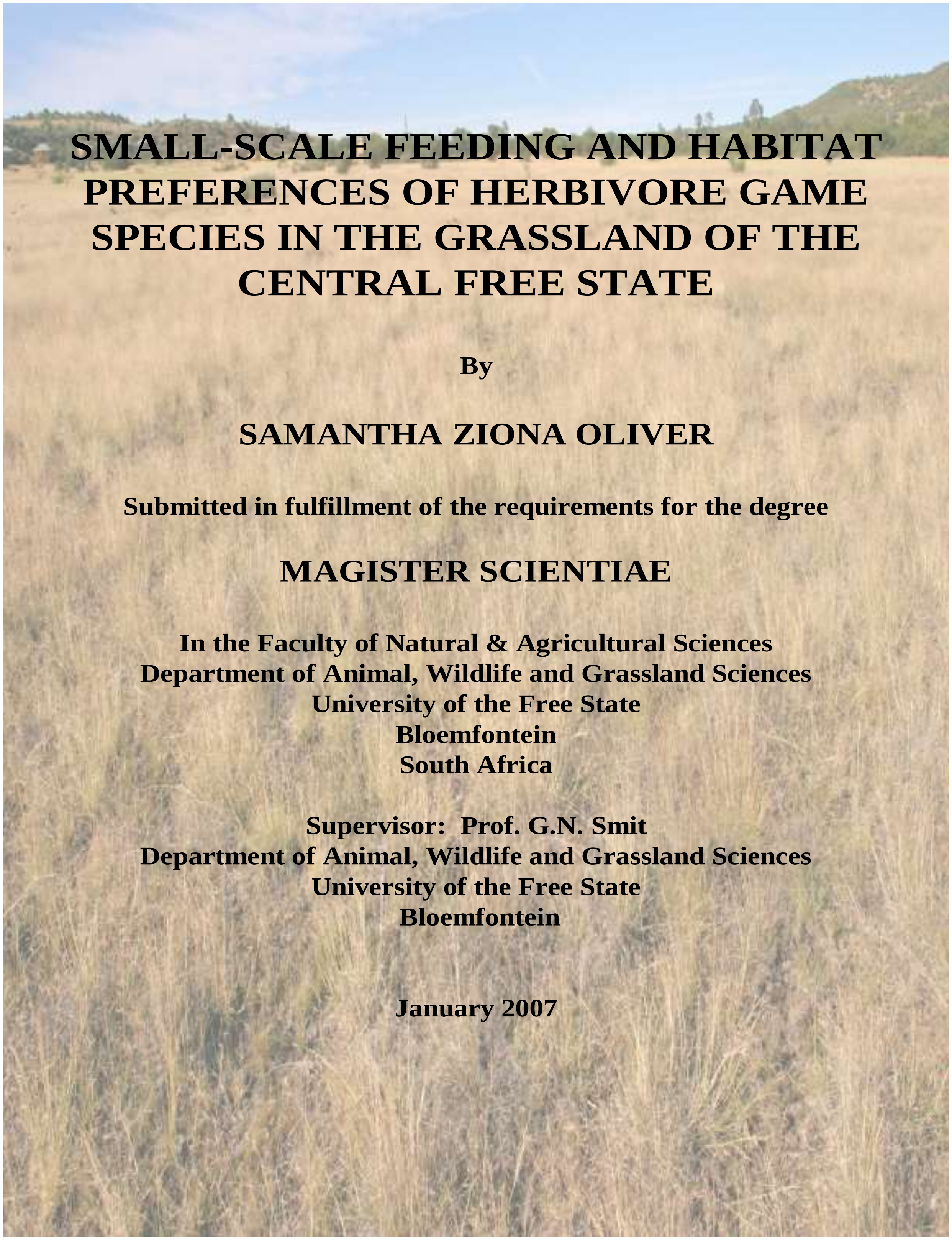

SMALL-SCALE FEEDING AND HABITAT PREFERENCES OF HERBIVORE GAME SPECIES IN THE GRASSLAND OF THE CENTRAL FREE STATE

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CHAPTER 1

INTRODUCTION

In South Africa game ranching is a recognised agricultural enterprise and is one of the fastest growing sectors in the agricultural industry (Bothma 1995; Gouws 1995; Eloff 1996; Smit 2003a). Game ranch owners have come to realise that the mere fencing of a piece of land and establishment of a variety of game species can cause just as many problems as having advantages. There is a growing need for specialised knowledge and professional advice to the game ranching industry. This requires an increase in the number of studies on the ecology of natural systems and the planning and management of game ranches (Bothma 2000).

Game ranching is far more complex than generally anticipated (Smit 2003a). In multi-species systems a greater number of variables need to be taken into account, which requires a broad knowledge base of ranch management. The rapid expansion of game ranching practices could lead to increasing competition within the industry. A scientific approach that includes both ecologically and economically sound principles will ensure a successful and more profitable long-term wildlife enterprise. It is only possible to measure objectively what has been achieved in range areas when stated goals have been set prior to their establishment (Savory 1988). Objectives are central to management since management is the means by which specific objectives are achieved (Coombes & Mentis 1992).

Game ranching in South Africa usually involves relatively small (< 5 000 ha) fenced-in areas (Behr & Groenewald 1990), where natural limitations of water availability, disease and large predators are often controlled (Du Toit 1995). Under these conditions, large herbivore populations often exceed natural densities (Du Toit 1995), which requires a more intensive management input (Trollope 1990; Bothma 1995; Van Rooyen *et al*. 2000). An example of this is the Mountain Zebra National Park, which in respect of grazing in practice is managed as a game ranch. Utilisation by large herbivores over a period of six years caused a decrease in *Themeda triandra* (red grass), which has a high grazing value in this area, and an increase in *Eragrostis obtusa* (dew grass), which has an average grazing value (Van Rooyen *et al*. 2000). Accompanied by drought, this caused such a decline in the grazing value of the veld that the buffalo (*Syncerus caffer*) populations totally collapsed. According to Van Rooyen *et al*. (2000), the same scenario occurred in the Willem Pretorius Nature Reserve in the Free State. He came to the conclusion that large herbivores have an important impact on the veld in small areas, and that intensive veld management is essential in these fenced areas. Therefore, management practices need to be properly adapted according to the environmental parameters influencing an area to ensure the long-term sustainability of the enterprise.

In contrast to the classification of Hofmann (1973), which focused on the feeding strategies of game species, Collinson & Goodman (1982) classified game mainly on the impact they have on the vegetation and habitat. These authors identified four main categories: Type I are species that are capable of causing an initial drastic change in the climax vegetation and the physical environment; Type II are species that decrease in abundance as a result of the disturbance and changes in vegetation caused by Type I species; Type III are species that increase in abundance as a result of the impact of Type I species and modify the vegetation further, and; Type IV species are influenced by changes in the vegetation brought about by species of Types I and III, and increase in abundance, but have little further impact on the vegetation.

In South Africa there is an increasing tendency to fence in relatively small areas (<100 ha) and stock them with mainly selective short grass grazers that are classed as Type III species. This habitat modification is a change in quality of the habitat so that it is no longer entirely suitable for the herbivore species, but not unusable. In the central Free State the most common game species such as springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*), black wildebeest (*Connochaetes gnou*) and gemsbok (*Oryx gazella*) can all be classified as Type III species. These species are usually the first to be established in an area. There is thus growing concern over the effect of this type of stocking on the natural resources (veld) of small fenced areas, which could result in environmental degradation and non-sustainable utilisation of valuable natural resources. Very little research, if any, has been done on this in the central Free State Province and was the main motivation for conducting the present study.

The primary objectives of this study, which was conducted in a small fenced property, were to:

(i) Analyse small-scale habitat preferences of springbok, blesbok and black wildebeest within the same vegetation type.

(ii) Study the small-scale feeding preferences of these game species in relation to the available above-ground plant production.

(iii) Study the associations between the soil, vegetation and grazing by the herbivore game species.

(iv) To determine whether the simulated influence of Type I herbivores on the sward structure will affect the small-scale habitat preferences of other species, notably the Type III species.

This study will provide useful information to small-scale game ranchers/farmers that can be used to implement more effective management strategies. This should ultimately ensure better long-term sustainability of the game ranch industry, improved utilisation of environmental resources, and greater profitability for game ranchers.

CHAPTER 2

LITERATURE REVIEW

2.1 INTRODUCTION

Man has always been associated with the destructive use of large wild herbivores throughout history. The keeping of wild herbivores has been documented for more than 2 000 years. Wildlife species sometimes served to enhance the splendour and the pleasure of their owners, and at times bring profit and revenue. This scenario doesn't differ much from what is practiced today.

2.2 OVERVIEW OF GAME RANCHING IN SOUTH AFRICA

Although South Africa is a dry country, it is well documented that it teemed with wildlife in previous centuries. The over-exploitation of these animals and the introduction of commercial cattle farming caused their numbers to decline. Multi-species utilisation of grazing by game was gradually replaced by mono-species utilisation. However, since the commercial value of wildlife has progressively increased, game numbers on private land have increased (Smit 2003a).

The game ranching industry has shown extraordinary growth during the past 40 years and is now a recognised agricultural enterprise in South Africa and one that is still expanding and growing economically (Gouws 1995; Eloff 1996; Bothma 2000; Scriven & Eloff 2003). Excluding national and provincial reserves, the area fenced in with game fences increased by 2.5% (300 000 ha) a year during 1998 and 1999 (Standard Bank 2000). Currently, there are about 5 000 game ranches and more than 4 000 mixed game and livestock ranches in South Africa. These cover some 13% of the country's total land area, compared with 5.8% for all officially declared conservation areas. National parks cover only 2.8% (Falkena & Van Hoven 2003).

Apart from generally poor soils and low rainfall, cattle farmers in South Africa have been confronted with extensive strategic challenges for more than a decade. Several evident challenges include: deregulation of the agricultural sector and loss of political leverage in Parliament, global warming, new labour legislation and labour problems, stock theft, the impact of aids and malaria, bush encroachment, livestock diseases and land claims (Falkena & Van Hoven 2003; Smit 2003a). Conversion to game ranching might be a possible economic solution to the above-mentioned problems. Wildlife is better adapted to the African environment, more difficult to steal than cattle and sheep, less susceptible to the effect of droughts, more disease- and parasite resistant, and far less labour intensive (Behr 1988; Falkena & Van Hoven 2003; Smit 2003a). These are possible reasons for the rapid expansion of the game ranching industry in South Africa.

Income from game ranching can be separated into non-consumptive and consumptive use of game. Non-consumptive use includes ecotourism activities and accommodation. Ecotourism is likely to provide a secondary income and is a potentially large earner of foreign currency (Van der Waal & Dekker 2000; Smit 2003a). It furthermore creates more job opportunities for skilled and semi-skilled labourers. The ecotourism industry accounts for at least R1 billion in added value, while its indirect augmenting effects (airlines, 4x4 trails, outdoor equipment and hotels) are roughly of similar value, which implies that the total turnover in this industry is approximately R2 billion (Falkena & Van Hoven 2003). Consumptive use includes trophy-, venison- as well as recreational hunting, and live game sales. About 60-70% of the total game ranching income is generated by hunting (Falkena & Van Hoven 2003). On average, about 6 000 trophy hunters visit South Africa annually. In the last decade the sales of animals increased from 8 292 in 1991 to 20 022 in 2002 (Scriven & Eloff 2003). Game gained record prices at game auctions with an average countrywide increase of 15% per annum for the period 1992-2002 (Smit 2003a). Additional income generated in this sector includes meat processing and taxidermy.

Non-consumptive as well as consumptive use has financial implications. Many game ranches operate on meagre profits, and some even at a loss. This is usually because their operations are too small, in terms of either land size and/or the sustainable utilisation of game stock, lack of range management, or the environmental attraction is not adequate to focus on ecotourism (Falkena & Van Hoven 2003). The only way in which any game ranch or game industry will be economically sustainable in the long-term is to run it within the framework of ecological sustainability (Smit 2003a). Unfortunately, there is a perception that game ranching/farming is easy with no realisation of the essentiality and complexity of correct ecological planning and management.

In rural areas, game utilisation is a source of income, which is an important ecological and socio-economical benefit. Casual labour is often employed on game ranches during the hunting season and where large construction projects are undertaken. Game ranching does not only create direct employment opportunities, but also involves employment opportunities in the fields of ecological and veterinary services, game capturing and transportation, culling of surplus animals, taxidermy, meat processing, fencing, building, and construction industries, amongst others.

The establishment of game ranches plays an important role in South African nature conservation. Game ranches will form an essential part of nature conservation in South Africa if they are planned and managed on a healthy ecological basis and can contribute largely to the preservation and conservation of all life on earth, which is a direct benefit for future generations.

2.3 GAME RANCHING IN THE FREE STATE PROVINCE

The Free State Province was once a land of vast grass-filled plains perfect for agriculture and stock farming. Over time, some farmers considered it more beneficial to return the land to its original inhabitants. The plains currently sustain springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*), black wildebeest (*Connochaetes gnou*), red hartebeest (*Alcelaphus buselaphus*), Burchell's zebra (*Equus burchelli*), eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), and a number of other species. In the Free State, a province not especially well known as a game ranching area, there are already an estimated 600 ranches and farms each containing more than 100 units of game (Smit 2003a). The number of farms being converted to game ranches is still increasing.

2.4 THE GRASSLAND BIOME

A biome is a broad ecological unit and represents a large relatively homogeneous natural area (Van Rooyen & Theron 2000a). The Grassland Biome is mainly found on the central plateau of South Africa, and the inland areas of KwaZulu-Natal and the Eastern Cape (Low & Rebelo 1996). Of the seven biomes in southern Africa, the Grassland Biome is the second largest (336 544 km^2). The species diversity is considered as relatively rich, and the biome houses several threatened animals as well as plants (Low & Rebelo 1996).

