by herbivores.

Burger (1974) reviewing studies on the effect of defoliation on production concluded that both frequency and intensity of defoliation exert an influence on production. In general, higher frequencies and lower intensities resulted in higher DM production. Obviously though, this is dependent on such factors as species studied, whether they be in natural veld or sown pastures, subject to fertilization or not, and whether the experiment was conducted in a controlled environment or under natural conditions.

5.1.2 Effect of defoliation on root growth and carbohydrate reserves

The work of Crider (1955) showed that root growth either slowed down or stopped completely when top growth was removed, the degree of root regrowth depending on the severity of the defoliation treatment. Similar conclusions were drawn by Tainton (1958), Du Toit, Rabie and Grunow (1973), Grobbelaar (1971) and Weinmann (1943, 1944).

Excessive defoliation results both in a die-back of roots as reserves are retranslocated to allow for top growth, and, of particular significance in a perennial sward, insufficient storage reserves to allow for initial growth in a subsequent growing season. Tainton (1979) observes that these effects are not equally pronounced in all species, in that species with a low habit and underground stems are more resistant to defoliation than upright species. Steinke and Booysen (1968) state that cutting grasses at "increasingly frequent intervals tends to deplete carbohydrate reserves progressively and results in decreased regrowth and in some cases even death of plants". Using an autoradiographic technique, it was further demonstrated (Steinke 1969) that reserve materials were translocated from storage organs (mainly root crowns) to new leaves produced after defoliation, and suggested that these materials were used for respiration and for the production of structural material.

The present study was conducted to examine the effect of height and frequency of defoliation on above ground DM production, root mass, and nitrogen content of *Digitaria eriantha* ssp *pentzii* and *Brachiaria nigropedata*. Controlled environment studies, whilst indicating overall trends, are obviously subject to limitations. Burger (1974) for example found that *Anthephora pubescens* tufts grown in pots in a controlled environment were smaller and shorter than those grown under natural conditions. He ascribed this to limited space for root development in the pots. Furthermore, tufts defoliated under natural conditions are subject to further variables such as competition from surrounding plants and fluctuations in water availability and temperature. In this study defoliation treatments were carried out both in a controlled environment, and in the study area at Nyslvley (hereafter referred to as *in situ*).

5.2. Methods

5.2.1 Controlled environment

5.2.1.1 Dry matter production

Asbestos pots of 7 litre capacity were utilized in this study. Drainage holes were provided at the base of each pot. Small stones were placed in each pot to a depth of *ca* 2 cm to prevent soil compaction and loss through the drainage hole. Sifted loamy soil, obtained from the University of Pretoria experimental farm was packed into each pot in layers, in order to obtain a reasonably uniform degree of compaction. Each pot was filled to approximately 2,5 cm from the top. Pots were watered thoroughly, allowed to stabilize and repacked. Pots were fertilized in the manner described by Burger (1974):- 1,6 g superphosphate, 0,32 g potassium chloride and 1,9 g limestone ammonium nitrate was applied to the surface of each pot and thoroughly mixed into the upper 10 cm of soil. This is equivalent to a fertilizer application of 500 kg superphosphate (41,5 kg P), 100 kg potassium chloride (50 kg K) and 600 kg limestone ammonium nitrate (28% N) (168 kg N) per hectare taking the mass of 1 hectare of soil 15 cm deep as being 2 200 000 kg (Burger, 1974).

Tufts of *D. eriantha* and B. *nigropedata* were excavated at Nylsvley on 7th March 1978 and transplanted into the asbestos pots. Half of the tufts of each species were lightly defoliated to aid establishment in the pots. Pots were placed in a greenhouse and watered every three days.

The heating system of the greenhouse was set to operate at a temperature of 17°C. Cooling was initiated at a temperature of 29 - 30°C. A day length of 14 hours was maintained throughout the period of study, using mercury vapour lamps when natural day length was less than 14 hours.

The *D. eriantha* tufts which were clipped at time of transplant became more successfully established than those not clipped which were accordingly discarded. *B. nigropedata* tufts mostly failed to establish after transplant. In April 1978 more tufts of this species were excavated. Sandy soil from Nylsvley was placed in the asbestos pots but this second batch of tufts also failed to establish. After a further failure in May 1978, further attention was confined to *D. eriantha*.

In April 1978 1 g LAN (88 kg $N.ha^{-1}$) was applied to each pot and on 3rd May 1978 pots were divided into five blocks each containing 15 pots. Division into blocks was done on the basis of tiller numbers:- although tufts were of similar size at time of transplant, there was nevertheless a variation in size and tiller number at the initiation of the experiment. This variation was slight but grouping on this basis resulted in the most homogeneous blocks possible.

Each pot in each of the five replicate blocks was randomly assigned to one of the following treatments: five clipping frequencies of 3, 6, 9, 12 and 36 weeks (the latter being equivalent to unchecked growth over the 36 week period of the experiment) and clipping intensities (heights) of 2, 5 and 8 cm in a 5 x 3 factorial design.

The initial treatments were applied on 4th May 1978, tufts being clipped using a stainless steel scissors. At this date a further 1 g LAN was added to each pot. A further 1 g LAN was applied at 6 weekly intervals and 18 weeks after the initiation of the experiment the full nutrient supplement, as applied at the start, was applied.

The pots within each block were rotated according to the method of Graven (1968) each week. At each harvest date, harvested material was bagged, dried in a forced-draught oven at 70°C to constant mass and weighed. As tufts increased in size use was made of sheep shears to defoliate. During the early stages of the experiment, prolific stolon growth was evident. At the time of harvest, stolons were raised vertically and clipped at the appropriate height, together with the leaf material.

After 36 weeks the experiment was terminated. After the final harvest the contents of the pots were carefully transferred to a sieve. The stubble and roots were thoroughly washed, separated, oven-dried at 70°C and the roots weighed. During the course of the experiment, DM was not separated into live and dead. Dead matter only accumulated in the 12 and 36 weekly defoliation treatments and all dead matter was included in DM yield.

5.2.1.2 Chemical Analyses

Samples of root material from each treatment combination were finely ground through a sieve and subjected to analysis for nitrogen and starch content.

Starch was determined according to the method described by Allen, Grimshaw, Parkinson and Quarmby (1974):- 1 g of material ground to pass through a 40 mesh sieve was heated in a test tube with 5 ml of water and 200 mg of fine sand. The tube was heated for 15 minutes in a boiling water bath to gel the starch, cooled to 30°C and 5 ml 60% $HC1O_4$ rapidly added whilst mixing. The tissue was ground with a glass rod against the side of the tube intermittently for 20 minutes, transferred to a 100 ml volumetric flask and diluted to volume. Aliquots (5 ml) were transferred to 50 ml volumetric flasks. A range of standards containing from 0,1 to 2,5 mg starch was prepared and transferred to 50 ml volumetric flasks. Standards and samples were then treated in the same way:- a few drops of phenol red indicator were added to each flask. NaOH was added until a red colour developed. HOAC (10% v/v) was added to destroy the colour, whereafter a further 2,5 ml was added. Then 0,5 ml KI (10% w/v) and 5,0 ml $KI\ O_3$ (0,0125 M) were added, the flasks well shaken and diluted to volume. Optical density was read at 680 nm using a colorimeter. Starch content of the samples was calculated by comparison with a calibration curve prepared from the standards, and the following :

$$\text{Starch \%} = \frac{\text{C(mg) x solution volume (ml)}}{\text{10 x aliquot (ml) x sample weight (g)}}$$

where C = mg starch, obtained from calibration curve.

Nitrogen contents were determined as follows: 0,5 g of root material ground to pass through a 40 mesh sieve were digested in concentrated H_2SO_4 and $K_2\ SO_4$, with the addition of glass balls to prevent 'bumping'. H_20_2 was added prior to digestion at 420°C for 30 minutes, to aid in breakdown of organic matter and to prevent foaming. The digestion tubes were cooled, diluted to volume and the contents analyzed for NH_4^+ in a Technicon$^{(R)}$ Autoanalyzer II : - a green ammonia-salicylate complex forms by the reaction of NH_4^+ in the sample with added sodium salicylate, sodium nitroprusside and sodium hypochloride in a buffered medium. This is read at 660 nm, and compared with standards of known concentration.

5.2.2 In situ

For the purpose of the design of the experiment, it was necessary to use tufts as replicates and consequently it was desirable that similar tufts should be used. A preliminary survey was undertaken to establish the distribution of tiller numbers per tuft, with a view to utilizing tufts from the modal class for the defoliation experiment. However, difficulty was experienced in actually counting tillers in the field. The results could not be reproduced on the same tufts to any acceptable degree. Therefore tuft diameter was used as the criterion for including tufts in the experiment.

Chosen tufts of the grasses *Digitaria eriantha* ssp *pentzii* and *Brachiaria nigropedata* were assigned in a randomized block design to one of the following treatments: 3, 6, and 9 weekly defoliation at heights of 2, 5 and 8 centimetres above 'crown' level. It was found that, especially in the case of *D. eriantha*, tufts were generally raised slightly above the surrounding soil level, and the stated defoliation heights would be meaningless in relation to ground level. The 2 cm height especially would in several cases have resulted in complete removal of 'above ground' biomass, including stem bases. The following method was thus adopted:- a dowel stick of 4 mm diameter was marked at intervals of 2, 5 and 8 cm from the base. The stick was carefully lowered into a tuft until resting on the top of the crowns inside the tuft (indicated by visual inspection and resistance to further gentle downward pressure). Using a stainless steel scissors, the tuft was then defoliated at the level of the marks on the dowel stick.