The vegetation is mainly monolithic as far as physiognomy is concerned, and is characterized by strong dominance of hemi-cryptophytes of the Poaceae family. The canopy cover is moisture-dependent and decreases with lower mean annual rainfall, while fire and grazing have a decisive influence on canopy structure (Rutherford & Westfall 1994). Trees are almost absent, except on riverbanks, rocky outcrops, and in the gorges of the eastern mountain ranges. The grassveld areas where the tree component is relatively prominent can be regarded as good game ranching areas.

The contribution of sweet and sour grass species to the herbaceous cover is influenced by rainfall. Sweet grasses have a lower fibre content, maintain their nutrients in the leaves in winter, and are therefore palatable. In contrast, sour grasses have a higher fibre content, tend to withdraw their nutrients from the leaves during winter, and are unpalatable (Low & Rebelo 1996; Van Oudtshoorn 1999). In higher rainfall areas and on more acidic soils, sour grasses prevail. C_4 grasses dominate throughout the biome, except at the highest altitudes where C_3 grasses become prominent (Low & Rebelo 1996; Van Oudtshoorn 1999). The sensitivity of C_4 grasses to low temperatures during the growing season appears to have a strong influence on their distribution (Caldwell *et al*. 1977). During photosynthesis C_3 plants use the Calvin Benson pathway exclusively and produce 3-carbon compounds as the first stable products. C_4 plants, unlike C_3 plants, produce 4-carbon compounds, which make it a more efficient plant in terms of productivity, photosynthesis and water loss (Ludlow 1976; Waller & Lewis 1979; Galston *et al*. 1980; Pearcy *et al*. 1987).

The Grassland Biome is presently under serious threat by agriculture, industrialization and urbanization. Large areas have been cultivated, restricting natural vegetation so that for the most part only overgrazed relics remain (Low & Rebelo 1996; O'Conner & Bredenkamp 1997).

2.6 HABITAT PARAMETERS THAT INFLUENCE HERBIVORE GAME SPECIES

Many biotic and abiotic factors influence the way an animal uses space, both in terms of where it goes and how long it stays in one area (Melton & Heard 1991). The habitat of an animal can be described as the area in which it lives, with both biological and physical features, as well as the presence of other species characterizing it. The term habitat includes plants and animals as the living component; and climate, geological formation, soil and water as the physical component (Joubert 2000; Van Rooyen & Theron 2000b).

Combined, they provide food, shelter and water to an animal. The higher the diversity in habitats or plant communities, the more game species can be accommodated. Even small, isolated and unique pieces of habitat can be important for the survival of a given type of species. According to Sinclair (1983), the diversity of herbivore game species in Africa reflects the wide variety of habitats available. Differential habitat selection is one of the principal relationships that permit game species to coexist (Rosenzweig 1981), as the species are restricted to particular vegetation types, consequently reducing competition for resources. The quality of a habitat is reflected by the reaction of the game species to its habitat (Melton & Heard 1991).

2.5.1 Terrain morphology

The landscape of a given area can be divided into a number of terrain morphological units. These units differ in terms of exposure to climatic factors, rockiness, slope, aspect, soil type and depth, nutrient status and soil water content (Van Rooyen & Theron 2000b). The latter factors influence the growing conditions of plants and the degree of shelter that is provided to animals. A high diversity in terrain morphological units leads to a higher heterogeneity in the landscape and vegetation composition (Van Rooyen & Theron 2000b). Consequently, this will create a greater diversity of game species that can be accommodated on the land.

At the landscape level, the combined influence of biotic and abiotic factors may determine the distribution patterns of herbivores (Redfern *et al*. 2003). Animals may have preferences for specific topographical features, for example slopes or level terrain, or for geological formations such as rocky outcrops or cliffs, while soil texture may also have an influence (Joubert 2000). Spatial choices position the animals in a landscape prior to selecting plant species or parts from among an aggregate of available plants (Stuth 1991).

2.5.2 Geology and soil

In the semi-arid regions of South Africa there is a clear correlation between the geological formations, soil types and plant communities. Meissner *et al.* (1996) found that in the Timbavati Private Nature Reserve the composition of the grass layer on gabbro formations consisted of more palatable plant species that might probably be associated with advantages in nutritive value. Soil texture affects the rate and depth of water infiltration, the root penetration of plants, leaching of nutrients, aeration, and soil temperature and structure (Van Rooyen & Theron 2000b). In the Eastern Cape, Martens *et al*. (1996) found that there is a significant correlation between the plant species distribution and soil characteristics such as soil depth, clay content and surface stone. Bredenkamp (1985) considered both chemical and physical properties of the soil as important habitat factors.

2.5.3 Climate

In its most general sense, climate can be described as the average weather of a region. This includes a wide variety of parameters such as daily net radiation, temperature, wind speed and direction, hail, frost, and precipitation type and intensity (Strahler & Strahler 1998). Temperature and precipitation are factors that most strongly influence the natural vegetation of a region. The natural vegetation cover is often a distinctive feature of a climatic region and typically influences the use of the area (Strahler & Strahler 1998). The development of soils, as well as the types of processes that shape landforms, is partly dependant on temperature and precipitation. Air temperatures have an important effect on precipitation. Warm air can hold more moisture than cold air, which means that colder regions generally have lower precipitation than warmer regions (Strahler & Strahler 1998).

2.5.4 Vegetation

The vegetation is probably the single most influential parameter of the habitat, and can reveal vital information on various aspects of the habitat. It is also one of the fundamental factors to evaluate and monitor when restoring damaged habitats. A plant community is an assemblage of plant species with a relatively uniform physiognomy, growing and interacting among themselves in a relatively consistent type of physical environment (Tainton 1999). Plant communities are largely described by the definition of an agro-ecological unit, which is one of the most important criteria used in the subdivision of management units on a game ranch (Van Rooyen & Theron 2000b). The potential of a plant community as a habitat for game species, and its ecological capacity and resilience to utilisation and drought, are the outcomes of the influences of environmental factors and earlier utilisation and management. Each plant community will react in a different way to vegetation management practices, fire and grazing (Wolfson 1999).

Species composition and structure of the vegetation represent important habitat parameters and determine its suitability to herbivores. The plant species composition will determine whether food resources are adequate. It has often been shown that the distribution of plant species, and especially plant communities, is the result of all the environmental factors present (Roberts 1970; Scott D. 1974; Scott J.T. 1974; Bredenkamp *et al*. 1983).

The structure of the vegetation plays an equally important role in determining the suitability of the habitat to herbivore game species. The structural attributes of a habitat are embodied in the concept of cover as it pertains to the functional needs of animals (Dasmann 1981). The distribution and habitat selection of many herbivores are determined, among other things, by forage availability and water, which is influenced by habitat structure (Joubert 2000; Dörgeloh 2001).

Some game species use vegetative cover for escape purposes whereas others prefer habitats with little or no vegetative cover. For example, impala (*Aepyceros melampus melampus*) and mountain reedbuck (*Redunca fulvorufula*) often utilise moderate or dense vegetation stands to either avoid detection by predators or to escape from predators following detection. In contrast, species such as blue wildebeest (*Connochaetes taurinus*) prefer open grassland habitats because the structural attributes of such habitats enhance these species' ability to spot predators from afar and to escape following detection, if necessary. Cover also benefits many game species by virtue of its inherent ability to modify environmental conditions by providing shade and insulation. There is also a strong interaction between vegetation cover and food in certain instances. For example, cover may directly enhance a herbivore game species' food supply if the primary cover species is a preferred forage species (Inglis 1985). Cover may also indirectly benefit certain herbivore game species by creating a micro-environment that enhances the establishment and growth of certain preferred forages and/or by providing a structure that impedes the utilisation of such species by competing herbivore game species (Barnes *et al*. 1991).

The structure of the vegetation may even affect the social structure of animal populations. According to Joubert (2000), the size of the social units or herds in which animals occur is directly related to the structure of the habitat. In dense vegetation, animals are solitary or form pairs or small groups. When the vegetation is less dense, the size of the animal units increases. The largest herds are usually found among animals that prefer large, open grassy plains (Joubert 2000). The 25 000 km^2 Serengeti ecosystem supports the earth's largest herds of free-ranging, unmanaged ungulates (McNaughton 1985). However, a further distinction can be made between open plains with tall grass and those with short grass cover.

Plant phenology has a major influence on animal movement patterns, habitat choice and feeding preferences, and consequently, on the physical condition, herd size and reproduction of the animals. The term "phenology" refers to the different growth phases in the life cycles of plants and animals that occur in reaction to the climatic patterns of the environment, and include the leaf, flower and fruit phases (Joubert 2000). The phenology of plant species indicates the availability of food plants such as grasses and leaves, and the quantity and condition of the different components through the season.

2.5.5 Water

Water is an essential element for the nourishment of all living organisms. Therefore, availability of water over time and space is a critical factor affecting the growth and survival of wildlife populations (Barnes *et al*. 1991). Water requirements, in terms of both quantity and quality, vary widely among game species. Differences are related to behavioural, morphological and physiological differences (Barnes *et al*. 1991). As a result of these differences, some large herbivore game species can survive extended periods without consuming water, whereas other species require a readily available supply of water.

According to Smit (2003a), game species can in broad terms be divided into water dependant and water independent groups. The latter group includes species such as gemsbok and eland (*Taurotragus oryx*). These species can survive for long periods without surface water. The water dependent group can be further sub-divided into mobile and non-mobile species according to the distance that they move daily from surface water resources. In the case of the non-mobile water dependent species, which include species such as impala and bushbuck (*Tragelaphus scriptus*), their densities decline drastically when they are found further than 5-6 km from standing water. The mobile water dependent species include species such as zebra (*Equus burchelli*), blue wildebeest, roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) antelope. These species occur more frequently in areas closer than10 km from standing water. In areas further than 10 km from standing water mainly water independent species occur on a more permanent basis.

2.5.6 Space

Although animals require space to survive, the amount of space required varies depending on the spatial distribution of food, water and cover across a landscape, as well as evolved behavioural attributes (Barnes *et al.* 1991). Many of the game species require large areas to achieve acceptable levels of reproductive performance whereby survival of a population is assured. According to Barnes *et al*. (1991) this need may be viewed primarily as an evolved behavioural response, wherein space requirements (i.e. isolation) are linked to physiological function.

2.5.7 Herbivore game species

Herbivore game species are not evenly distributed while they are foraging, but they rather favour certain habitat types over others (Jarman 1974; Pienaar 1974; Hirst 1975). Different parts of the environment represent habitats of varying quality in terms of opportunities such as food and in terms of risks such as predators (Melton 1987). The habitat quality therefore affects the individual's ability to survive and reproduce within the area (Dekker *et al*. 1996). Knowledge of the specific habitat requirements of herbivore game species as well as a detailed survey of the available habitats on the farm are thus essential. Social behaviour patterns play a key role in determining the means by which different game species utilise their habitats, and therefore, play an important role in determining the densities in which different species can be kept in a specific area.

2.5.8 Disturbances

Disturbances caused by human actions include cultivation, roads, dams, urban development, pollution, fragmentation of habitats through fencing and many more. The reclamation of overgrazed veld, erosion and bush control are important management actions that have to be dealt with in order to improve the overall habitat (Van Rooyen & Theron 2000b).

2.6 DIET SELECTION OF HERBIVORE GAME SPECIES

Animals need food to provide the energy needed to keep them alive and to maintain homeostasis, for external activities, reproduction and for the supply of specific substances for their upkeep and growth (Swenson 1977; Schmidt-Nielsen 1997). These specific substances include proteins, amino acids, vitamins, certain essential nutrients, and various minerals and other trace elements, some of them in such low quantities that it is difficult to establish their physiological role in the animal (Schmidt-Nielsen 1997). Each population employs an evolutionary strategy directed toward maintenance of fitness. Reported scientific studies indicate that most economically important herbivore game species forage optimally and are energy maximizers. That is, they maintain fitness by feeding optimally to consume the greatest amount of energy and/or other nutrients (Schoener 1971, Charnov 1976, Pyke *et al*. 1977; Krebs & Davies 1978; Belovsky 1978, 1981a, 1981b; Hixon 1982; Owen-Smith & Novellie 1982; Black & Kenney 1984; Kenny & Black 1984; Belovsky 1986a, 1986b; Belovsky & Sable 1986).

Game species have the ability to select from a variety of feeds on offer only those that supply them with the nutrients needed to maintain their basic bodily functions (Forbes 1986). Even with a highly concentrated diet that fulfils the individual's nutrient requirements in a couple of bites, it will continue to feed beyond this point because its digestive tract is still largely unfilled. Herbivore game species therefore have to select a diet that meets their nutritional requirements and makes them feel satiated. The mechanisms for achieving these objectives are uncertain (Kleiber 1961; Stephens & Krebs 1986).

2.8 FACTORS THAT INFLUENCE THE DIET SELECTION AND FEEDING BEHAVIOUR OF HERBIVORE GAME SPECES

Voluntary food intake constitutes the amount of food eaten by an animal during a given period of time while it has free access to food, but exactly which foods are taken depends on a number of factors relating to the animals, the environment, and the food (Forbes 1986). Amongst others, these factors include: the physiological condition of the animal, its previous grazing experience (Owen-Smith 1999; Van Hoven 2000), the surrounding conditions (e.g. the presence of other animals and topography of the landscape) (Owen-Smith 1999), the animal's level of hunger, species of animal and its basic anatomical and physiological adaptations, age of the animal (Campling & Lean 1983; Van Hoven 2000), relative palatability of plant species and plant parts available, and the physical accessibility of plant material (Owen-Smith 1999). In ruminant animals, taste and smell, as well as learned feeding habits, are the most important in the feeding situation (Forbes 1986). Forage plants have developed defences against defoliation, while herbivores have in turn developed foraging strategies to overcome these defences (Van Soest 1994).