Each treatment combination was replicated 15 times for both *D. eriantha* and *B. nigropedata*. The number of tufts of each species was therefore 3 x 3 x 15 equalling 135.

Tufts were marked by inserting wire pins close by. Each pin was coded in varying colour combinations to facilitate relocation. Aluminium garden markers were fixed to each pin and a code corresponding to the particular tuft's treatment combination was engraved on the garden marker.

The particular part of the study area was open to grazing by indigenous herbivores and insects but no sign of mega- or mesoherbivore activity was encountered in the immediate vicinity of marked tufts. Insect consumption is a normal feature of the herbaceous layer of savanna and was accepted, within the context of this study, as being an environmental variable.

On 18-10-1978, all tufts were clipped to their respective heights and thereafter at the appropriate time intervals. Regrowth was oven-dried at 70°C to constant mass in a forced-draught oven and weighed. It was intended to continue the experiment for 36 weeks but after May 1979 no further regrowth was measured so the experiment was terminated after 27 weeks.

After the final clip five replicates of each treatment combination were excavated. Care was taken, as far as possible, to include all roots. The roots were washed to remove sand; roots and stubble were separated, and roots weighed. Roots were subjected to analyses for starch.

In March 1980, all remaining tufts were examined and the percentage which had died in each treatment was calculated, in order to assess the longer-term effect of the treatments on the tufts.

5.3 Results

5.3.1 Dry matter yields of *Digitaria eriantha* ssp *pentzii* in a controlled environment

The total yields of each treatment combination averaged over the five replicates are presented in Table 28 .

Table 28 : Total yield (g) of each frequency (F) x intensity (I) treatment combination for *Digitaria eriantha* ssp *pentzii* over a 36 week period, in a controlled environment

Frequency (weekly)	Intensity (cm)			Average yield of each F over all levels of I
	2	5	8	
3	10,35	29,85	28,52	$22,92^a$
6	32,05	41,23	39,68	$37,65^b$
9	26,53	41,64	41,99	$36,72^b$
12	37,56	37,09	38,48	$37,71^b$
36	31,51	35,67	32,97	$33,38^b$
Average yield of each I over all levels of F	$27,60^a$	$37,10^b$	$36,33^b$	33,68

LSD (I over levels of F): 6,19 (p = 0,05)
7,79 (p = 0,01)

LSD (F over levels of I): 9,35 (p = 0,05)
11,33 (p = 0,01)

a, b : figures with letters in common do not differ significantly (p = 0,05)

From the table it is apparent that total average dry matter yield of the 3-weekly clipping frequency over all levels of intensity was significantly lower than the other frequencies. The latter (6, 9, 12 and 36 weekly) did not differ significantly from each other. The total average yield at the 2 cm intensity was significantly lower than the average yield of the 5 cm and 8 cm intensities, which did not differ significantly from each other. There was no significant interaction between frequency and intensity of clipping (Appendix 4).

The average yield of each frequency over the levels of intensity is shown in Fig. 28, in which the following trend is discernable: the three weekly clipping frequency resulted in the lowest total dry matter yield, particularly at the 2 cm clipping height. The 2 cm clipping height did not appear to reduce yield, relative to the 5 and 8 cm intensities, at the 12 and 36 weekly frequencies, as illustrated by the slope of the plots of these frequencies in Fig. 28. This is further illustrated in Fig. 29., in which it is also apparent that the 5 and 8 cm clipping heights resulted in similar yields over all levels of clipping frequency.

5.3.2 Below ground dry matter yield of *Digitaria eriantha* ssp *pentzii* in a controlled environment

The average mass of root material for each treatment combination is shown in Table 29.

Table 29 : Average mass (g) of root dry matter for each frequency(F) x intensity (I) treatment combination, for *Digitaria eriantha* ssp *pentzii* in a controlled environment.

Frequency (weekly)	Intensity (cm)			Average mass of each F over all levels of I
	2	5	8	
3	1,69	12,30	17,34	10,44^{a}
6	24,27	29,85	33,78	29,30^{b}
9	15,50	32,53	50,08	32,70^{b}
12	45,47	36,75	28,40	36,87^{b}
36	28,80	26,45	40,60	31,95^{b}
Average mass of each I over all levels of F	23,15^{a}	27,58^{ab}	34,04^{b}	28,25

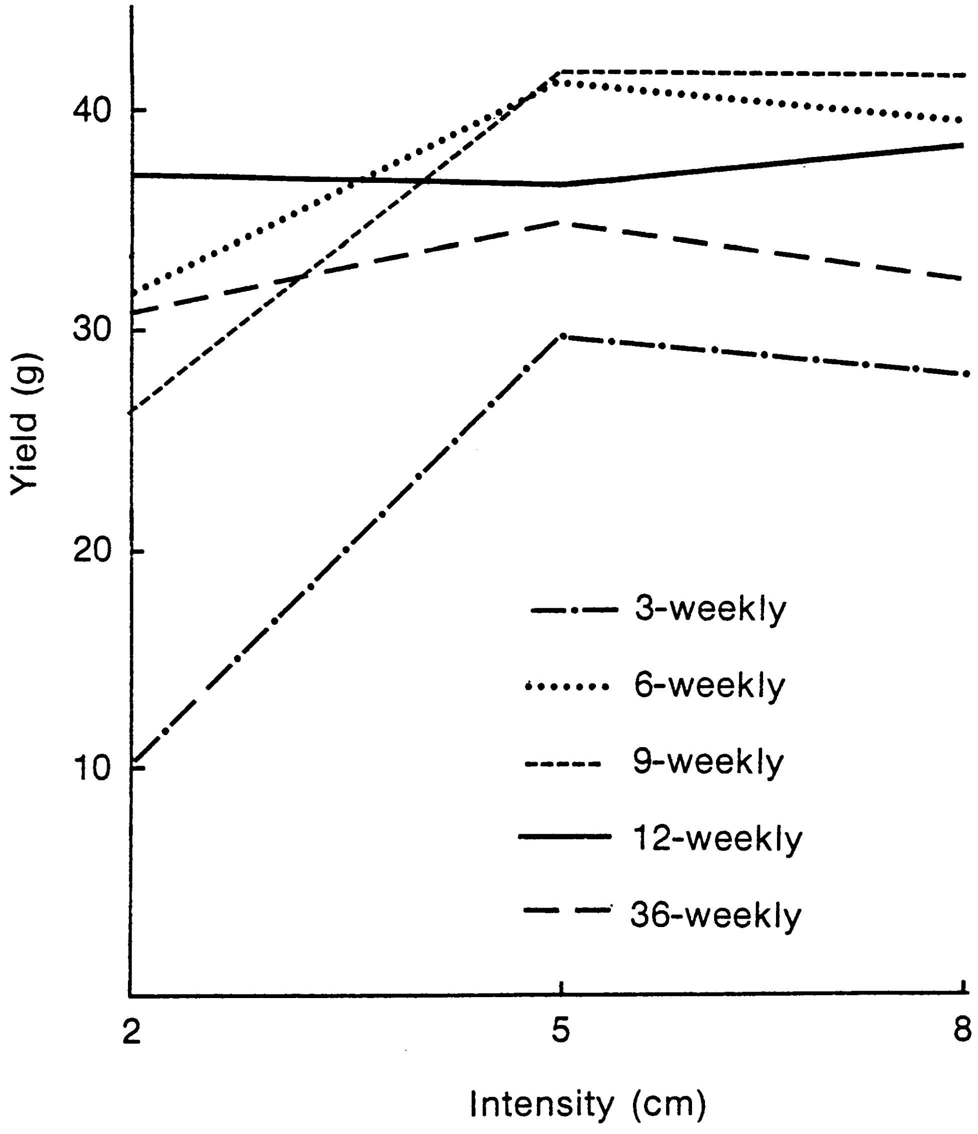

Fig. 28. Average above-ground dry matter yield (g) of each clipping frequency over the levels of intensity, for *Digitaria eriantha* ssp *pentzii* in a controlled environment.

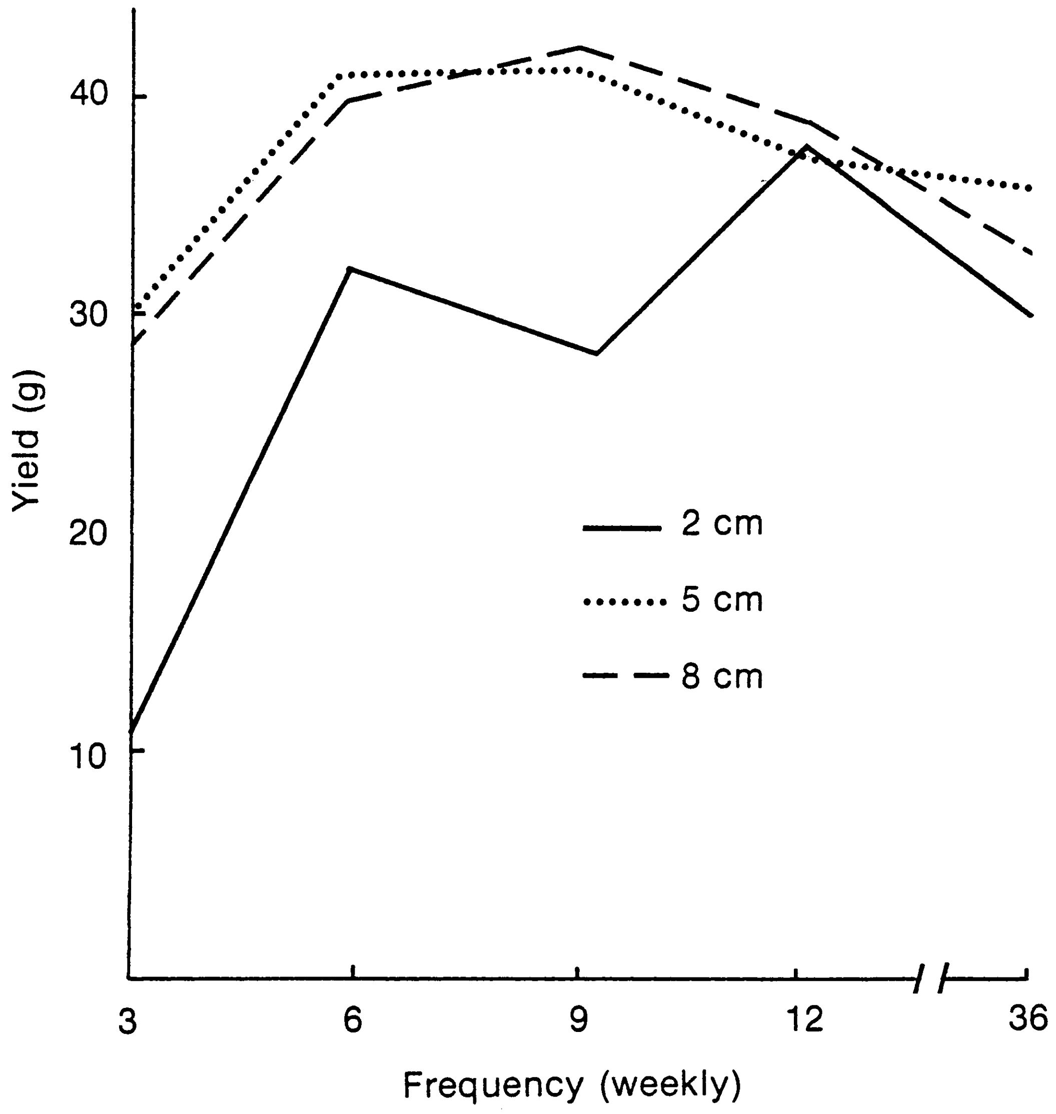

Fig. 29. Average above-ground dry matter yield (g) of each clipping intensity over the levels of frequency for *Digitaria eriantha* ssp *pentzii* in a controlled environment.

LSD (I over levels of F) : 9,86 (p = 0,05)
11,43 (p = 0,01)

LSD (F over levels of I) : 14,87 (p = 0,05)
18,00 (p = 0,01)

a, b, : figures with letters in common do not differ significantly (p = 0,05)

The relations between root mass and frequency and intensity of clipping are further illustrated in Fig. 30 and 31 respectively. Root mass, averaged over all levels of intensity, increases from the low value obtained for the 3 weekly clipping frequency, to the higher values obtained at the less frequent clipping intervals: the root dry matter obtained from the plants clipped at 3 weekly intervals differed significantly (p = 0,05) from that obtained at the 6, 9, 12 and 36 weekly intervals, which did not differ significantly from each other (Table 29, Fig. 30). The root mass of the 2cm clipping height, averaged over all frequencies, was significantly lower than the 8 cm intensity, but all other intensity comparisons were non-significant (Table 29, Fig. 31). There was no significant interaction between frequency and intensity of clipping combinations (Appendix 4), although the most severe defoliation treatment of a 2 cm clipping height at 3-weekly intervals resulted in only 1,69 g of root dry matter accumulating over the period of the experiment.

5.3.3 Chemical analyses of storage organs

Using the method described for ascertaining starch content of storage organs, no appreciable amounts of starch were detected in roots of any of the treatment combinations. Nitrogen contents of the roots, expressed as percentages of root mass, are shown in Table 30.

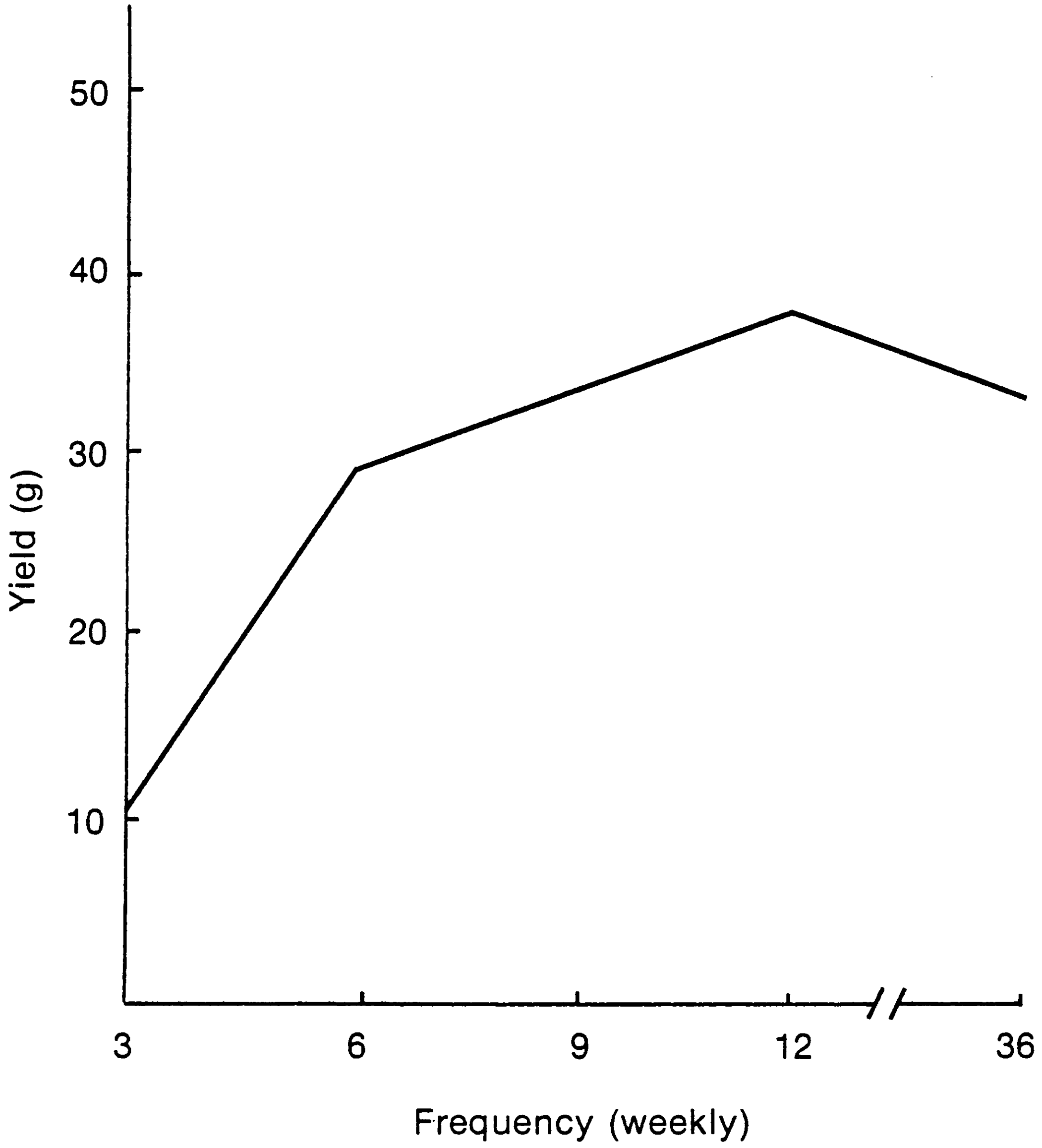

Fig. 30. The relation between root dry matter yield (g)and clipping frequency of Digitaria eriantha ssp pentzii, over all intensities, in a controlled environment.