2.7.1 Animal related determinants of diet selection

Based on anatomical factors and grazing utilisation, different herbivore game species can be divided into different utilisation classes, namely: (a) bulk feeders - which consume large amounts of roughage. (They are less selective and because the average nutritional value of their food is low they have to consume large quantities food. They are often grazers rather than browsers); (b) concentrate feeders - which are highly selective feeders. (The nutritional value of their food is much higher than the averages of the plant communities as a whole that they feed on); (c) grazers – which include species that mainly feed on grasses. (They can be further sub-divided in to long and short grass grazers); (d) browsers – which include species that mainly consume woody plants (dicot foliage); and (e) intermediate or mixed feeders - species that select both grass and browse depending on the specific circumstances (Hofmann & Stewart 1972; Hofmann 1973; Grunow 1980; Van Hoven 2000; Smit undated a). Hofmann (1973) suggested that these adaptations are the major ecological dichotomy separating ruminant species.

2.7.1.1 Influence of body size

An animal's size has a fundamental influence on its metabolism and hence on its food and energy needs. Animals need chemical energy to carry out their various functions, and their overall use of chemical energy is often referred to as their energy metabolism (Schmidt-Nielsen 1997). The basal metabolic rate, which determines their energy requirements, varies among animal species according to their body mass (French 1985; Owen-Smith 1999).

Van Hoven & Boomker (1981) found, by using the formula 293 $kJ/kg^{0.75}$ body mass/24h, that the daily maintenance energy requirement of the black wildebeest is 12 116 kJ. The specific metabolic rate and, therefore, relative energy consumption per unit of body mass decline as the animal's mass increases (Owen-Smith 1999). Schmidt-Nielsen (1997) also found the same striking relationship between the body size and oxygen consumption, i.e. that the rate of oxygen consumption per gram decreases consistently with increasing body size. He stated that other physiological variables such as food intake must be similarly affected. Rogerson (1968) found that the metabolic rates measured for wildebeest are about 50% greater than their size would suggest. In contrast, Meissner (1976) found that blesbok have fairly low metabolic rates for their size. The metabolic rate is also affected by the reproductive state, lactation (Owen-Smith 1999; Swenson 1977; Van Hoven 2002), mobility (Schmidt-Nielsen 1997; Owen-Smith 1999), weather conditions (Owen-Smith 1999), and growth (Swenson 1977). Aspects such as body composition and body insulation may also influence the standard metabolic rate (Owen-Smith 1999).

The metabolic rate per unit of body mass decreases as body mass increases, and as a result the daily food intake as a fraction of body mass declines with increasing body size. Small herbivore game species therefore require a relatively high amount of energy per unit body mass, owing to higher metabolic rates, than larger herbivore game species. In order for a smaller herbivore game species to meet its high mass-specific energy requirements, Geist (1974) and Owen-Smith (1999) suggested that the animal must select a diet that is high in nutritive value, which can provide a high rate of energy return. This is made possible, firstly, by virtue of its low absolute energy requirement. Secondly, small ruminant herbivore game species have relatively more foraging time per unit amount of material consumed compared to large ruminant herbivore game species, which have less time to be selective due to their high absolute energy requirements per day. Thirdly, due to their small mouths, small species are capable of selecting small items of concentrated foods (Hanely 1982; Gordon & Illius 1996; Owen-Smith 1999). Meissner (1982) and Hudson & Christofferson (1985) found that small, growing animals of the same species also metabolise more energy per unit body mass. Thus, the metabolic rate of the body dictates the type of grazing and the frequency of intake (Van Hoven 2000). The proportion of high quality items in the diet therefore increases with a decrease in the size of the herbivore game species (Bell 1970; Blankenship & Qvortrup 1974). Murray & Illius (2000), studying topi (*Damaliscus korrigum jimela*) in the Serengeti, found that greater selectivity alone provided topi with an energy intake estimated to be 16% higher than that of blue wildebeest.

Large herbivore game species cannot afford to be as selective for plant parts as small herbivore game species because they individually consume a greater total amount of food per day. Nevertheless, they still prefer the best quality material that is available (Owen-Smith 1999).

2.7.1.2 Influence of anatomical mouth features and feeding mechanisms

The rate of food consumption depends on the number and size of bites per minute, which is a function of both the pasture (grass height and density) and the herbivore game species (incisor width or diameter of tongue sweeps) (Grunow 1980; Illius & Gordon 1987; Welch & Hooper 1988). Ungar *et al*. (1991) found that bite size, and therefore intake rate, is reduced on shorter swards, and with successive grazing.

Mouth size also determines the degree of selectivity that is instinctively possible for the forager to exhibit, and the time and energy costs of selective foraging on specific plant parts or individuals (Hanley 1982). Herbivore game species with small mouths are more capable of being selective of plant parts than species with large mouths are (Jarman 1974). According to Hanley (1982), mouth size and body size seem to be highly correlated, apparently because of the overall time-energy constraints on forage selectivity. Murray & Illius (2000) found that blue wildebeest, which have relatively wide mouths, could graze down vegetative swards to a height below that which can be tolerated by the topi, which have a narrower mouth. The topi, however, can reduce the leafy component of differentiated swards through selective feeding to a level below that which can be tolerated by wildebeest.

Grazing ungulates have high-crowned cheek teeth with a finely ridged surface, which facilitates grinding the fine, fibrous leaves of grasses. In ruminants, incisors are absent in the upper jaw (Welch & Hooper 1988; Van Hoven 2000). In the lower jaw, grazing antelope have protruding incisors of similar size (Janis & Ehrhardt 1988) that aid in the plucking of grass leaves. According to Janis & Ehrhardt (1988), the greater incisor width of grazers serves to maximize the bite size when feeding on a continuous distribution of grasses. Due to the structure of their lower jaw, bulk feeders seldom graze lower than 12 to 14 mm from the ground (Van Hoven 2000).

Grazing and browsing ruminants differ in muzzle width relative to body size (Jannis & Ehrhardt 1988). Grazers preferring short grass have relatively wide muzzles compared to those favouring rather taller grass. Wildebeest, for example, have wide muzzles, and therefore favour short creeping grass and low-growing forms (Owen-Smith 1999). A narrow muzzle is beneficial in taller grass swards as it makes it possible for the animal to pluck only green leaves from within the tall sward. Differences in the muzzle width affect the performance of species feeding on swards of different structure. Owen-Smith (1999) has, for example, found that wildebeest can maintain an adequate rate of intake, even when the grass is as short as 50 mm. Murray & Illius (2000) found that blue wildebeest in the Serengeti could maintain a positive energy balance on 20 mm swards. Small ungulates can effectively feed on both tall and short grass, but tend to prefer the latter (Owen-Smith 1988).

By comparing the lips of different species, the anatomical adaptations that permit some animals to graze closely and others to browse selectively is revealed. According to Welch & Hooper (1988), selective feeders have well developed upper lips that enable them to pluck desirable leaves from, for example, among thorns, while animals that are quite unselective in their choice of feed have relatively immobile lips, and rely primarily on their tongues to bring feed into their mouths.

2.7.1.3 Influence of digestive system

A major anatomical difference among herbivore game species is that of ruminants (foregut fermenters) and non-ruminants (hindgut fermenters). Ruminants have a fermentation chamber (rumino-reticulum) anterior to the acidic stomach (abomasums). The stomach of a ruminant consists of four compartments, namely the rumen (large stomach), reticulum, omasum and abomasum (true digestive stomach) (Schmidt-Nielsen 1997; Owen-Smith 1999), which keeps the recently swallowed food separate from the food that has been swallowed for a second time. Intake in ruminants depends on the capacity of their digestive tracts, especially the rumen, and largely determines the differences in intake of different game species and their forage. The relative size of each stomach compartment in respect to one another, and with regard to body mass, is specific for grazers, browsers and intermediate feeders respectively (Van Hoven 2000).

The animal's digestive processes and the movement of food residues through the digestive tract influence the level of rumen fill. Because the volume of a ruminant's digestive tract is much larger than in monogastric animals, it increases the ruminant's need for bulky feeds and reduces its tolerance to highly concentrated feeds (Swenson 1977). Consequently, ruminants will eat until a certain degree of fill is achieved. The rate of forage disintegration in the rumen is closely related to the abundance and nature of the cell wall constituents in the forage, since these constituents depress fermentation and outflow. Gordon & Illius (1996) found that when animals of a range of body masses are fed the same food, fermentation rate per unit mass of digesta in the rumen is lower in large animals, which is a result of the decline in the concentration of digestible nutrients. Van Hoven & Boomker (1981) found that the mean rumen fermentation rate for black wildebeest in the Golden Gate Highlands National Park also varies seasonally, and increased from 166μmol gas g^{-1} DM h^{-1} in December to 203μmol gas g^{-1} DM h^{-1} in March.

Concentrate selectors have a limited capability to digest fibre, yet they pass digesta quite rapidly through the gastro-intestinal tract. They consume relatively low-fibre forage that ferments rapidly (Mysterud 1998). Their ability to select only the parts of the plant that are most digestible is essential to their survival (Van Soest 1994). The feeding strategy of the roughage or bulk feeders could be considered as "more is better" and "quantity, not quality". Digestive tract fill as a percentage of total capacity tends to be greater in large nonselective grazers (Van Hoven & Boomker 1985), largely due to the need to retain food in the tract for a longer period of time, to optimise digestion. Grazers have capacious rumens that enable them to retain the slow-fermenting leaves of grasses for long enough to extract most of the digestible energy the leaves contain. These animals derive significant energy from digesting the cell walls of plants (Mysterud 1998). Mixed feeders have the digestive capacity of a grazer, but other adaptations similar to those of browsers (Hofmann & Stewart 1972; Hofmann 1973). They are less discriminating in what they eat than are the selectors, but they are incapable of continuously consuming large quantities of highly fibrous feeds. Both the amount that they can eat and the duration of that feed being retained in the rumen, are limited by the capacities of their digestive systems (Welch & Hooper 1988).

The more rapidly food is digested and passed through the animal (i.e. the higher the quality of the food), the greater the potential for food intake, and the more likely it is to increase the animal's level of production (Meissner *et al*. 1999). Animals can, to a certain extent, buffer variable food intake by anatomical or physiological means. Anatomical buffering structures are temporary storage organs such as mouth pouches, the crop, rumen, etc. Physiological pathways that buffer food intake are body fat depots and the interchange ability of metabolic fuels, for instance, proteins that can be catabolized to obtain energy during periods of insufficient energy intake (Rogers & Blundell 1991; McDonald *et al*. 2002). Voluntary intake is therefore a function of both the food and the type of digestive system the animal possesses (Campling & Lean 1983).

2.7.2 Vegetation related determinants of diet selection

Feeding behaviour can be divided into habitat preference, feeding preference, behaviour patterns, herd and social behaviour, and migration (Grunow 1980). Feeding preference refers to the selection of vegetation layers (feeding height), taxonomic classes of plants, plant species and plant parts. The most important factors that influence the feeding behaviour of animals are the availability, acceptability, digestibility and chemical composition of their food. Feeding behaviour forms the link between the animal and the vegetation in its environment. This behaviour can be flexible in that animals have adapted different feeding strategies to sustain themselves under changing and unfavourable environmental conditions. Some maximise the quality of the feed they eat by careful selection, some consume large quantities of poor-quality feeds, while others adopt an intermediate approach to diet selection (Crampton 1964; Welch & Hooper 1988). The intrinsic anatomical, physiological and behavioural differences among animal species also have a fundamental influence on their feeding patterns.

The landscape level of diet selection is characterized by those physiognomic and thermal features of a management unit that influence animal movement patterns. A given landscape unit (pasture) is characterised by boundaries, distribution of plant communities, degree of accessibility and distribution of water, and thermal and mineral foci (Stuth 1991). Evidence suggests that the animal's selection of a given plant community is largely related to those attributes of a site that influence its ability to harvest nutrients. Senft *et al*. (1987) established that forage quantity and quality was closely related to the ratio of amount of time spent grazing in a community relative to the area occupied within the landscape. The abundance of seasonally preferred plant species also influences the patterns of plant community use (Senft *et al*. 1985). Preferred grazing areas have high occupancy:area ratios and high utilisation:herbage mass ratios (Stuth 1991). The major bulk of the herbivore game species' forage is derived from these areas. Grazing areas avoided contain forage with a low value or are inaccessible to the animal(s).

An animal's feeding station is established when it stops walking, moves the orientation of its head (upwards or downwards) and bites a plant. Certain sensory cues cause the animal to stop searching and to select a species or combination of species it considers as profitable. The pattern of feeding stations is strongly related to the distribution and profitability of patches in a community, the size of the community, and the geographical relationship of the community to the animals' grazing path (Novellie 1978; Ruyle & Dwyer 1985). At this level forage behaviour can be categorised as search time, time spent roving between feeding stations, biting rates and duration of biting while at a feeding station (Stuth & Searcy 1987).

Herbage intake is related to both the amount of time spent grazing and the rate of consumption (Welch & Hooper 1988). Intake is mostly determined by the amount of pasture available, plant spacing, plant height or accessibility, herbage digestibility, water content, the presence of metabolites, botanical composition, and palatability of the plant species (Allden & Whittaker 1970). Several factors influence the amount of time an animal spends eating, namely herbage density in a sward, photoperiod, temperature, weather, quality and form of feed, and physiological status of the animal. According to Owen-Smith (1988), both the day-night feeding ratio and the proportion of time devoted to foraging vary with body mass of the animal. Eating patterns and intake differ among animals in different reproductive states. Animals in oestrus decrease feed consumption, as do animals in the periods before and after calving. Van Wieren (1992) found that cattle had a very high intake during growth and lactation. According to Meissner *et al*. (1999), the nutritive value (chemical and nutrient composition) of the plants that are fed on, their digestibility, and the rate of feed intake are the main factors that determine animal performance. Several studies have been done on the influence of plant communities on ingestion rates (Allden & Whittaker 1970; Chacon & Stobbs 1976; Arnold & Dudzinski 1978; Arnold 1981; Forbes *et al*. 1985). Gordon & Illius (1996) concluded that food properties rather than anatomical adaptations are of greater significance for the nutritional ecology of some ruminants.

Searching between feeding stations appears to be an adjustment mechanism associated with forage quality. According to Bell (1970, 1971) and Jarman (1974), the feeding niches of African ruminant game species have often been classified in terms of three principal properties of the vegetation, namely its quality, quantity and botanical composition. The major factor affecting diet selection in most herbivore game species is quantity and quality of food available. This is substantiated by the fact that the diet composition of any game species varies over time (season) and space (location) in response to variations in quantity and quality of available food (Barnes *et al*. 1991). The quantity and quality of forage eaten not only determine the production of an animal species and reflect its behaviour and habitat (Milne 1991), but also provide reliable information on the value of those plants in addressing the nutritional needs of the individual. Sometimes, the material ingested by free-ranging herbivore game species simply does not contain sufficient nutrients to meet the animal's requirements. It is often stated that ruminants can only satisfy an animal's appetite when the yields of young, desired forage exceed 2 t ha^{-1}, and grazing is unrestricted (Minson 1990). However, these yields are seldom achieved in arid and semi-arid conditions, on dystrophic rangelands and during periods of poor pasture quality (Van der Merwe & Smith 1991). It is, therefore, often difficult for free-ranging herbivore game species to ensure a forage intake of sufficient quantity and quality.

2.7.2.1 Influence of plant species composition

Veld is typically heterogeneous and comprises a mixture of species of varying acceptability and palatability, which is determined by the species composition (Bothma 2000). Animal biomass and productivity is in a complex way related to the characteristics of plant species comprising the grazing community (Hudson & Christofferson 1985). Based on the herbaceous species composition and biomass, and on feeding studies of the relevant animal species, it is possible to determine the amount of suitable forage currently available for the specific species (Venter 1994).

Preference, which is essentially behavioural, involves proportional choice of one plant species from among two or more species. The preference status of a plant species is largely dependent upon its natural abundance, its morpho/phonological characteristics, the array of species on offer and the herbivore game species in question (Stuth 1991). Preference constantly changes as abiotic factors (i.e. season) alter the nature of the plant community. In grazing herbivore game species, diet selection relies on preferred and principal foods. Preferred species are taken in a greater proportion than their representation in the feeding area, irrespective of the extent to which the specific plant species contributes to the total diet (Petrides 1975; Grunow 1980; Mentis 1981). Preferred species enhance the diet nutritionally, resulting in better than normal animal performance. Principal species are those with a large contribution to the total diet selected by an animal, irrespective of its preference, relative to other plant species on offer (Grunow 1980; Mentis 1981). These species are not generally as high in nutrients as the preferred species but provide the animal the opportunity to maximize instantaneous intake rates (Stuth 1991). Plant species not readily consumed generally make up a lesser percentage of the diet in comparison to the percentage of their availability in the vegetation. Consumption of this undesirable or avoided selection group is highly condition specific (Stuth 1991). Diet selection can also be used to identify dietary preferences for different forage species. Dietary preference is the ratio between the abundance of a plant species in the diet of a herbivore game species, compared to the abundance in the herbage layer (Petrides 1975). By using the dietary preference ratio, the forage species can be ranked according to their preference under various grazing intensities. According to Grunow (1980), grass and browse species fall into four classes, namely preferred species, principal food species, intermediate species (taken under rather high grazing pressure), and non-forage species (which are either not taken at all or only when grazing and browsing pressure has become very high).

2.7.2.2 Influence of sward structure

Studies that were done on communities of African grazing ungulates have indicated that sward structure, as determined by leaf densities, leaf heights and leaf to stem ratios, is an important factor in the determination of niche separation between different animal species (Bell 1971; Grobler 1983; McNaughton 1985). Almost all natural grasslands display complex patterns of heterogeneity (Coughenour 1991), with some patterns being related to the landscape. For instance, short grasses tend to be widespread on summit areas where the soil is shallowest, medium tall grasses predominate on the slopes, while plains may be dominated by either tall or short grasses, depending on various factors (Owen-Smith 1999). Tall grasses tend to predominate in situations where defoliation is moderate, as their height gives them an advantage during competition for light (Novellie

1989). In the case of severe defoliation, short grasses, and in particular those with a prostrate growth form, are favoured over taller species (Stuart-Hill & Mentis 1982).

Different herbivore game species have diverse abilities - largely by virtue of variation in their mouth structure - to graze grass plants of different lengths. The rate of intake can, however, to a limited extent compensate for the influence of changing grass height. The variations in grass height play an important roll in preference changes for particular grass species. The highest intake rate can, in some situations, be achieved from quite short grass because the biomass concentration or bulk density is highest in this state. Aggregation of grazing ungulates in herds, such as in wildebeests, together with patch-selective grazing, can promote the development of short grass lawns (Novellie 1989), which increases feeding efficiency (McNaughton 1984). Laca *et al.* (1994) found that taller patches had more herbage mass and allowed a greater bite mass than shorter ones, and that the intake curves had steeper slopes and higher asymptotes for taller patches. Some wild herbivore species exploit the catenary pattern by moving seasonally among the different grassland types, but others have very definite preferences. Bell (1970, 1971) found that the order of movement of different animal species in the Serengeti Plains was related to the different tolerances of the animals to long and short grass. Page & Walker (1978) found that the height of the grass layer is the most important variable relating to niche separation of large herbivores in the Hluhluwe Game Reserve in KwaZulu-Natal.

2.7.2.3 Influence of dry matter production

Although the quality of individual food items has a profound influence on the condition of individual herbivores, the quantity of forage, also taking into consideration the species composition, ultimately determines how many animals can exist within a habitat (Venter 1994). During a study done in the semi-arid savanna of the Northern Cape Province, Mbatha & Ward (2006) concluded that ranchers should only lightly stock open savanna habitats in spite of high standing biomass, because they have low vegetation quality and may be particularly susceptible to degradation and invasion by poisonous and unpalatable plants. The term grazing capacity is used to describe the capability of rangeland to support animals. Stoddart & Smith (1955) defined grazing capacity as the maximum number of animals that can graze each year on a given area of the range, for a specific number of days, without inducing a downward trend in forage production, forage quality or soil condition. Grazing intensity affects herbage quality indirectly through its effect on growth rate and relative maturity of the plant (Meissner *et al*. 1999), as young re-growth is usually more nutritious, digestible and palatable than older plant material. In the Giant's Castle Game Reserve, the introduction of black wildebeest was not very successful due to habitat destruction brought about by severe over-grazing, this resulted in the removal of almost all of the animals in 1976 (Rowe-Rowe 1983).

Increased competition between herbivore game species due to high stocking rates or reduced abundance of preferred forages in the natural vegetation due to deteriorating rangeland condition, reduces the abundance of preferred forages in the diet. This forces the game species to change their diet selection pattern. Other forage species that are normally avoided may now be taken in disproportionably large quantities since the preferred forages have been depleted or are not abundant enough. The intake rate of grasses is predictable from estimates of pasture biomass, because bite size is directly related to grass biomass (Short 1985). If the quality of food selected by the animal species and the amount they eat during different times of the year are known, nutritional requirements can be calculated for the purpose of predicting grazing capacity (Pietersen *et al*. 1993).

A wide variety of factors and variables are involved in the estimation of grazing capacity, such as the reaction of the veld to use pressure, seasonal fluctuations, and the effect of biological and climatological conditions on the nutritional value of forage. Competition between plant and animal life may also alter grazing capacity. The ideal grazing capacity may be regarded as the balance between plant production and animal production. Rowe-Rowe (1983) found that the numbers and proportions of the five most abundant herbivore species in the Giant's Castle Game Reserve were determined by the amount of suitable habitat and the degree of specialization of the individual species. Various methods have been developed to measure grazing capacity. Among them are the estimate method, energy method, and the large-animal stock-unit method (Van Hoven 2000). Herbivore game species, due to the local plant species diversity, are capable of more thorough resource utilisation. As a result, more game (than domestic livestock) can be carried by a given area, if expressed in kilograms of body mass (Van Hoven 2000).

Water availability is the main environmental determinant of plant production (Snyman 1988). Snyman (1999) found that rangeland condition in interaction with the soil water content is the main determinant of optimal plant production and water-use efficiency. Pieterse & Grunow (1985) described an S-shaped production curve for five different grass species in natural veld of the Limpopo Province. They also found that the month of peak production might differ between species. Production can be influenced by a number of factors including plant genetics (Grossman *et al*. 1980), soil (Snyman 1997), drainage patterns, periodic droughts, and a variety of factors relating to temporal and spatial variation in habitats and surface water (Hudson & Christofferson 1985).

Above-ground phytomass production decreases when plant cover decreases, or when range and soil condition declines (Snyman 1997, 1999). In the Free State, Snyman (1993b) found that defoliation of *Themeda triandra* and *Eragrostis lehmanniana*, while they are at a temporary wilting point in the early growing season, resulted in decreased production in the subsequent season. Studies done by McNaughton (1979) in the Serengeti National Park showed that net above-ground primary productivity of grasslands (concentration areas of the wet-season) was strongly regulated by the grazing intensity of large ungulate fauna. He also found that moderate grazing stimulated productivity up to twice the level encountered in ungrazed areas, depending on soil moisture availability.

According to Grunow *et al*. (1977), the rate of re-growth of cultivated grasses is slow during the growing season, followed by a quick increase in dry-matter production over a period of nine weeks. In the late growing season the rate of quick growth lasts for a period of five to eight weeks. In all cases he found that the protein and *in vitro* digestible organic material contents declined between four to six weeks after defoliation. It is recommended by Grunow *et al*. (1977) that a resting period of four to six weeks is allowed before the next defoliation. This defoliation will coincide more or less with the early flowering stage, when the quantity and quality of the material is sufficient for maximum production. Grass species in natural vegetation also differ in their reactions to defoliation frequency. A defoliation frequency of six to nine weeks should be maintained to make provision for the needs of all the species (Pieterse & Grunow 1985).

2.7.2.4 Influence of plant chemical composition

Herbages contain various chemical compounds, consisting of primary and secondary plant substances, which serve as nutrients for herbivores. These chemical constituents can be divided into cell wall constituents (carbohydrate cellulose, hemicellulose and lignin) that are either indigestible or poorly digestible, and cell contents (proteins and soluble carbohydrates), which are highly digestible (Van Soest 1967; Schwartz & Hobbs 1985). Primary plant substances include components such as starches, lipids, proteins, vitamins, and minerals (Stuart-Hill & Mentis 1982) and play an important role in the metabolism of the animal species. Secondary plant substances include glucosides, saponins, tannins, alkaloids, essential oils and organic acids, which have no significant role in the metabolism of the animal.

According to Simons & Marten (1971) and Levin (1976), these chemicals are primarily controlled by genotype and not by environmental factors. However, the level of expression appears to be environmentally determined (Louw *et al*. 1967). Secondary plant substances provide plants with specific chemical resistance to feeding animals

(Fraenkel 1969). Secondary plant substances may be non-toxic; however, many are toxic and cause ill effects in animals, and sometimes even death. They have been shown to have a negative effect on herbivore fitness and a deterrent effect on herbivore grazing (Rhoades 1979). Conversely, animals have developed the ability to detoxify and/or build up a tolerance to these chemicals (Stuart-Hill & Mentis 1982).

Proteins, vitamins and minerals are essential components of the animal's diet and are required in a proper balance if animals are to perform adequately. Proteins are often the constituent that are most limiting to the performance of animals on veld (Meissner *et al*. 1999). The protein requirements of an animal are influenced by the species (Pieterse & Grunow 1985; Meissner *et al*. 1999), age (McDonald *et al*. 2002; Meissner *et al*. 1999), physiological functions such as growth or lactation (Meissner *et al*. 1999) and seasons (Pieterse & Grunow 1985; Fourie *et al*. 1986). Plant proteins occur at a higher concentration in young and rapidly growing plants than in old and mature plants (McDonald *et al*. 2002; Meissner *et al*. 1999), following the same trend as digestibility. Pieterse & Grunow (1985), for example, found that grass species such as *D. eriantha* and *S. pappophoroides* have a higher percentage crude protein (%CP) and *in vitro* digestible organic material (IVDOM) than species such as *E. rigidior*, *T. triandra* and *H. contortus*. In the Free State, Fourie *et al*. (1986) found that the %CP and IVDOM reach a peak during the growing season and a low during the dormant season. It was also found that cultivated forage has a higher %CP and IVDOM (Grunow *et al*. 1977) than natural forage (Pieterse & Grunow 1985). This may be due to the management practices that are being followed or due to fertilisation with nitrogen (Roberts & Scott 1968). According to Meissner *et al*. (1999), ruminants generally require a minimum of between 7% and 8% crude protein, and high producing animals require a level approaching 13% to 14%. However, it appears that game species have a lower level of crude protein requirements.

Inadequate levels and imbalances of minerals in forages may cause physiological disorders and suppress an animal's performance (Meissner *et al*. 1999). The concentration of minerals in forage plants is largely determined by the maturity of the plant material. Mineral content of the forage declines with age. However, the rate and extent varies with the time of the year, and is influenced by seasonality, soil type and nutrient levels of the soil (Meissner *et al*. 1999). Structural constituents of plant material can be divided into matrix polysaccharides, such as hemicellulose and peptic substances, and fibre polysaccharides, such as cellulose, lignin and proteins (Jones & Wilson 1987). Vitamins are normally required in small amounts, the most important one being vitamin A, chemically known as retinol (McDonald *et al*. 2002), which is usually deficient in dry veld (Meissner *et al*. 1999).