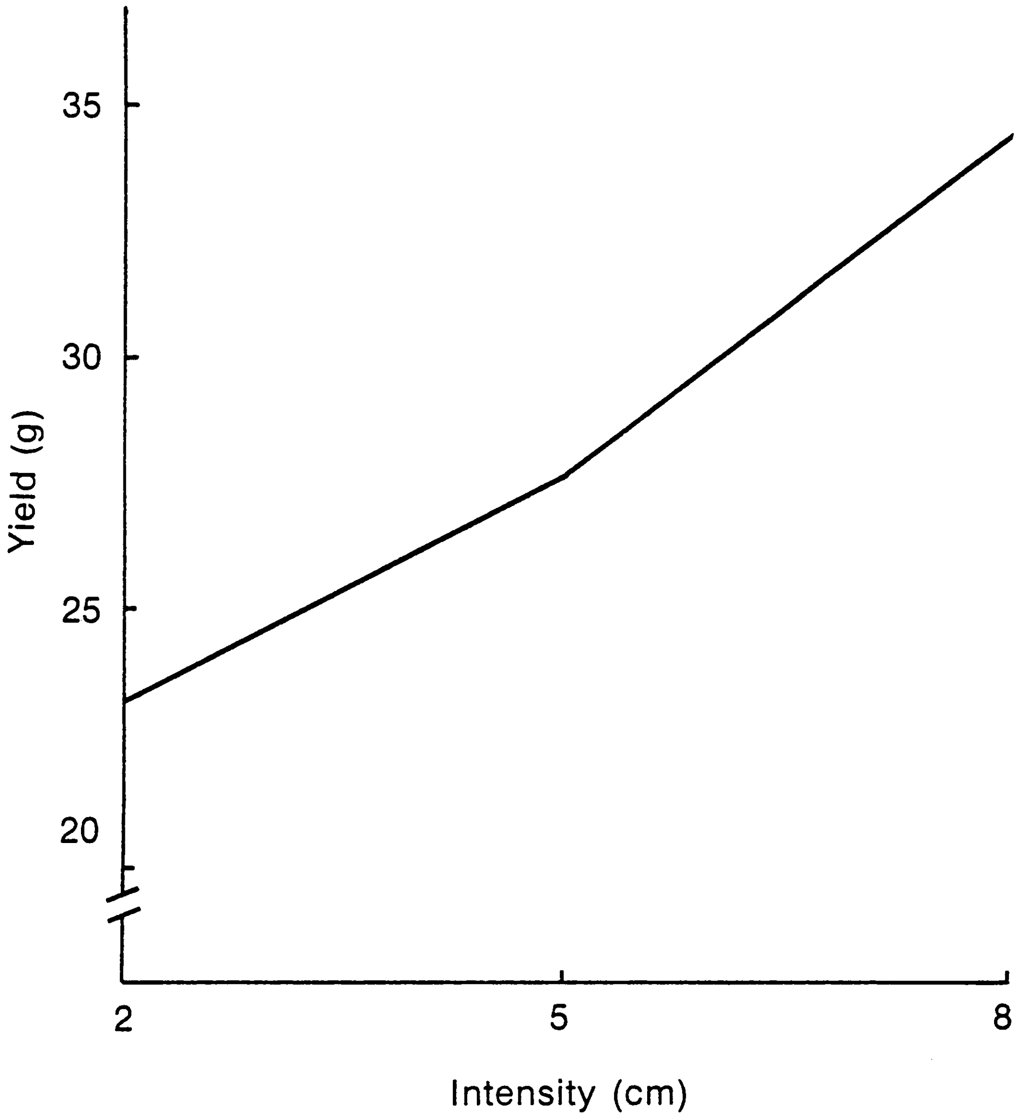

Fig. 31. The relation between root dry matter yield (g) and clipping intensity of <u>Digitaria eriantha</u> ssp <u>pentzii</u>, over all frequencies, in a controlled environment.

Table 30 : Mean percentage nitrogen content of Digitaria eriantha spp pentzii roots, in a controlled environment, for each frequency (F) x intensity (I) treatment combination

Frequency	Intensity (cm)			Average % N content of each F over all levels of I
	2	5	8	
3	*	0,665	0,700	0,683
6	0,582	0,678	0,564	0,608
9	0,737	0,581	0,457	0,592
12	0,413	0,602	0,553	0,523
36	0,715	0,663	0,517	0,623
Average % N content of each I over all levels of F	0,612	0,638	0,558	0,603

LSD (over all I's and F's) : F value NS
* : insufficient material for analysis

No obvious trends are readily discernable. It would appear that percentage nitrogen content of root material is not noticeably influenced by differing clipping treatments.

5.3.4 *In situ* above-ground dry matter yields of *Digitaria eriantha* ssp *pentzii* and *Brachiaria nigropedata*

In Table 31, the total yield of each frequency x intensity treatment combination, averaged over replicates, is shown for *Digitaria eriantha*.

Table 31 : Total yield (g) of above-ground dry matter for each frequency (F) x intensity (I) treatment combination for *Digitaria eriantha* ssp *pentzii* at Nylsvley.

Frequency	Intensity (cm)			Average yield of each F over all levels of I
	2	5	8	
3	0,45	0,47	0,54	$0,48^{ab}$
6	0,52	0,56	0,54	$0,54^{b}$
9	0,45	0,36	0,34	$0,38^{a}$
Average yield of each I over all levels of F	$0,47^{a}$	$0,46^{a}$	$0,47^{a}$	

LSD (F over levels of I) : 0,13 (p = 0,05)
0,20 (p = 0,01)

LSD (I over levels of F) : F value NS

a, b, : Figures with letters in common do not differ significantly

In contrast to the experiments conducted in the controlled environment, the 2 cm clipping height did not result in the lowest above-ground DM yield in the case of *Digitaria eriantha*. There was no significant difference between intensities. The 6-weekly defoliation frequency, averaged over all levels of intensity, resulted in a significantly greater DM yield than the 9-weekly frequency. The average yield obtained from the 3-weekly clipping frequency did not differ significantly from those obtained from either the 6- or 9-weekly clipping frequencies. There were no significant interactions between clipping frequency and intensity combinations (Appendix 4).

The results of the in-situ clipping experiments on B. nigropedata are shown in Table 32.

Table 32 : Total yield (g) of above-ground dry matter for each frequency (F) x intensity (I) treatment combination for Brachiaria nigropedata at Nylsvley

Frequency (Weekly)	Intensity (cm)			Average yield of each F over all levels of I
	2	5	8	
3	1,00	0,95	0,94	$0,96^{a}$
6	1,10	0,96	0,84	$0,97^{a}$
9	1,15	0,82	0,72	$0,90^{a}$
Average yield each I over all levels of F	$1,08^{a}$	$0,91^{ab}$	$0,83^{b}$	0,94

LSD (F over levels of I) : F value NS

LSD (I over levels of F) : 0,19 (p = 0,05)
0,24 (p = 0,01)

a, b, : Figures with letters in common do not differ significantly

The DM yield at the 2 cm clipping height, averaged over the levels of clipping frequency, was significantly greater than at 8 cm but not than at 5 cm. There was no significant difference between DM yields at different frequencies of defoliation. There was no significant interaction between defoliation frequency and intensity combinations (Appendix 4).

5.3.5 *In situ* root dry matter yields of *D. eriantha* ssp *pentzii* and *B. nigropedata*

The total root DM yields of each treatment combination, averaged over the five replicates excavated from the field, are shown below for *D. eriantha* (Table 33) and *B. nigropedata* (Table 34).

Table 33 : Total yield (g) of root dry matter for each frequency (F) x intensity (I) treatment combination for *Digitaria eriantha* ssp *pentzii* at Nylsvley

Frequency (Weekly)	Intensity (cm) 2	5	8	Average yield of each F over all levels of I
3	0,31	0,44	0,51	0,42
6	0,26	0,32	0,29	0,29
9	0,51	0,47	0,44	0,47
Average yield of each I over all levels of F	0,36	0,41	0,41	0,39

LSD (over all I's and F's) : F value NS

There were no significant differences between any of the treatments.

Table 34 : Total yield (g) of root dry matter for each frequency (F) x intensity (I) treatment combination for Brachiaria nigropedata at Nylsvley

Frequency (weekly)	Intensity (cm) 2	5	8	Average yield of each F over all levels of I
3	0,97	1,40	0,75	1,04
6	1,11	0,91	1,31	1,11
9	1,01	0,98	1,11	1,03
Average yield of each I over all levels of F	1,03	1,10	1,06	1,06

LSD (over all I's and F's) : F value NS

As in the case of *D. eriantha*, no significant differences were detected between any treatments or treatment combinations.

5.3.6 Starch content of storage organs

As in the case of *D. eriantha* tufts grown in the controlled environment, no starch was detected in the storage organs of the *in situ* defoliated *D. eriantha* tufts. The starch contents of the roots of *B. nigropedata* proved to be negligible. Upon separation of roots and root crowns however, detectable quantities of starch were recovered from the root crowns of *B. nigropedata*. The results are shown in Table 35.

Table 35 : Starch contents (percentages of dry matter) of the root crowns of *Brachiaria nigropedata* tufts, for each frequency (F) x intensity (I) combination

Frequency (Weekly)	Intensity (cm)			Average yield of each F over all levels of I
	2	5	8	
3	1,2	3,1	3,6	2,6^{a}
6	2,3	3,5	2,6	2,8^{ab}
9	2,3	4,5	5,8	4,2^{b}
Average yield of each I over all levels of F	1,9^{a}	3,7^{b}	4,0^{b}	3,2

LSD (I over levels of F) : 1,1 (p = 0,05)

LSD (F over levels of I) : 1,5 (p = 0,05)

a, b, : figures with letters in common do not differ significantly

The severe 2 cm clipping intensity, averaged over all levels of frequency, resulted in a significantly lower starch percentage than the 5 or 8 cm intensity. The 3 weekly frequency resulted in significantly less starch than the 9 weekly frequency whilst the starch percentage of the 6 weekly clipping frequency did not differ significantly from that of either the 3 or 9-weekly frequencies. There was no significant interaction between frequency and intensity (Appendix 4).

5.3.7 *In-situ* tuft mortality

The percentage of the remaining *in-situ* tufts which were dead during examination in March 1980 are shown below in Tables 36 and 37 for *D. eriantha* and *B. nigropedata* respectively:

Table 36 : Percentage mortality of *Digitaria eriantha* ssp *pentzii* in each frequency (F) x intensity (I) treatment combination, as recorded in March 1980 at Nylsvley

Frequency (Weekly)	Intensity (cm)			Average of each F over all levels of I
	2	5	8	
3	80	10	0	30
6	40	0	0	13,3
9	10	10	0	6,7
Average of each I over all levels of F	43,0	6,7	0	16,7

Table 37 : Percentage mortality of *Brachiaria nigropedata* tufts in each frequency (F) x intensity (I) treatment combination, as recorded in March 1980 at Nylsvley

Frequency (Weekly)	Intensity (cm)			Average of each F over all levels of I
	2	5	8	
3	30	10	0	13,3
6	10	0	0	3,3
9	0	0	0	0
Average of each I over all levels of F	13,3	3,3	0	5,5

The more severe clipping combinations resulted in the greatest mortality of tufts of both species, although *D. eriantha* tufts were particularly deleteriously affected by the 2 cm x 3-weekly treatment combination.