2.7.2.5 Influence of plant digestibility

The digestibility and primary and secondary nutrient contents of food are a primary measure of their value to the animal as a source of energy (McDonald *et al*. 2002). Digestibility is estimated as the difference between the amount of feed ingested and the amount excreted. Since the total energy recorded in the excreta is not derived from the forage, and all the energy is only partially accounted for in metabolic rate determination during feeding trials, only the apparent digestible energy content is represented by this amount (Meissner *et al*. 1999). Usually the relationship between digestibility and feed value is positively related to the concentration of nutrients and intake of the forage. Feed can therefore be more easily digested if the quantity of nutrients in the feed is larger (Meissner *et al*. 1999; Van Hoven 2000). This association is, however, influenced by factors such as the animal species, level of feeding, intake, and growth rate of the animal (McDonald *et al*. 2002). In the Netherlands, Van Wieren (1992) found that the digestibility of the diet appears to be the single most important factor limiting food intake of cattle, although other factors are also involved.

Digestibility is also related to the lignin contents (French 1957), fibre content and the proportion of structural material in the food (McDonald *et al*. 2002), which includes cellulose and hemicellulose (Minson 1971). Tropical grasses are generally less digestible than their temperate counterparts because their leaves contain more vascular bundles (lignin) and they have dense masses of cells that resist invasion by micro-organisms (McDonald *et al*. 2002). In southern Kenya, Georgiadis & McNaughton (1990) found that nutritional values, as indicated by the fibre properties, were at all times higher in areas of high intensity herbivore use than in areas of low intensity herbivore use. Plant species, plant age, climate, seasonality, temperatures, fertilisers, soil nutrients and moisture stress have a direct influence on digestibility, while grazing management has an indirect influence (Meissner *et al*. 1999). The availability of moisture has a much greater effect on herbage quality than most other factors (Wolfson 1999).

2.7.2.6 Influence of plant palatability and acceptability

Palatability is the absolute attractiveness of feed to animals, as determined by factors of the forage and the environment (Mentis 1981). It refers to those factors inherent to a plant species that elicit a selective response by the animal. Owen-Smith (1993) describes palatability as the inherent properties of potential foodstuffs that influence the inclination of animals to consume them. According to Marten (1978), only relative palatability can be measured, because of the many factors that influence the extent to which a feed is consumed. Potentially palatable feed can be unacceptable, and unpalatable feed can be made acceptable by, for example providing licks (Meissner *et al*. 1999). There appear to be associations between plant palatability and leaf chemistry, soil nutrient level, and seedling growth rate (Owen-Smith & Cooper 1988). Owen-Smith & Cooper (1987) found that plants known to have chemical defenses against vertebrate herbivory are prominent on nutrient-deficient soils, while those with structural defenses are prominent on fertile soils. Due to their high digestibility, component elements of the cell content (proteins, minerals, water, etc.) tend to be positively associated with acceptability, in contrast to comprising elements of the cell wall, such as fibre and lignin, which are negatively correlated with digestibility (Meissner *et al*. 1999).

Acceptability is also strongly influenced by the physical properties and structure of the plant. Plant structure may influence acceptability by affecting the accessibility of leaves to the grazing animal. Thorns and spines may reduce the bite size, biting rates (Cooper & Owen-Smith 1986) and acceptability (Mentis 1981; Stuart-Hill & Mentis 1982; Cooper & Owen-Smith 1986) of certain woody browse species below levels that would be expected. Acceptability may also be reduced by the hairiness, toughness (Dyne *et al*. 1980; Stuart-Hill & Mentis 1982; Wright & Illius 1995), stickiness (Dyne *et al*. 1980; Mentis 1981), coarseness or harshness of the leaves (Shewmaker *et al*. 1989).

Plant secondary metabolites, such as tannins and alkaloids, are relatively scarce in grasses. When they do occur, they reduce digestibility and acceptability, as in *Elionurus muticus* (Stuart-Hill & Mentis 1982; Meissner *et al*. 1999), *Bothriochloa insculpta* and *Cymbopogon* spp. (Stuart-Hill & Mentis 1982). Tannins and structural carbohydrates, such as cellulose and lignin, increase the fibre content of the plant. When tannin-containing food is consumed, the tannins form relatively indigestible complexes with protein. Because this combined molecule is difficult to digest, the available proteins in the food are not released as energy (Rhoades 1979). Tannins inhibit a wide variety of animal and microbial digestive enzymes (Van Sumere *et al*. 1975) and reduce the ability of micro-organisms to break down proteins (Owen-Smith 1993), thereby lowering the nutritional value of plant species (Cooper & Owen-Smith 1985), rendering herbage less acceptable to animals and thus limiting intake (Meissner & Paulsmeier 1995). The presence of tannins (Stuart-Hill & Mentis 1982) and lignin (Schwarts & Hobbs 1985) depresses the total rate of digestion, which reduces the digestibility of the forage. This may lead to the deterioration of the animal's condition despite a protein-rich diet of high quality. Ingestion of natural concentrations of secondary chemical compounds can either lead to death or severe physiological impairment. However, herbivores are capable of detoxifying and eliminating secondary compounds (Freeland & Janzen 1974). Grazing and browsing ungulates differ in anatomical features related to deactivation or detoxification of tannins and other xenobiotics (Owen-Smith 1993).

The circumstances under which a plant grows also influence its acceptability. Other neighbouring plant species may change a plant's acceptability by masking its chemical cues and restricting the animals from grazing nearby due to their smell, or by physically reducing access to the plant (Crawley 1983). The relative abundance and preference for other plant species growing in the same area may also influence acceptability. In pastures where there are manure pads, there is a zone of aversion around each manure deposit where animals will not graze unless no other feed is available (Welch & Hooper 1988). This unacceptability might be due to the smell or taste of the grass that is closely associated with the dung pad.

2.7.3 Seasonality as a determinant of diet selection

According to Tolsma *et al*. (1987), knowledge of the nutrient status of the various plant organs and their changes during the growing season is necessary for proper assessment of the effects of these changes on the functioning of the ecosystem. Most ungulates living in the temperate zone, experience periods of food stress on a seasonal basis. During the winter season, there can be a substantial decline in food quality and quantity (Van Soest 1982; Schwartz & Hobbs 1985; Van Wieren 1992). The body condition of the animals can be seriously affected by this period of winter stress and may eventually lead to death at the end of the winter and early spring (Mitchell *et al*. 1977). Van Wieren (1992) found that weight losses occurred in cattle during the winter period in the Netherlands, and he postulated that the lower daily metabolisable energy intake of cattle during the winter is the main reason for this weight loss.

Dekker *et al*. (1996) found that the highest spatial separation of ungulates in Mopani veld occurred in the warm dry season, which coincides with the period at which resources are most limited. In the Serengeti, some grazers, particularly wildebeest (*Connochaetes taurinus*), increase their range of movement during the early part of the dry season to seek out green flushes associated with rainstorms (McNaughton 1979). According to

Owen-Smith & Cooper (1988), plant species neglected at one time of the year may become favoured at another time, due to changes in food abundance and/or in relative leaf chemistry. Ben-Shahar (1991) found apparent seasonal patterns in wildebeest diet, showing high preferences during the winter months for grass species that were rejected during summer. During the dry season there is a decrease in intake of grass leaves at the expense of leaf sheath and stems (French 1985).

Studies of the foraging behaviour of blesbok and springbok revealed that in both species seasonal changes in foraging behaviour were correlated with chemical and structural changes in the sward (Novellie 1978). Cooper *et al*. (1988) found that during the dry season, plant species were added to the diet of some browsing ruminants, approximately in the order of their relative protein:condensed tannin difference. During the late dry season, the ranges of grazers become restricted to the proximity of surface water points (Owen-Smith 1992). Pettifer & Stumpf (1981) suggested that the availability of surface water is probably the most important factor influencing the seasonal movements of impala (*Aepyceros melampus*) in the Loskop Dam Nature Reserve. Seasonality affects quality, quantity and palatability of forages so that the diet of herbivore game species varies throughout the year. Most plant growth, especially of the herbaceous plants, occurs during the rainy season. In the more arid parts of southern Africa, plant growth is erratic and consequently affects animal behaviour, especially feeding behaviour (Ellis 1995).

2.7.4 Habitat overlap as a determinant of diet selection

The problem of competition among sympatric herbivore species is frequently encountered in wildlife management. Not only is the quality and quantity of the available food important for wild herbivores, but also the interaction between various species of herbivores when competing for the same food resources. Increasing grazing pressure by one animal species can force another species into their less preferred food group resulting in reduced performance, decreased harvest efficiencies or both (Stuth 1991). If resource abundance varies with season and there is evidence of seasonal shortage (Andere 1981), particularly during the dry season or winter (Jenkins & Wright 1987), more niche overlap occurs among herbivores and interspecific competition is increased (French 1985; Jenkins & Wright 1987). According to Bonser & Reader (1995), both competition and herbivory have a greater effect on plant growth in areas with higher biomass. However, in areas with a relatively low biomass herbivory has less of an effect on plant growth than competition.

Novellie (1978) found that blesbok and springbok, which share the same habitat, change their foraging behaviour in order to overcome overlapping. The size of the animal often determines its feeding habits. Smaller herbivores usually have a split upper lip that enables them to feed closer to the ground (Owen-Smith 1999). The findings of Murray & Illius (2000) in the Serengeti indicate that bite quantity competition may apply on short grazing lawns and that bite quality competition is expected on differentiated swards with a limited supply of green leaf. They suggest that herbivory by one species can modify the vegetation in a way that makes it less profitable to competing species, which is a critical component of resource competition in herbivores. It is not only the ability of the food to supply energy, but also the competition between the herbivores, that is important for animal production. In terms of feeding, the aforementioned tend to separate the herbivores in times of food shortage, when competition for food would be detrimental. Therefore, forage selection provides a great deal of insight into competition and resource partitioning in ungulate communities (Hanley 1982). Page & Walker (1978) emphasized niche overlap as being of great importance when determining carrying capacity.

2.7.5 Other environmental factors as determinants of diet selection

There is a consistently large amount of complicated environmental factors impacting on animals, which directly or indirectly influence their physical and psychological well-being and needs. Stress-related problems often occur at sub-clinical levels and may not be readily obvious, or occur during limited periods of the year and are related to unusual weather conditions, seasonal variations and animal susceptibility (Young 1988). According to Young (1988), the impact of environmental stress on ruminants often involves some nutritional cost. Grazing animals usually eat during daylight, particularly in the early morning and at sunset, and in hot conditions animals increase their nocturnal grazing time to avoid grazing during the heat of day. Hot conditions and heat-stress can reduce feed intake markedly and lower animal productivity, especially if associated with high humidity or solar radiation. Cold conditions, in contrast, generally increase feed intake, which can reduce the digestive efficiency. However, the main reason for the increase in nutrient requirements of an animal is to compensate for the increase in metabolic activity to keep warm, and the increase in metabolic intensity associated with cold acclimation (Young 1988). Young (1988) further mentioned that other environmental conditions such as high moisture (rain, snow, mud, etc.), unusual sound levels, and gaseous contaminants can also be stressful on ruminants and can cause a reduction in productivity, primarily through a decline in appetite. Some gaseous contaminants are highly toxic, can affect the animal’s health, and can even be fatal (Young 1988).

2.8 THE INFLUENCE OF HERBIVORE GAME SPECIES ON VEGETATION

Rangeland condition, relating to some functional characteristic of the range such as its maximum forage yield or its resistance to soil erosion (Tainton 1999), reflects the effect of herbivory on vegetation, although grazing is not the only parameter that shapes vegetation (O’Connor 1994; O’Connor & Roux 1995). Trends in rangeland condition are commonly used to determine whether herbivore game species have a positive, neutral or negative effect on the vegetation. Therefore, diet selection is the true interface between herbivore game species production and vegetative processes that react to defoliation by the foraging species (Emmans 1991; Prache *et al*. 1998).

The direct impact of grazing animals on the physical properties of soils and growth of plants together with the indirect impacts on soil aggregate stability, plant food reserves, and effective precipitation, combine to markedly affect not only plant competition and community composition, but also subsequent spatial configuration of forage resources. These small shifts and changes in plant community composition and the spatial relationships of these plants lead to long-term changes in the landscape (Stuth 1991). Milchunas & Lauenroth (1993) found that the changes in species composition with grazing are primarily a function of aboveground net primary production and the evolutionary history of the grazing of the site, with the level of consumption third in importance. They also found that changes in species composition increased with increasing plant productivity and with longer, more intensive evolutionary histories of grazing.

Patch grazing is often the most obvious early sign of landscape reconfiguration. The new available green foliage of a patch that was grazed clean, results in intense patch defoliation and re-defoliation. Such frequent defoliation in turn alters the hydrologic condition of the patch/community, ultimately to the point where plant species composition shifts and forage production declines. Furthermore, repetitive defoliation results in expansion of the size of the patch and in some cases leads to the loss of most plant material and consequent development of eroded areas. Once soil loss accelerates to the point of erosion, a permanent reconfiguration of the grazing area occurs. Results from a study done by Tsholofelo & Brits (2006) on the impact of domestic and wild herbivores on herbaceous forage around artificial watering points indicated that the herbaceous vegetation only occurred further than 10 m from watering points in the case of wild herbivores. However, domestic herbivores had a greater impact on the vegetation.

The grazing patterns of the animals are influenced by the occurrence of palatable and unpalatable plant species. If a ranch has a small area of unpalatable grazing, that area will be utilised last and will not be overgrazed. However, if only a small area of palatable grazing occurs on a ranch that has predominantly unpalatable grazing, that small area will be utilised first and will usually result in over utilisation or destruction of that area. Lütge *et al*. (1996) found that patch-selective grazing changes the species composition of the specific area, and due to limiting forage availability the animals increase the size of existing patches and/or create new patches. Therefore, proportional species composition of the herbage on offer usually has an important influence on grazing capacity (Barnes *et al*. 1984).

In extensive animal production systems, where the animals are free to forage in the natural vegetation (Pagot 1992), the ability of an animal to select feed from the variety of plant species available becomes vital to its well-being (Rogers & Blundell 1991). Therefore, in relation to the often large variation among grass species with regard to structure, nutrient content and palatability, it is common that different grazer species exhibit marked grazing preferences (Smit 2003a). Selective grazing is thus common among grazers to varying degrees.

Herbivores select food in a hierarchical fashion, making different decisions at different spatial scales ranging from the plant part or bite to the landscape and region (Jarman 1974; Senft *et al*. 1987; Stuth *et al*. 1993). Whether or not selectivity is a significant advantage depends on the composition of the available forage. The more uniform the forage, the less beneficial selective grazing will be. Due to the more continuous dispersion of many grasses (Jarman 1974), they tend to be rather homogeneous. Therefore, grazers are expected to choose diets based on the characteristics of the patch, pasture or landscape, rather than those of individual plants or plant parts (Shipley 1999). For instance, grazers may select patches that provide the tallest, youngest or most nutritious grasses (Langvatn & Hanley 1993). When the quality of mature and immature parts of the plant differ to a great extent, as found in tropical grasses, careful selection may make it possible for an animal to survive in an environment in which less selective feeders cannot survive. According to Ben-Shahar (1991), the patterns of dietary habits indicate that selectivity appears to be a means of compensating for variations in local conditions in order to maximise nutrient intake. Melton & Heard (1991) found that waterbuck (*Kobus ellipsiprymnus*) decrease area selectivity with a decline in the habitat quality. After the removal of many recognisable competitors, selectivity increased markedly.

According to Tainton (1999), various types of selection can be distinguished, namely:

- plant part selection – animals select for specific plant parts,
- within plant type selection – animals select between plants of the same species,
- plant type selection – animals select for specific plant species from amongst other species,
- area selection – animals select for a specific veld type, e.g. hillsides and grass plains,
- spot selection – more local than area selection, thus the area of selection is smaller,
- stratum selection – occurs when the vertical utilisation is not even,
- seasonal selection – preference for different plant species varies over the season,
- interspatial overgrazing – a type of forced selection that occurs when high growing plants obstruct the movement of the animals,
- progressive selection – the manner or method through which many types of selection take place,
- controlled selective foraging – the animals are allowed to only eat some plant species, and
- the division of grazers as tall and short grass feeders, which is just another form of selective feeding based on certain grass height preferences.

2.9 THE IMPORTANCE OF MANAGEMENT IN GAME RANCHING

The increasing interest in game ranching and privately owned reserves accentuates a need for improved methods of game and veld management. Managing wildlife populations depends largely on a perceptive and predictive analysis of their habitat preferences (Pienaar 1974; Dekker *et al*. 1996; Dörgeloh 2001), and the diet of the specific animal species, including species of plants eaten (Scotcher 1979; Hanley 1982; Hobbs *et al*. 1983). An understanding of the abundance and distribution of game species is important to be able to judge which species may be introduced in a certain area (Pienaar 1974). The smaller the area being used for game, the more intensively it must be managed (Pietersen *et al*. 1993). Amongst other factors, this requires implementation of a realistic standard whereby the carrying capacity of veld for game species can be determined. A principal factor in such calculations is the animal's food intake, since carrying capacity or stocking rate is primarily a function of the grazing and browsing capacity of the veld (Trollope 1990). Based on the plant community diversity and information about the palatability of the vegetation present, the grazing capacity, and veld condition - management plans can be developed to allow a reliable choice of suitable game species. This, in turn, determines the number and ratio of the different feeding classes that can be sustained by the area (Van Rooyen & Theron 2000b).

CHAPTER 3

STUDY AREA AND TRIAL LAYOUT

3.1 INTRODUCTION

Sangiro Lodge was established in 2002 and is situated on the farm Annex Wildealskloof No. 260 Bloemfontein, a sectional title of the farm Bergendal. The developer identified a need for accommodation and conference facilities close to the N1 highway. With the prior consent of the local municipality, and subject to such conditions imposed by the local municipality, chalets and related facilities were established on this property. Endemic game was introduced into the area as part of the ecotourism attraction. The land was previously used for grazing by cattle. In the surrounding area land is predominantly used for agriculture.

3.2 GEOGRAPHICAL LOCATION AND SIZE

The study area is situated approximately 5 km north of Bloemfontein in the central Free State Province, South Africa (Figure 3.1). It is located at 29˚02´47.3″S, 26˚13´37.1″E, at an altitude of approximately 1 380 meters above sea level. The total game fenced area occupies 78.8 hectares and consists of a few chalets, a restaurant, conference facilities and a game viewing area.

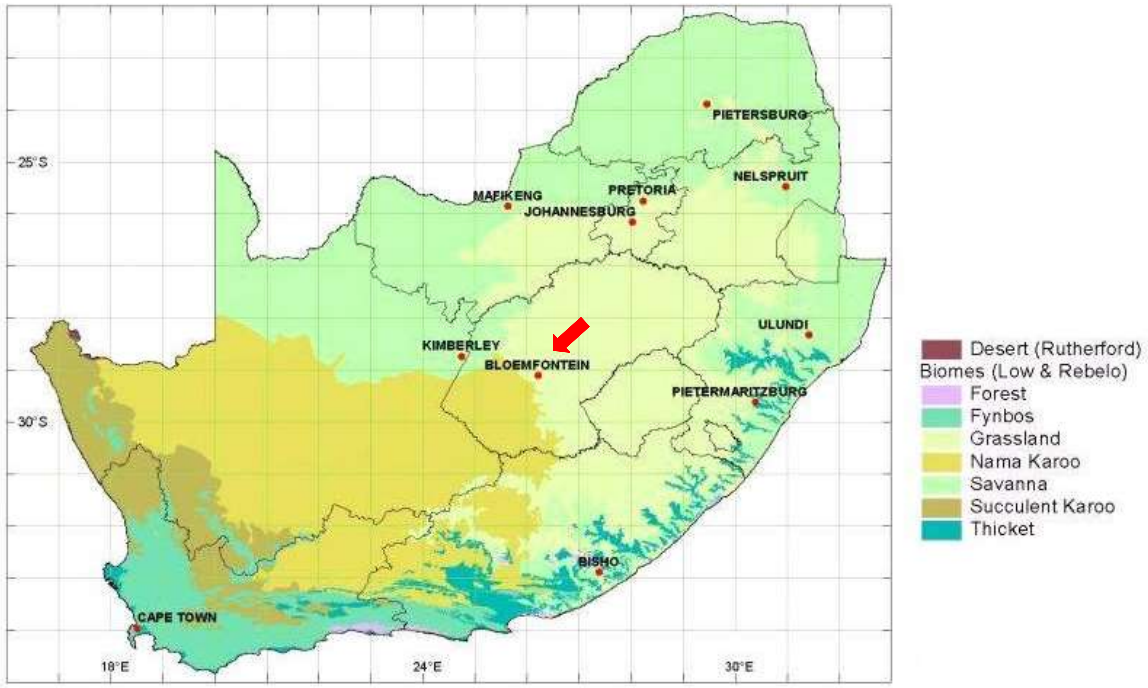

Figure 3.1: Map of biomes in South Africa, indicating the location of the study area in the central Free State north of the city of Bloemfontein. (Low & Rebelo 1996, map provided by South African National Biodiversity Institute).

3.3 CLIMATE

The climatic data received from the Bloemfontein Weather Station [0261516B0], approximately 20 km south-west of the study area, was used to provide an indication of the prevailing climatic conditions of the central Free State.

3.3.1 Rainfall

3.3.1.1 Long-term rainfall patterns

The study area is situated in the summer rainfall region of South Africa. The mean long-term seasonal rainfall (July - June) for the period 1994/95 to 2004/05 was 552.3 mm.

More than 70% of the total mean annual rainfall occurred from November to March (Figure 3.2). The highest mean monthly rainfall was received during January (94.2 mm) (Figure 3.2).

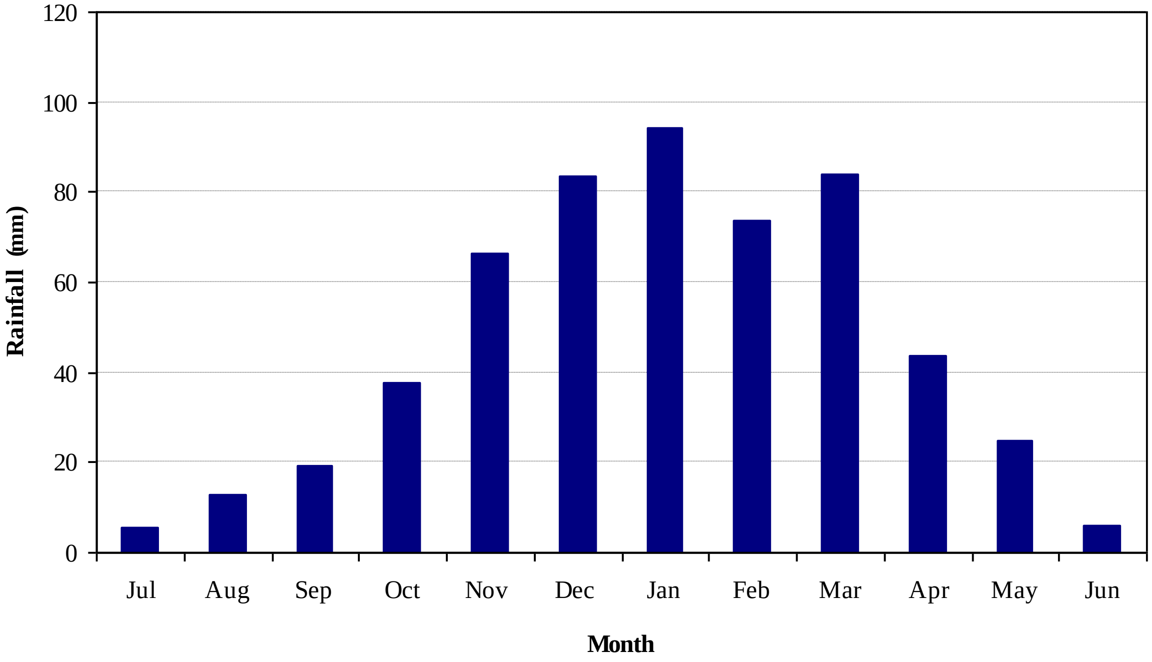

Figure 3.2: Mean monthly rainfall for the period 1994/95 to 2004/05, as measured at the Bloemfontein weather station.

3.3.1.2 Rainfall during the study period

The study was conducted from July 2004 to June 2005. During this period precipitation at the study site was measured with a standard cone-shaped rain gauge (127 mm diameter). For comparison, the monthly rainfall data for the previous season (2003/04) was obtained from the nearby National Botanical Gardens. Compared to the mean seasonal rainfall of 552.3 mm, the rainfall for both the seasons was below average. It can be seen in Figure 3.3 that the rainfall at the study area was irregularly distributed and largely unpredictable.

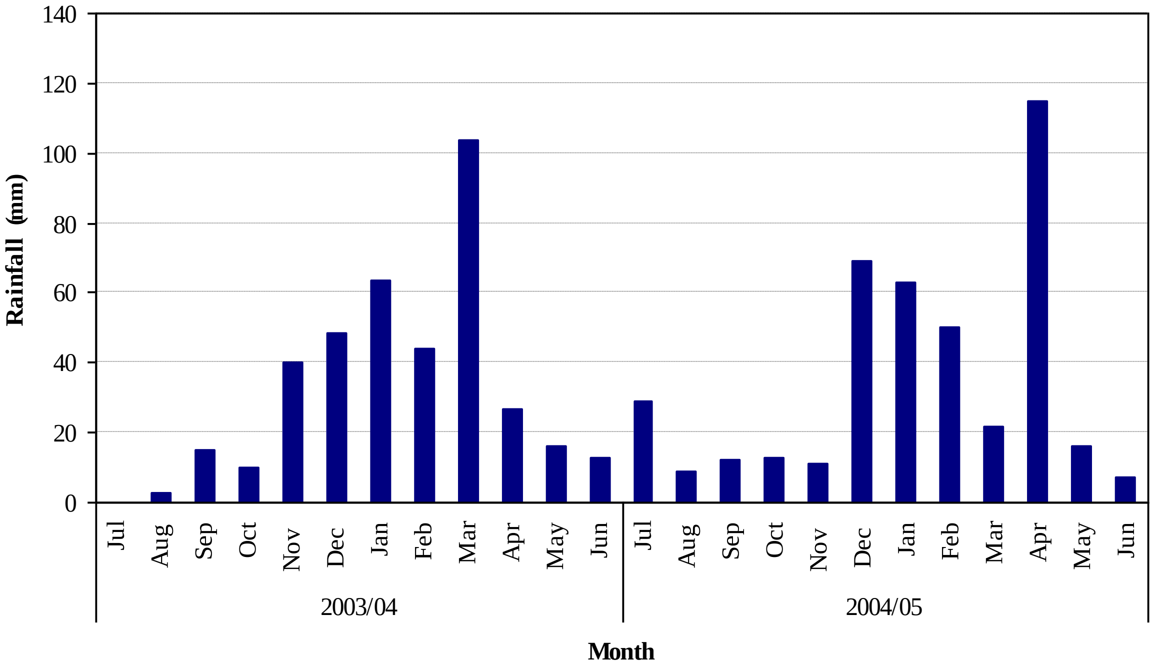

Figure 3.3: Monthly rainfall measured at the study area during the 2003/04 and 2004/05 growing seasons.

3.3.2 Temperatures

The study area is situated in a region well known for its semi-arid climate and temperature extremes. The mean daily temperatures for the period 1994/95 to 2004/05 peaked from December to February and reached a low during June and July (Figure 3.4). The mean daily minimum and maximum temperatures were 13.2˚C and 29.9˚C for December and -1.9˚C and 18.7˚C for June.