Several of the *B. nigropedata* tufts clipped at the 2 cm intensity, whilst not dying completely, exhibited die-off of central tillers, with new regrowth occurring peripherally. This is illustrated in Fig. 32. The regrowth of a clipped leaf from the intercalary region is also obvious.

5.4 Discussion

The greatest DM yields of *D. eriantha* grown under controlled conditions were recorded at the more moderate levels of defoliation. The most severe clipping intensity of 2 cm and the most severe clipping interval of 3 weeks resulted in the least amount of above ground DM yield over the period of the experiment. The three weekly clipping interval furthermore resulted in the lowest yield of root DM in the case of *D. eriantha* tufts clipped in the controlled environment. In contrast, there were no significant differences between the above-ground DM yields of *D. eriantha* subjected to three clipping intensities under natural conditions, whilst the moderate interval of 9 weeks resulted in a significantly less above-ground DM yield than the 6-weekly interval. It should be noted however, that the more severe clipping treatments resulted in the highest degree of mortality of the tufts defoliated *in-situ*.

Fig. 32. A Brachiaria nigropedata tuft clipped at a 2 cm height at 3-weekly intervals. The death of central tillers and development of peripheral growth is visible. Regrowth of clipped leaves is apparent from the clipped ends of some leaves.

The tufts grown in the controlled environment were subjected, unnaturally in relation to those treated in-situ, to highly favourable conditions as regards moisture, temperature and nutrient supply. The potgrown D. eriantha tufts were considerably taller and generally more robust than those growing in-situ, in direct contrast to the findings of Burger (1974) on Anthephora pubescens. Whilst the average height (excluding elevated flowering culms) of pot-grown tufts was 19 cm, prior to the initiation of the clipping treatments, the greatest height of any in-situ growing tuft was 11,5 cm at time of anthesis. Furthermore, average maximum yield of in-situ clipped D. eriantha tufts (0,56 g) was only 1,33% of the average maximum yield of the tufts grown in the controlled environment.

As is evident from the results of the botanical survey presented earlier (Table 24), the species composition of the Nylsvley sward is somewhat poor from a grazing viewpoint. The dominant palatable species is D. eriantha ssp pentzii and it is probable that this species was heavily utilized during the past, when Nylsvley was a cattle ranch. A combination of this and the above mentioned factors favouring the tufts grown in the controlled environment, were probably responsible for the reduced vigour of the in-situ tufts as compared with those grown in the controlled environment.

In the case of the in-situ clipped B. nigropedata tufts, no significant differences in above or below ground DM yields were caused by the different clipping frequencies. The most severe intensity of 2 cm resulted in a significantly greater above-ground DM yield than the moderate 8 cm clipping height. However, on average, 13,3% of the tufts clipped at the 2 cm height died compared to 100% survival of tufts clipped at the moderate 8 cm height.

The fact that no significant differences were recorded between in-situ root DM yields of the various treatment combinations is possibly a reflection of the variation between the replicates. Only five replicates were utilized, in the case of both species, as ten of the original fifteen replicates were left in order to assess the longer-term effects of the different treatments.

The starch contents of the root crowns of B. nigropedata were found to be lowest at the severe 2 cm clipping intensity. The 3-weekly clipping intervals resulted in significantly less starch in the root crowns than the 9-weekly intervals. Weinmann (1944) reported that root reserves of highveld grasses were similarly reduced by increased clipping frequency. Steinke (1969) concluded, from studies on the effects of defoliation on Eragrostis curvula, that about three weeks were required after defoliation before storage organs' reserves were restored to their pre-defoliation levels. A further defoliation would result in slower regrowth and increased root damage. In the present study the more severe clipping treatments resulted in greatest degree of mortality in both species.

It is likely that the curtailed root development caused by these severe treatments contributed to the death of tufts, particularly during the drier periods experienced.

The method employed to analyse starch is intended as a rapid proximate technique for ecological studies. As such, the failure to detect starch in D. eriantha storage organs may indicate the lack of sensitivity of this technique, rather than indicating that carbohydrates are stored in a different form in this species.

The treatment combinations imposed did not appear to affect the percentage nitrogen content of the D. eriantha roots taken from the plants grown in the controlled environment. Weinmann (1959) states that the complex nitrogen compounds are not as readily mobilized and translocated as the carbohydrate reserves. Whereas percentage nitrogen content has been shown to change seasonally (Weinmann, 1944) it is probable that the clipping treatments imposed did not cause a relatively rapid retranslocation of nitrogenous compounds within the plant.

The peripheral growth and die-off of central tillers in B. nigropedata tufts clipped at the 2 cm x 3 weekly treatment combination is noteworthy. Youngner (1972) states that removal of apical meristems of tillers reduces hormonal inhibition of lateral tiller development. Branson (1953) stated that elevation of grass growing points to a height of 2,5 cm renders tham vulnerable to removal by grazing animals. It is likely that at least some of the growing points were removed by the 2 cm intensity, resulting in the development of 'daughter' tillers from axillary buds and the peripheral growth shown in Fig. 32.

The findings of this study may be stated, in terms of practical animal ranching, as follows: an interval of about 6 weeks between grazing periods would appear to result in relatively favourable above-ground grazeable D M without affecting root D M (and in the case of *B. nigropedata*, carbohydrate reserves) adversely. Whilst it is difficult to relate the defoliation intensities applied to percentage removal of leaf material, this study would emphasize that the severe defoliation levels induced by too high stocking rates is deleterious to the plant as a whole, as evidenced by reduced starch content and high mortality even in the relatively short term, of those plants clipped at 2 cm.

CHAPTER 6

ESTIMATES OF NET ABOVE-GROUND PRIMARY PRODUCTION

In preceding chapters there has been reference to 'production'. As defined previously, this is not synonymous with 'true' net primary production *sensu stricto*, which may be conceptualized as follows:

$$NPP = GPP - R$$

where

NPP = net primary production
GPP = gross primary production
R = loss of photosynthate due to respiration.

The 'production' thus far referred to has been reflected by biomass and biomass changes which, whilst of value in indicating relative amounts and vigour of the sward in a variety of situations, do not meet the requirements of a more refined estimate of 'true' net primary production.

During the course of this study, no quantification of below ground herbaceous biomass was undertaken. In order to accurately quantify 'true' net primary production, such measurements are essential, as photosynthate is continually being relocated from aerial to underground organs. Furthermore, photosynthate is lost in the form of exudates and leachates, and is consumed by herbivores.

In the studies described, no account can be made for most of these losses. Examination of reports on other studies of a similar nature reveals that such losses are generally not accounted for, and a rather loose estimate of 'net annual above-ground production' '<u>sensu lato</u>' is derived. Frequently such results cannot be compared and contrasted because the methods used to derive them differ considerably.

Quantification of net annual above-ground production (<u>sensu lato</u>) in a perennial sward is confounded by residual or 'carry-over' biomass from a previous to a current year. A comparison of September biomass, generally representing the end of a year, and the October values representing the start of a new year's growth, reveal that there is always considerable biomass carried over from a 'previous' to a 'current' year at Nylsvley (Table 3.8). This effectively excludes the use of peak biomass as an estimate of net annual above-ground production.

<u>Table 38</u> : Biomass (g m^{-2})* recorded in September and October at Nylsvley between 1975 and 1978 (1975, 1976 and September 1977 data from Grunow and Bosch, 1978)

Year	September biomass	October biomass
1975	36	27
1976	22	28
1977	16	51
1978	17	24

* Figures rounded to nearest whole number.

As residual biomass dies and flows to necromass, the 'baseline' against which biomass increment is being measured, will decrease, so that the sum of sequential biomass increments will underestimate net annual above-ground production in such a perennial