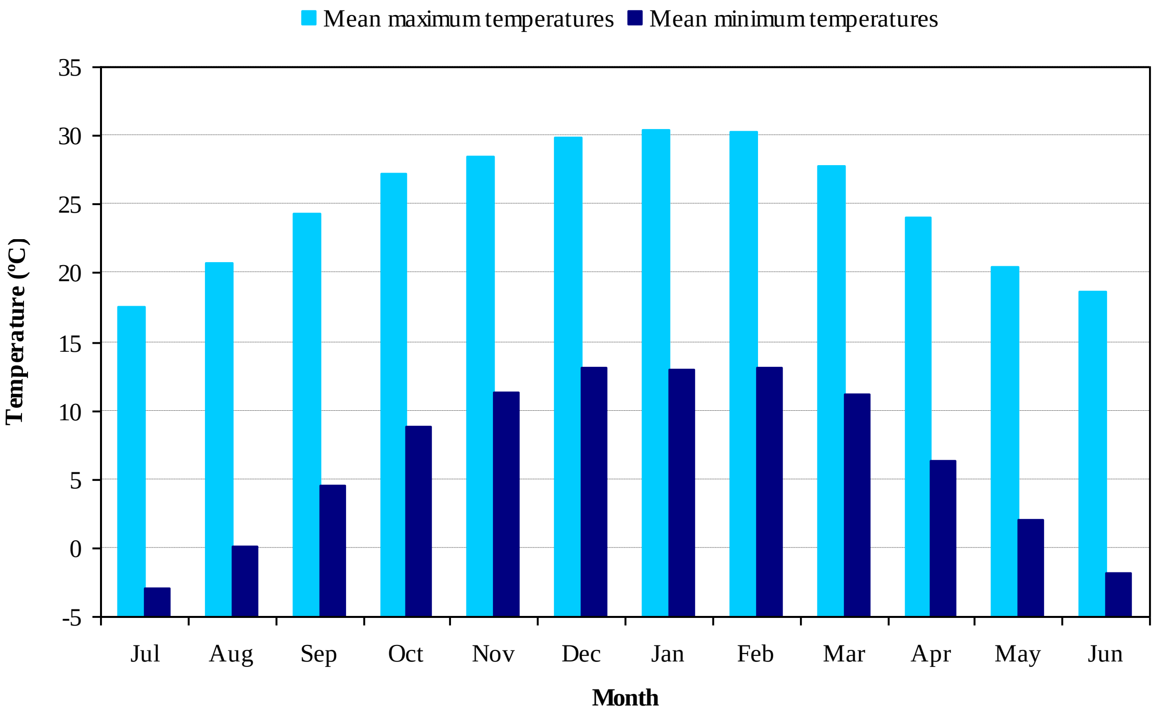

Figure 3.4: Mean daily minimum and maximum temperatures for the period 1994/95 to 2004/05, as measured at the Bloemfontein weather station.

3.4 GEOLOGY AND SOIL

The study area is located in the Adelaide subgroup of the Beaufort Group of the Karoo Sequence. The soil consists mainly of green or blueish gravel, reddish and purple mudstone, submissive gravel, and fine grain sandstone. Dolorite intrusions are also common in this area. The slopes of the dolerite hill are covered in a very shallow layer of soil and outcrops of sandstone are also visible. A more detailed description of the soil composition is presented in Chapter 4.

3.5 VEGETATION

The vegetation of the study area is described by Bredenkamp *et al*. (1996) as Dry Sandy Highveld Grassland (vegetation type 37), while Acocks (1988) classified it as Dry

Cymbopogon-Themeda Veld. The dominant grass species occurring in the area are *Aristida bipartita*, *Eragrostis chloromelas*, *Setaria incrassata* and *Themeda triandra*. Prominent tree and shrub species include *Rhus lancea* (common karee), *R. erosa* (broom karee), *R. burchelli* (kuni bush), *Acacia karoo* (sweet thorn) *Diospyros austro-africana* var. *microphylla* (fire-sticks) and *Protasparagus laricinus* (wild asparagus). Most of these species, except *A. karoo* and *P. laricinus*, generally occur on rocky ridges and hillocks and are not found in open grassland. The most common forbs are from the Lamiaceae and Asteraceae family.

3.6 GAME POPULATIONS AND EXPERIMENTAL ANIMALS

Between August and October 2002 eight herbivore game species were introduced into the game fenced area. The number of each species during the study period is presented in Table 3.1. The increase in numbers observed was due to breeding during the season.

Table 3.1: Number of each herbivore game species during the study period.

Scientific name	**Common name**	**Number (2003/04)**	**Number (2004/05)**
Antidorcas marsupialis	Springbok	27	40
Cervus dama	European fallow deer	4*	4*
Connochaetes gnou	Black wildebeest	5	8
Damaliscus pygargus phillipsi	Blesbok	4	6
Oryx gazella	Gemsbok	4	4
Raphicerus campestris	Steenbok	4*	5*
Redunca fulvorufula	Mountain reedbuck	5	5
Sylvicapra grimmia	Grey duiker	4*	4*

* Indicates uncertainty due to limited sightings

Four of the eight species occurring in the enclosure, namely European fallow dear (*Cervus dama*), steenbok (*Raphicerus campestris*), mountain reedbuck (*Redunca* *fulvorufula*) and grey duiker (*Sylvicapra grimmia*), are browsers and inhabit the woodland and/or hillsides. As a result, these four species were excluded from the study, since the study was conducted exclusively on grazers occurring in the open grassland.

3.7 TRIAL LAYOUT

3.7.1 Selection of experimental plots

At the onset of the study the concentration and diurnal activity of the four game species included in the study were intensively observed for a number of days. It was noted that they largely avoided the area close to the chalets and also the area close to the fence near the very busy and noisy N1 highway. They also avoided the wooded area covered by *A. karroo* as well as the rocky ridges and mainly concentrated in an open grassland area in the lower half of the fenced property (Figure 3.5). As a result, the three plains dwelling game species utilised only a small area of the total 78.8 ha of the fenced property. It was subsequently decided to select this area only for the study. This approach also suited the intensive nature of the planned survey and vegetation monitoring of the study, which would be impossible to apply on a lager area.

A relatively homogeneous area of 250 x 200 m (5 ha) in the middle of the open grassland area was subsequently selected for intensive study. With the aid of a black and white stereo photograph (scale 1:50 000), GPS (Geographical Positioning System) and tape measure the selected area was subdivided into twenty blocks of 50 x 50 m (0.25 ha). The corners of the blocks were marked with painted droppers in such a way that any block within the 5 x 4 grid pattern could be identified from a distance, using binoculars and the colour coding of the droppers. Each of the twenty blocks were allocated an identification code based on its position within the grid, e.g. A1, A2, A3, A4, B1, B2, etc. (Figure 3.5). The measurements and data collected within these blocks will be described in subsequent chapters.

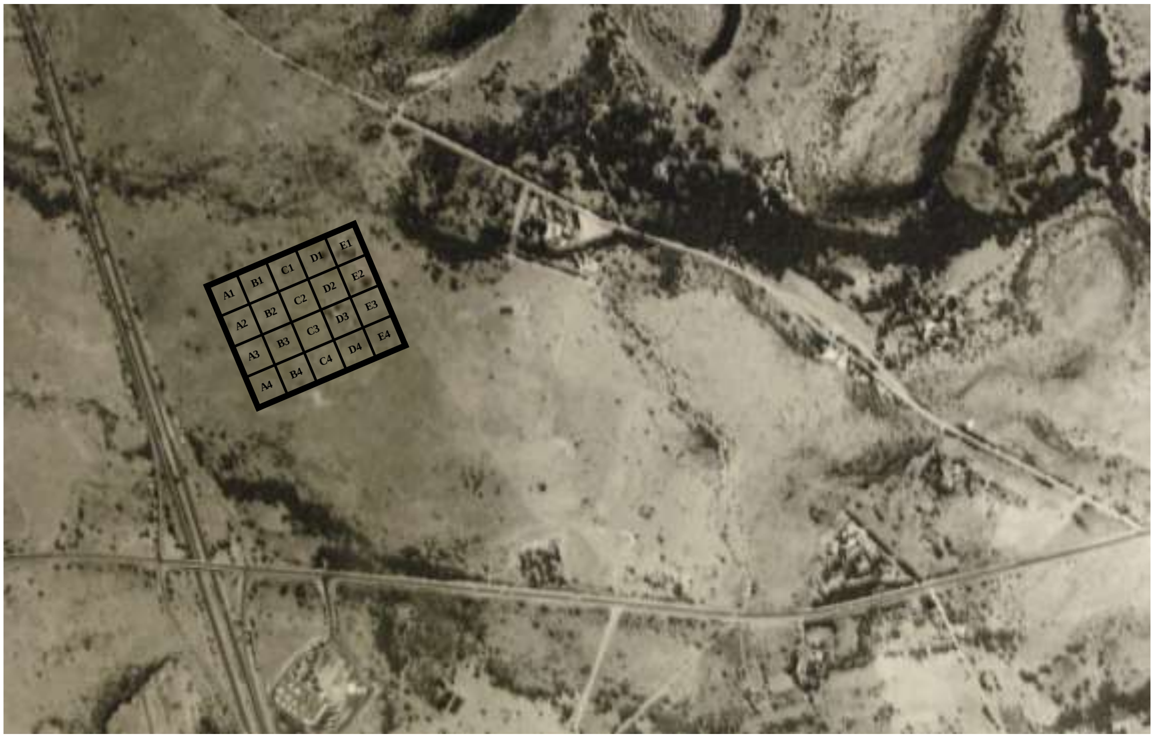

Figure 3.5: The position of the experimental plots in relation to the topographical units and vegetation.

3.8 TERMINOLOGY

The terminology used in this thesis is in accordance with Trollope *et al*. (1990), unless otherwise referenced or described.

CHAPTER 4

A PHYSICAL AND CHEMICAL CHARACTERISATION OF THE SOIL OF THE STUDY AREA

4.1 INTRODUCTION

The interactions between plant and soil processes in grassland ecosystems have received a great deal of attention (Wedin & Tilman 1990; Huenneke *et al*. 1990; Schlesinger *et al*. 1990; Elberse & Berendse 1993; Berendse 1994; Vinton & Burke 1995; Wedin 1995; Schlesinger *et al*. 1996, and many others). Many studies focus on the interaction between the botanical composition and soil organic matter and nutrient availability, and the influence of plant presence and absence on the accumulation of organic matter and nutrient availability under individual plants. Individual plant characteristic, such as life-span, biomass allocation, and tissue chemical composition have been shown to have significant effects on ecosystem processes such as soil organic matter and nutrient dynamics (Melillo *et al*. 1982; Pastor *et al*. 1984; Pastor & Post 1986; Vitousek *et al*. 1987; Berendse *et al*. 1989; Matson 1990; Binkley & Valentine 1991; Johnson & Damman 1991). In a study done by Burke *et al*. (1998) it was concluded that there is a strong interaction between plant community structure, plant diversity and soil attributes, and that the reverse influences of soil on plant communities are also strong. Nutrients, such as nitrates, phosphorus, a series of anions and cations, and various trace elements are essential to the nutrition of plants (Bell 1982), and act as determinants of the botanical composition, plant diversity, plant structure and productivity of the vegetation (Burke *et al*. 1998). Soil, therefore, plays a vital role in the determination of the vegetation, and consequently will have an influence on the habitat selection and feeding preferences of herbivores.

The objectives of this study were:

(i) to provide an accurate description of the soil properties of each experimental plot, and

(ii) to determine if small scale differences in the soil properties of these plots existed.

With the above mentioned objectives achieved the interaction between the soil and vegetation in the study area could be determined. This will be discussed in Chapter 8.

4.2 PROCEDURE

4.2.1 Soil sampling

Soil sampling was conducted at the end of the growing season (February 2005). During sampling, topsoil samples (to a depth of 150mm) were taken with an auger in each of the 20 experimental plots at five random locations per plot. Each set of 5 samples was bulked, thoroughly mixed and one subsample of approximately 1 kg taken for analysis. Before analysis, each soil subsample was oven dried for a period of one week to ensure that the soil was completely dry.

4.2.2 Soil analyses

Analyses conducted included texture (% silt, clay and sand), pH (H_2O) and pH (KCl), total nitrogen (N), organic carbon (C), phosphorus (P) (Bray I), exchangeable cations, *viz*. sodium (Na), potassium (K), magnesium (Mg) and calcium (Ca), zinc (Zn) content and the electrical resistance (Ω). The soil analyses were done in the soil chemistry laboratory of the Department of Soil, Crop and Climate Sciences of the University of the Free State, South Africa, according to the standards of the Non-affiliated Soil Analyses Work Committee (1990).

4.2.3 Data analyses

The CEC values for each experimental plot were calculated from the exchangeable cation contents. It was assumed that the CEC was a function of only the cation (Ca, K, Mg and Na) contents of the soil. The Al^{3+} and H^+ values also contributed to the CEC values, but they were not measured in this study. In order to convert the exchangeable cation values (mg kg^{-1}) to equivalent values ($cmol_c$ kg^{-1}), the values for calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) were divided by 200, 391, 122 and 230, respectively (Du Preez personal communication[*]). The ratios between the different cations were also determined and compared to the accepted "normal" values of soil (Fertilizer Handbook 2003). It is important to keep in mind that the "normal" values are only relative values and that small variations from these values may not be significant.

The Exchangeable Sodium Percentage (ESP) and Exchangeable Potassium Percentage (EPP) were calculated by using the following formulas:

$$ESP = \frac{Exchangeable\ Na}{CEC} \times 100$$

$$EPP = \frac{Exchangeable\ K}{CEC} \times 100$$

where CEC = Cation Exchange Capacity ($cmol_c$ kg^{-1})

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[*] Du Preez C.C., Department of Soil, Crop and Climate Sciences, P.O. Box 339, University of the Free State, Bloemfontein, 9300, South Africa.