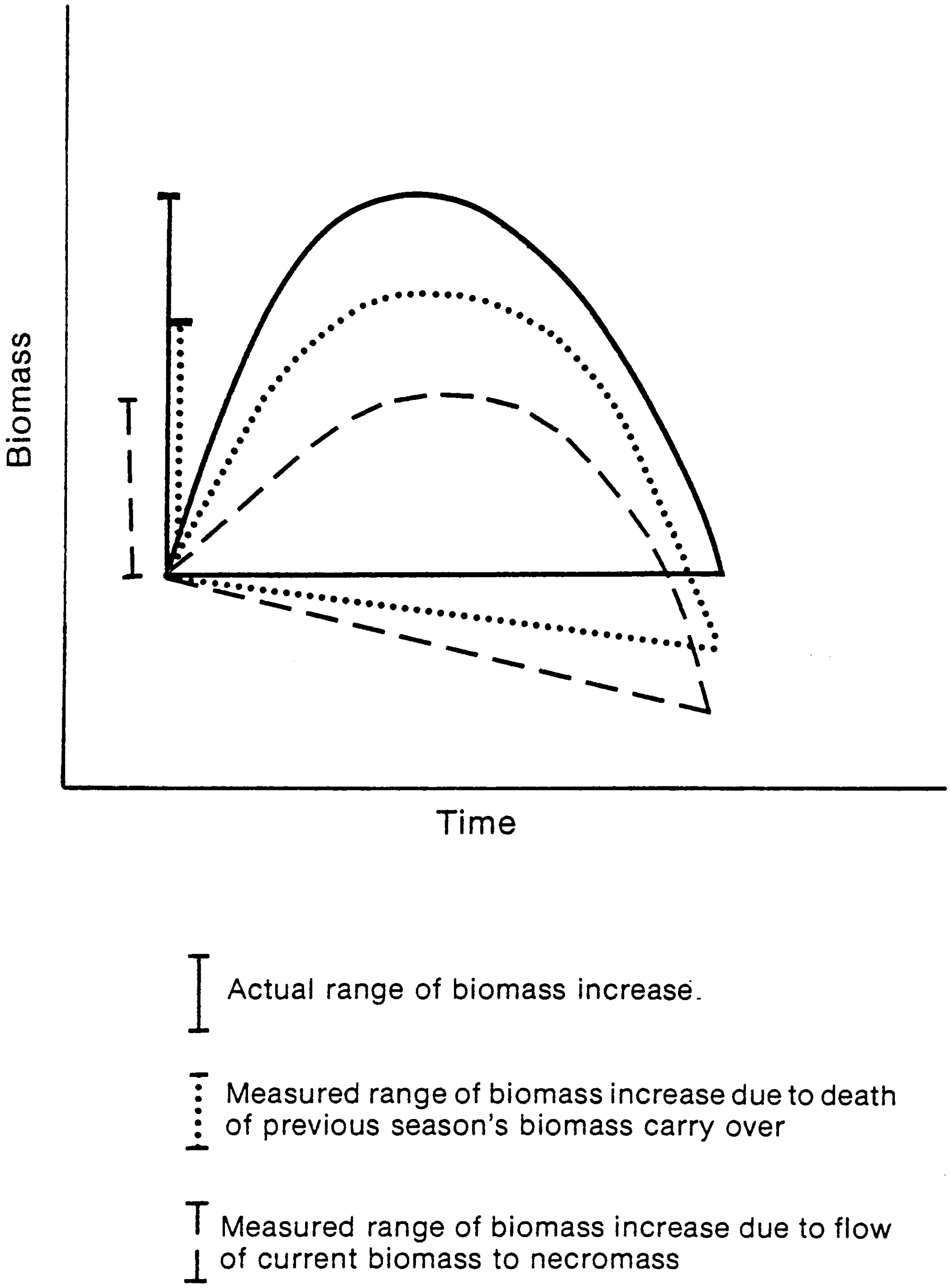

Fig. 33. Hypothetical relative dynamics of a current and a previous year's biomass.

sward, as will a 'peak/trough' increase. The situation is made potentially more complex by death of 'current' year's biomass before the peak biomass is attained. The hypothetical situation is illustrated in Fig. 33.

Examination of published data reveals that, although often not discussed, residual biomass is encountered in other unburnt perennial swards (e.g. Huntley, 1972; Rutherford, 1976; Williamson, 1976). Penfound (1964) denuded areas prior to measuring biomass increment, thereby overcoming the confounding influence of previous years' biomass.

In the light of these considerations, estimates of net annual aboveground primary production on the burnt plots can be made:-

on the burnt plots described earlier, as well as on Camp 2 which was burnt during September 1978, it was possible to quantify actual biomass increase more accurately than on the unburnt sward, as residual biomass was not a confounding factor. Similarly, necromass accumulation could be measured on these burnt areas. Furthermore, an indication of necromass accumulation could be gained from the data recorded in the 8-weekly clipping treatments described earlier.

In Table 39, the actual measured increases in biomass and necromass and necromass expressed as percentages of standing crop, are shown for the burnt sward.

Table 39 : Total biomass and necromass increments (g m^{-2}) on two different burnt areas of the sward, and necromass increase expressed as a percentage of total standing crop increase

Treatment	Total biomass increase to peak	Total necromass increase to peak	Necromass increase as % of standing crop increase
September 1978 burn (Camp 2)	71,2	17,5	19,8
September 1978 burn (Site 3)*	49,9	12,3	19,8

* "Site 3" - site of the plots to which the backfire was applied (Appendix 3).

Net annual above-ground production, calculated from biomass and necromass increases is 62,2 g $m^{-2}yr^{-1}$ on the burnt plots on Site 3 (backfire) and 88,7 g $m^{-2}yr^{-1}$ on Camp 2 which was subjected to a headfire. These values are considered to be the most accurate possible from the field date obtained in this study. A major assumption is that flow to litter, before peak biomass is reached, would be minimal. Huntley (1972) presents data which show that six months after a fire in savanna, litter accumulated was only 10,7% of herbaceous standing crop accumulated over the same period.

Insect herbivory is extremely variable, but would account for ± 10 $g\ m^{-2}\ yr^{-1}$ (Gandar, 1978) which could be added to the above values. It is noticeable that the headfire resulted in a higher estimate of net annual above-ground production than did the backfire. This is in part due to the proliferation of the forb Solanum panduraeforme in parts of Camp 2. Forbs formed 26,6% of total biomass in the Camp 2 site, compared with only 8% of total biomass on the plots burnt by the backfire.

Throughout this presentation, reference has been made to the fact that estimates of net annual above-ground production are an expression of the method used to derive them. In Table 40 estimates are presented using the following methods:

(1) Total biomass increment to peak

(2) Total biomass and necromass increments to peak (may only be calculated on burnt or defoliated sward)

(3) Peak biomass

(4) Peak standing crop

(5) Peak/trough difference

(6) Integral of growth curve from equation developed by Grunow, et al (1980) to model biomass change.

Table 40 : Estimates of net annual above-ground primary production (g $m^{-2}yr^{-1}$) in different subhabitats and burnt and unburnt areas, calculated by six different methods

Subhabitat/Treatment	Method used to estimate production*					
	1	2	3	4	5	6
OPEN subhabitat	38,4	**	55,5	95,7	38,4	51,2
Under *Burkea africana*	25,7	**	42,6	80,8	25,6	33,0
Under *Ochna pulchra*	20,9	**	33,3	50,5	16,3	18,9
Unburnt plots	27,9	**	44,9	98,5	27,9	44,4
September burnt plots (backfire)	49,9	62,2	46,6	58,9	46,6	47,2

* see text

** incalculable

All these estimates apply to grazeable production. Stubble biomass varied between 80 and 260 g m^{-2} over a year, with the average standing crop:stubble ratio being 1/1,662 (Grunow, 1976). The variation in NAAP estimates is illustrated by the range of values obtained for each subhabitat or treatment, according to the method employed.

As stated previously, it is felt that the estimate obtained for the sward on the burnt plots using biomass and necromass increase (62,2 g $m^{-2}yr^{-1}$) is the most accurate possible using the field date. Methods 1 and 5 generally resulted in low estimates of NAAP, compared to the other methods, in unburnt areas. This is due to the confounding influence of residual biomass and the 'baseline decrease' described earlier. Method 4 (peak standing crop i.e. peak biomass and necromass) resulted in the highest estimates of NAAP in all unburnt areas, due to the presence of residual necromass (Table 40).

It is postulated that net annual above-ground production in a similar perennial sward will be closely estimated by the following relationship, which accounts for the major losses:

$$\text{NAAP} = \left[\left[\text{RB} + \sum_{n=1}^{k}(B_n - B_{n-1})\right] \times C_1 \times C_2\right] + \text{IC} \quad \text{, where}$$

k = number of incremental periods

RB = residual biomass carried over from previous year

B = biomass

IC = insect consumption

C_1 = empirical constant to account for losses to necromass

C_2 = empirical constant to account for loss to litter

The constants C_1 and C_2 for the Nylsvley savanna sward are 1,25 and 1,1 respectively.

The following rationale was used to derive the above relationship:

(1) Measured necromass accumulation was about 25% of biomass accumulation over the same period on both burnt areas where such calculation was possible. Hence this loss can be added

to biomass accumulation.

(2) It is considered that residual biomass will have largely died by the time the last biomass increment is recorded (cf Rutherford, 1976) and hence this component may be added to account for the underestimation caused by 'baseline' drift described earlier.

(3) The amount of 10% litter production to the time of peak biomass was obtained from data of Huntley (1972) and may also be added.

(4) Insect consumption is a loss factor most easily measured and may be added (ca 10 g $m^{-2}yr^{-1}$ on average, Gandar 1978).

An assumption made is that growth after peak is reached (usually around February/March) is negligible compared to growth up to peak).

Using the above relationship, an estimate of net annual aboveground production of 78,9 g $m^{-2}yr^{-1}$ is obtained for the burnt plots on Site 3. This value is 1.58 times greater than the estimate obtained using biomass increment (49,9 g $m^{-2}yr^{-1}$). On the unburnt plots, a value of 71,9 g $m^{-2}yr^{-1}$ is obtained using the above relationship, which value is 2,57 times greater than estimated by biomass increment. Grunow et al (1980) estimated NAAP as 76 g $m^{-2}yr^{-1}$ on average on the same veld between 1974/75 and 1976/77 using Method 6. Two main points are further emphasized by these values:

(1) a greater underestimation of production is obtained in an unburnt perennial sward than in a burnt sward, when biomass increment is the basis for such calculations;

(2) estimation of production in an unburnt perennial sward is more than doubled, relative to biomass increment, by accounting for major losses (cf. Williamson, 1976).

CHAPTER 7

CONCLUDING REMARKS

The major form of land-use in _Burkea africana_ savanna is extensive beef and stud cattle ranching (Grossman and Gandar 1980), using the natural rangeland. At the time of this study, the cattle ranching industry was in a somewhat depressed condition. In an economic analysis of the north western Transvaal farming industry, van Zyl (1980) reported that the average _net_ income derived from cattle ranching was - R737 per annum per farm! The Commission of Inquiry into Agriculture (2nd Report, 1970) stated that the position of the extensive cattle ranching industry in the "bushveld" regions was a source of grave concern. The reasons for the unsatisfactory situation were, _inter alia_:

i sub-division of farms into uneconomic units,

ii the low level of management expertise,

iii lack of infrastructure, and

iv deterioration of the veld (Commission of Inquiry into Agriculture, 1968-72*; Coetzee, 1971)

In terms of point iv, the herbaceous layer of _Burkea africana_ savanna is dominated, over large areas, by the unpalatable species _Eragrostis pallens_. Coetzee (1978) considers that this species is encouraged by burning of the sward. Injudicious burning is felt to have contributed to the success of this species in this savanna vegetation type. Ranchers are however trapped in a circle:- _E. pallens_ is generally only acceptable to cattle when newly burnt (Coetzee, 1978) so ranchers burn the veld which further encourages

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* See under 'Republic of South Africa' in Reference list.

the undesirable E. pallens. Present opinion holds that the herbaceous layer of Burkea africana veld should rarely be burnt; Coetzee (1978) is of the opinion that E. pallens, if spared from fire and grazing, will die out in three years. The findings of a section of this study would indicate that (at least) six years of sparing from fire, together with only light grazing or protection from grazing, have certainly resulted in this species becoming increasingly moribund. It is considered that the sward improvement resulting from the backfire described in Chapter 4, presents a means of increasing the land-use potential of those areas of Burkea africana savanna where similar conditions pertain.

The significance of the canopied subhabitat in savanna vegetation in general, has been confirmed for Burkea africana savanna in particular by the findings presented in Chapter 3. Present available estimates indicate that the cost of aerial spraying with an effective arboricide is of the order of R25 per hectare (Van Niekerk, 1980). In order to prevent the subsequent increase of undesirable species at the expense of palatable species more usually associated with the canopied subhabitat (c.f. Barnes, 1979) it is conceivable that broadcast of seed would be necessary after tree removal, causing further expense. In terms of the findings of this study, it is unlikely that such radical transformation is required in areas of B. africana savanna where a similar open : canopied relation exists.

The two important forage species D. eriantha and B. nigropedata, appear to be reasonably productive when defoliated at a 6-weekly interval. In terms of grazing management, any rotational system would need sufficient camps to ensure at least such a period of absence between periods of stay. As the severe defoliation height (2 cm) caused relatively high mortality after a season, stock rates would of necessity have to be geared to ensuring that such severe grazing did not occur. It is considered that the average of 2,7 camps per herd reported for the north-western Transvaal bushveld by Coetzee (1971) is too low to achieve optimum sustainable utilization of Burkea africana rangeland.

The estimate of net annual above ground production (sensu lato) of 71,9 g m^{-2} yr^{-1} for the present study is of the same order as the average obtained by Grunow etal (1980) for the same veld between 1974/75 and 1976/77 (76 g m^{-2} yr^{-1}). Using data from Table 6 and Table 16, it is apparent that some 45% of the grazeable biomass consists of forage and intermediate species. Assuming total consumption of this biomass, a large stock unit (= 454 kg) requiring 10 kg DM per day would require 11,3 ha throughout the year or 7,6 ha for 8 months.

In fact, total consumption of the forage and intermediate species annual grazeable production would be rather severe. A stocking rate of something less than one large stock unit per 12 hectares throughout the year, or 8 ha for 8 months, would probably be better suited to the requirements of rational rangeland management in similar areas of Burkea africana savanna. This would apply at least until such time as the botanical composition was swung over more to the forage and intermediate species. Rational and sustainable utilization of the herbaceous sward is essential to prevent further deterioration of both the natural resources and the land-use enterprise.

SUMMARY

The main objectives of this study were to quantify the amounts and rates of accumulation of herbaceous biomass under a variety of situations.

Using the harvest technique, biomass (live) and necromass (standing dead material) quantity and quality were determined periodically over the period of one year in the following situations:

i under the dominant *Burkea africana* trees
ii under *Ochna pulchra* shrub clumps, and
iii in the uncanopied, between-tree subhabitat

The sward was divided into forage and non-forage categories, on the basis of herbivore feeding preference. It was found that, in the case of the sward as a whole, there was a significantly greater amount of biomass, over the year, in the open subhabitat than under *Burkea africana* trees or *Ochna pulchra* shrub clumps. The palatable forage species biomass was, however, of the same order under *Burkea africana* trees as in the open over the year, that under *Ochna pulchra* remaining significantly lower than in the other two subhabitats. In the case of the unpalatable, non-forage species group, it was found that a significantly greater amount of biomass was present in the open subhabitat than in the two canopied subhabitats. Peak biomass values recorded in each subhabitat were, in the case of the sward as a whole,

55,4 g m^{-2}	in the open
42,6 g m^{-2}	under *Burkea africana*
and 33,1 g m^{-2}	under *Ochna pulchra*

Forbs formed, on average, 10,3% of total biomass in the open subhabitat, 12,7% under *Burkea africana* and 12,2% under *Ochna pulchra*. *In-vitro* digestible organic matter contents ranged from almost 65% at the onset of the growing season, to less than 50% during July. The in-vitro digestible organic matter contents of forage species were consistently higher than those of non-forage species.

Crude protein contents of the forage species category under *Burkea africana* were generally greater than in the other subhabitats.

In the absence of fire for several years, there has been a notable accumulation of necromass. This component contributed 42,1% of the total standing crop (biomass + necromass) around time of peak biomass in the open subhabitat.

A correlation coefficient (r^2) of 0,77 was obtained using linear regression of biomass accumulation rate against rainfall in the case of the under *Burkea africana* subhabitat, and r^2 = 0,76 for the open subhabitat. The mean biomass accumulation rates recorded in the case of the sward as a whole, were

0,203 g m^{-2} day^{-1} in the open
0,156 g m^{-2} day^{-1} under *B. africana*
and 0,179 g m^{-2} day^{-1} under *O. pulchra*

In order to monitor herbaceous response to a fire, parts of the sward were burnt during September 1978. An intense backfire was applied. Over the following year, 29,4% less biomass was measured on the burnt plots compared with unburnt plots, in the case of the sward as a whole. This was however due to the significant reduction in biomass and basal cover of the somewhat moribund unpalatable species, primarily Eragrostis pallens. Basal cover of this species decreased significantly from 1,47% measured prior to the fire, to 0,69% recorded on burnt plots eighteen months after the fire. An eight-weekly clipping treatment was imposed on burnt plots and unburnt plots. The greatest biomass accumulation rate was recorded on unburnt plots subjected to the eight-weekly clipping treatment, in the case of the sward as a whole. Burning followed by eight-weekly clipping reduced the biomass accumulation rate of the non-forage species relative to unburnt, unclipped non-forage species. The "double defoliation" of burning followed by clipping however stimulated the rate of forage species biomass accumulation when compared with those in the undefoliated sward. It would appear that the backfire was deleterious to the large tufted unpalatable species, without adversely affecting the smaller, leafier palatable species.

On an area open to grazing by indigenous ungulates, the sward was burnt during September and exclosures were erected. Different exclosures were removed 29, 67 and 101 days after the fire. During the February after the fire, at time of peak standing crop, all previously protected sites were harvested.

Within Burkea africana areas, sites protected from herbivores for the longest period (101 days after the fire) had significantly greater February standing crops than sites opened to herbivores 29 or 67 days after the fire.

In order to determine the effects of different frequencies and intensities of defoliation on two important forage species, tufts of Digitaria eriantha ssp pentzii and Brachiaria nigropedata were clipped at 3, 6 and 9 weekly intervals at heights of 2, 5 and 8 cm in the veld. Digitaria eriantha ssp pentzii tufts, grown under controlled conditions, were subjected to clipping heights of 2, 5 and 8 cm at intervals of 3, 6, 9, 12 and 36 weeks in a separate experiment. The six weekly clipping interval resulted in favourable dry matter yields of D. eriantha ssp pentzii both in controlled and under natural conditions, compared with more or less frequent intervals. A similar defoliation interval resulted in relatively good yields of B. nigropedata, without adversely affecting starch reserves. The 2 cm defoliation height resulted in least amount of starch recorded in B. nigropedata root crowns, and in the greatest mortality of tufts of both species. The 8 cm clipping height resulted in 100% survival. No significant interactions between frequency and intensity of defoliation were obtained.

In order to gain an estimate of net grazeable above ground production, the results obtained using six different methods are compared. Using available data, and accounting for major losses, a relationship is derived which results in an estimate of net annual grazeable above ground production of 71,9 g m^{-2} yr^{-1} on the unburnt sward. This estimate is 2,57 times greater than the estimate obtained using only measured biomass increases.

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APPENDIX 1

Principal species in the herbaceous layer categories, Nylsvley.

i) Forage and intermediate species (FI)

Andropogon schirensis Hochst. ex A. Rich.
Brachiaria nigropedata (Munro ex Ficalho & Hiern) Stapf
Brachiaria serrata (Thunb.) Stapf
Digitaria eriantha Steud. subsp. *pentzii* (Stent) Kok (ined.)
Diheteropogon amplectens (Nees) W.D. Clayton
Heteropogon contortus (L) Beauv. ex Roem. & Schult.
Hyperthelia dissoluta (Nees ex Steud.) W.D. Clayton
Justicia minima A. Meeuse
Panicum maximum Jacq.
Rhynchelytrum villosum (Parl.) Chiov.
Schizachyrium jeffreysii (Hack.) Stapf
Themeda triandra Forsk.

ii) Non-forage species (NF)

Aristida argentea Schweickerdt
Aristida congesta Roem. & Schult.
Aristida diffusa Trin.
Aristida stipitata Hack.
Cyperus margaritaceus Vahl
Elionurus muticus (Spreng.) Kunth
Eragrostis gummiflua Nees
Eragrostis pallens Hack.
Eragrostis rigidior Pilg.
Fimbristylis hispidula (Vahl) Kunth

Perotis patens Gand.

Pogonarthria squarrosa (Roem. & Schult.) Pilg.

Trachypogon spicatus (L.f.) O. Kuntze

Urelytrum squarrosum Hack.

iii) *Non-forage non-grasses (NFNG)*

Cleome maculata (Sond.) Szyszyl.

Dichapetalum cymosum (Hook.) Engl.

Indigofera sp

Lippia sp

Parinari capensis Harv.

Pygmaeothamnus zeyheri (Sond.) Robyns

Rhynchosia sp

Vernonia spp

APPENDIX 2

Statistical analyses of the differences in BARs were attempted but proved unsatisfactory in view of the following : although the number of sampling units (quadrats) was sufficiently great to result in acceptable error limits, the actual number or replicates was low. In fact, four replicates were used for the experiments reported on in Chapter 3, and three replicates (plots) were used for the burning experiments reported on in Chapter 4. Particularly during drier periods, when low BARs were measured, it happened that in the case of some replicates an increase in biomass was measured between two harvest dates, whilst in other replicates a decrease in biomass was recorded over the same period. In calculating BARs, only increments are added. It thus occurred that the BARs calculated separately for each replicate did not, when averaged, result in the same BAR as calculated by using the mean of the sums of the replicates. This is illustrated using the following example :-

	Harvest date 2	Harvest date 1	BAR (over 30 days)
Replicate 1	22 g m^{-2}	18 g m^{-2}	0,133 g $m^{-2}day^{-1}$
2	26 g m^{-2}	21 g m^{-2}	0,166 g $m^{-2}day^{-1}$
3	23 g m^{-2}	25 g m^{-2}	BAR is-ve
Mean	23,66	21,33	

BAR as calculated from:

a) mean of date 2 - mean of date 1

$$= \frac{23,66 - 21,33}{30} = 0,077 \text{ g } m^{-2} day^{-1}$$

b) BAR calculated from the mean of the sum of the BARs of each individual replicate

$$= \frac{0,133 + 0,166 + 0^{*}}{3} = 0,099 \text{ g m}^{-2}\text{day}^{-1}$$

* By definition, increments only are added

In statistical analyses of variance, the criterion used to determine whether measured differences are significant is the LSD. In view of the fact that the mean BARs calculated for use in the statistical analysis are not equal to the actual mean BARs obtained using the equation, an LSD in this particular case would be a misleading value.

APPENDIX 3

The study area, Nylsvley, showing the approximate location of sites referred to in the text.

CT: 'Camp 2' (site of headfire, Chapter 4).

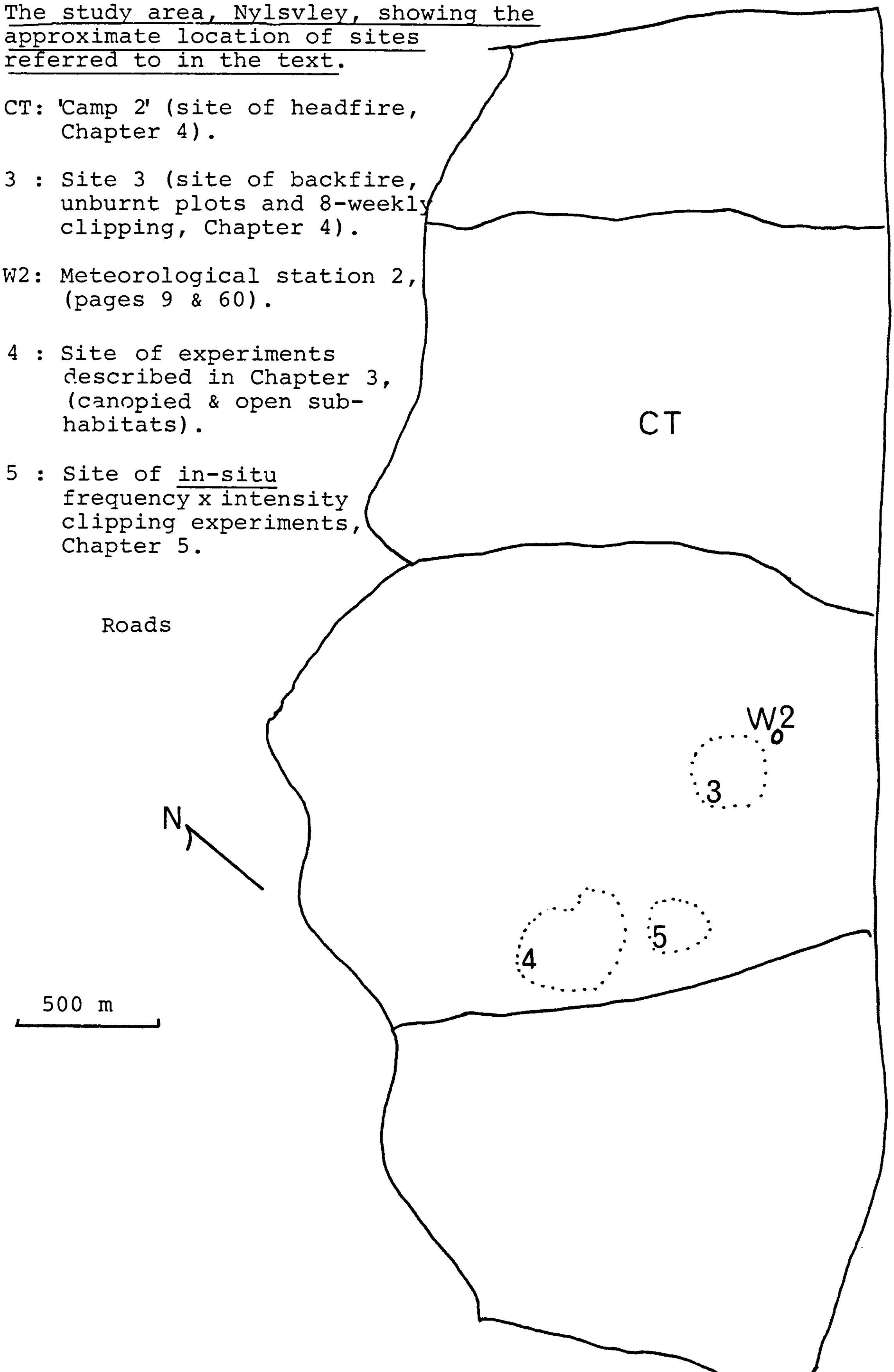
3 : Site 3 (site of backfire, unburnt plots and 8-weekly clipping, Chapter 4).

W2: Meteorological station 2, (pages 9 & 60).

4 : Site of experiments described in Chapter 3, (canopied & open sub-habitats).

5 : Site of *in-situ* frequency x intensity clipping experiments, Chapter 5.

Roads



APPENDIX 4

Table 4.1 : Analysis of variance of the effect of different frequencies and intensities of clipping on above-ground dry matter yield of *Digitaria eriantha* ssp pentzii under controlled conditions (Chapter 5, Table 28)

Source	DF	Mean Square	F Value	Pr > F
Replicates	4	170,50	2,06	NS
Frequency	4	666,17	8,05	**
Intensity	2	485,05	5,86	**
Frequency X Intensity	8	88,74	1,07	NS
Error	56	82,75		
Total	74			

C.V = 26,6%

Table 4.2 : Analysis of variance of the effect of different frequencies and intensities of clipping on root dry matter yield of *Digitaria eriantha* ssp *pentzii* under controlled conditions (Chapter 5, Table 29)

Source	DF	Mean Square	F Value	Pr>F
Replicates	4	370,57	1,77	NS
Frequency	4	1147,83	5,48	**
Intensity	2	723,89	3,46	*
Frequency X Intensity	8	318,5	1,52	NS
Error	56	209,35		
Total	74			

C.V = 51,2%

Table 4.3 : Analysis of variance of the effect of different frequencies and intensities of clipping , on above-ground dry matter yield of *Digitaria eriantha* ssp *pentzii* under natural conditions (Chapter 5, Table 31)

Source	DF	Mean Square	F. Value	Pr>F
Replicates	14	0,123	1,84	*
Frequency	2	0,349	5,20	*
Intensity	2	0,009	0.13	NS
Frequency X Intensity	4	0,061	0.91	NS
Error	112	0,067		
Total	134			

C.V = 52,7%

Table 4.4 : Analysis of variance of the effect of different frequencies and intensities of clipping on above-ground dry matter yield of *Brachiaria nigropedata* under natural conditions (Chapter 5, Table 32)

Source	DF	Mean Square	F Value	Pr> F
Replicates	14	1,060	7,26	**
Frequency	2	0,048	0,33	NS
Intensity	2	0,723	4,95	**
Frequency X Intensity	4	0,206	1,41	NS
Error	112	0,146		
Total	134			

C.V = 40,3%

Table 4.5 : Analysis of variance of the effect of different frequencies and intensities of clipping on the starch content of root crowns of <u>Brachiaria nigropedata</u> (Chapter 5, Table 35)

Source	DF	Mean Square	F Value	Pr> F
Replicates	4	0,63		NS
Frequency	2	2,04	4,97	*
Intensity	2	1,66	4,04	*
Frequency X Intensity	4	0,59		NS
Error	32	0,41		
Total	44			

C.V = 43,4%