In order to create a schematic representation of the relevant tested soil, four intervals were established for each soil variable. The minimum and maximum values were used for the first and last interval, and by using the formulas below the third (Y) and fourth (X) intervals were calculated. The third interval represented ⅓ of the difference between the maximum and minimum value and the fourth interval ⅔ of the difference.

$$Y = Min + \left(\frac{Max - Min}{3} \right)$$

$$X = Min + 2\left(\frac{Max - Min}{3} \right)$$

4.3 RESULTS

4.3.1 Soil texture

The results of the soil texture analysis are presented in Figure 4.1. A more detailed description is given in Appendix A_1 Table 1. Regardless of a high sand content in some plots, 90% of the plots also had a high clay content (more than 30% clay). Silt had a relatively low occurrence in all the plots. A schematic representation of the percentage of sand, silt and clay in the twenty plot grid is presented in Figure 4.2. By using a texture triangle a more detailed soil texture name was determined for each plot (Table 4.1). All the plots, except B1&2, C3, D4 and E1-4, had clay soil.

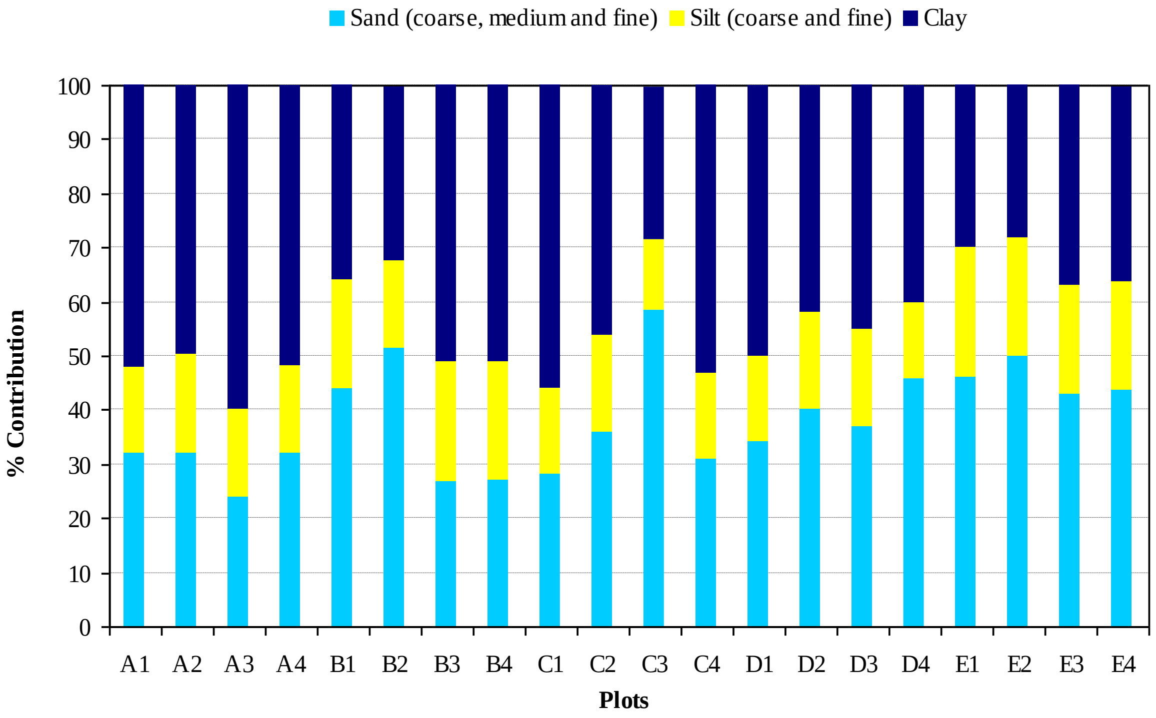


Figure 4.1: Percentage contribution of sand, silt and clay to topsoil samples taken in each experimental plot.

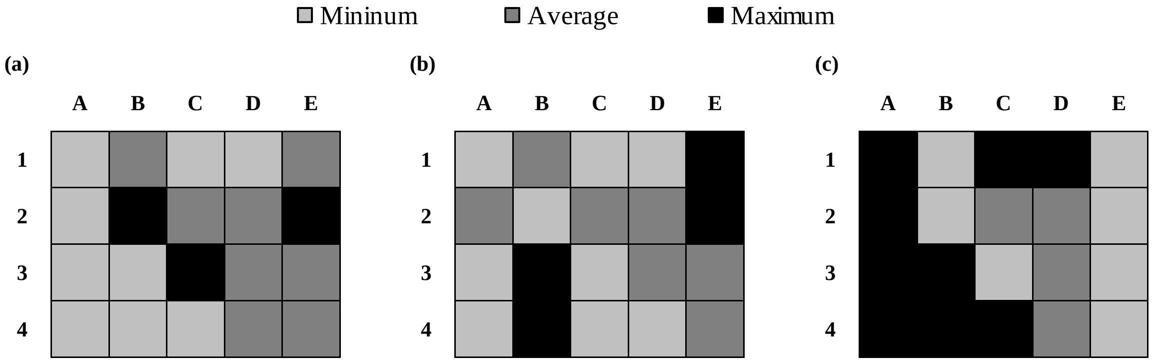


Figure 4.2: Schematic representation of the percentage of (**a**) sand (min = 24-36, ave = 36-47, max = 47-59), (**b**) silt (min = 14-17, ave = 17-21, max = 21-24) and (**c**) clay (min = 28-39, ave = 39-49, max = 49-60) in the twenty plot grid.

Table 4.1: Soil texture name of the soil of each experimental plot, according to the soil texture triangle (Miller & Gardiner 1998).

Plot	Soil textural name
A1	Clay
A2	Clay
A3	Clay
A4	Clay
B1	Clay loam
B2	Sandy clay loam
B3	Clay
B4	Clay
C1	Clay
C2	Clay
C3	Sandy clay loam
C4	Clay
D1	Clay
D2	Clay
D3	Clay
D4	Sandy clay
E1	Sandy clay loam
E2	Sandy clay loam
E3	Clay loam
E4	Clay loam

4.3.2 Soil pH

The pH (H_2O) and pH (KCl) values for each plot are presented in Figures 4.3 & 4.4, respectively. The differences in the pH (H_2O) values between the plots were marginal. All the plots, except E1-3, had a pH (H_2O) value near or above neutral (pH 7). The pH (KCl) followed a similar pattern than that of the pH (H_2O). The pH (KCl) values were more acidic and on average 1.5 pH units lower than the pH (H_2O) values. A schematic representation of the pH (H_2O) and pH (KCl) is presented in Figure 4.5.

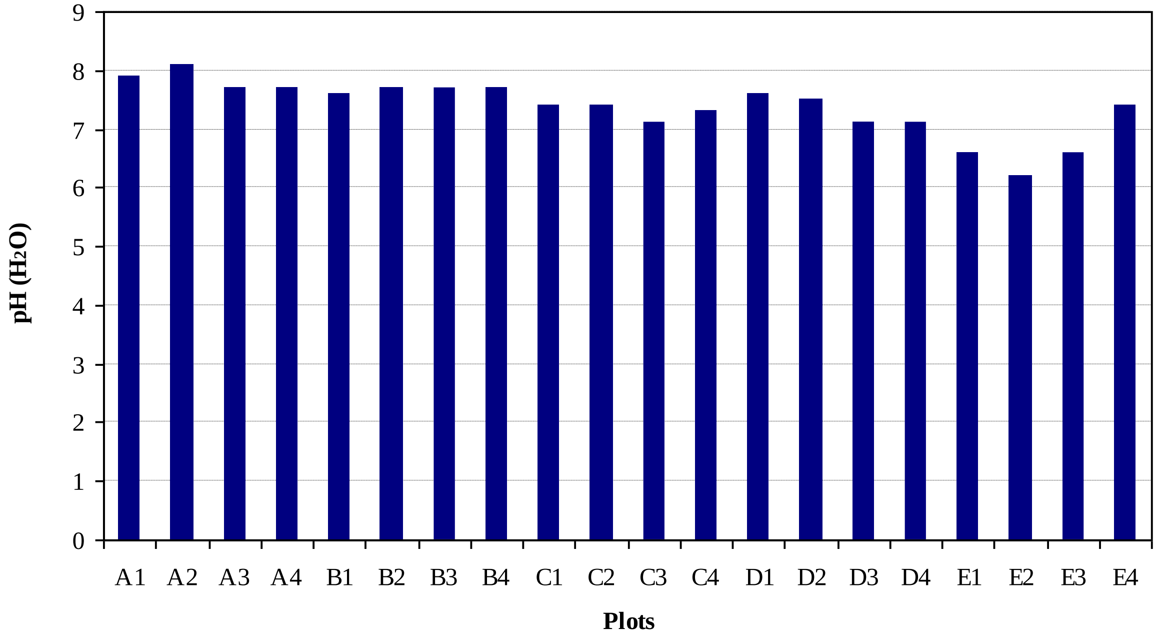


Figure 4.3: The pH (H_2O) of topsoil samples taken in each experimental plot.

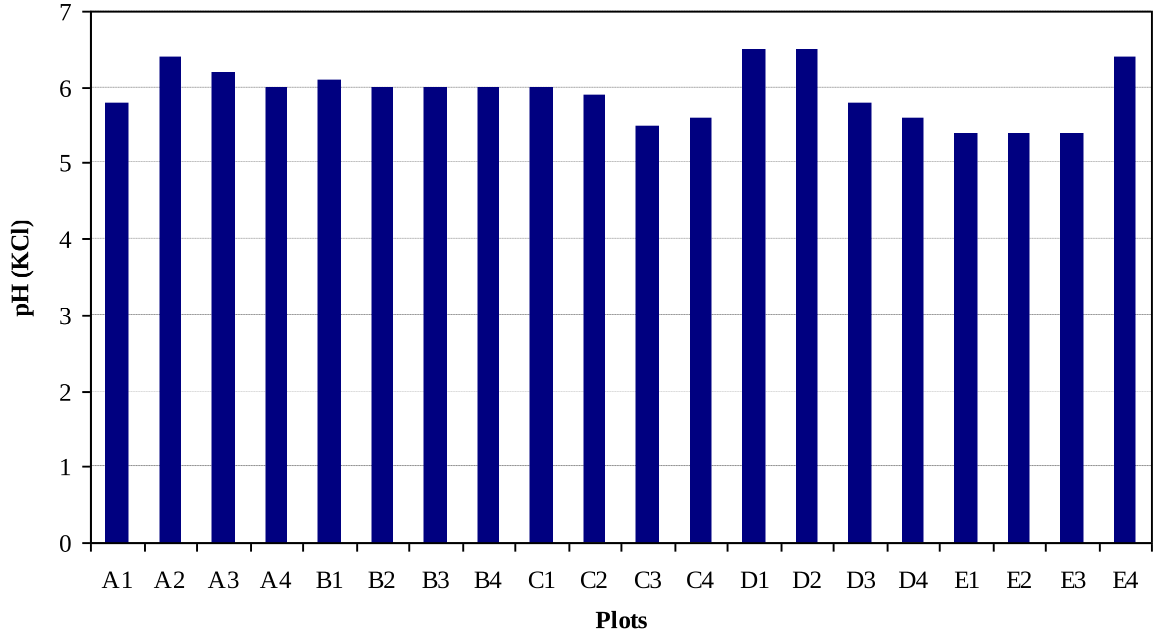
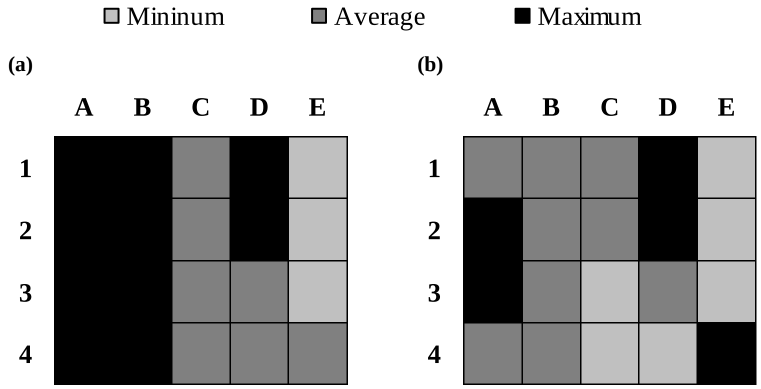


Figure 4.4: The pH (KCl) of topsoil samples taken in each experimental plot.



░ Mininum ▓ Average ■ Maximum

(a)

	A	B	C	D	E
1	■	■	▓	■	░
2	■	■	▓	■	░
3	■	■	▓	▓	░
4	■	■	▓	▓	▓

(b)

	A	B	C	D	E
1	▓	▓	▓	■	░
2	■	▓	▓	■	░
3	■	▓	░	▓	░
4	▓	▓	░	░	■

Figure 4.5: Schematic representation of the (**a**) pH (H_2O) (min = 6.2-6.8, ave = 6.8-7.5, max = 7.5-8.1) and (**b**) pH (KCl) (min = 5.4-5.8, ave = 5.8-6.1, max = 6.1-6.5) values in the twenty plot grid.

4.3.3 Nitrogen (N), Organic Carbon (C) and Carbon : Nitrogen ratio

The total N and organic C values are presented in Figures 4.6 & 4.7. It is clear from Figures 4.6 and 4.7 that the total N and organic C contents were the highest in plots E2&3 and E1&2, respectively, and the lowest in plot A4. Organic C and total N, to a lesser extent, showed a general increase in plots on the southern side. With the exception of plots A4, B2&4, the organic C contents did not show extreme variations between the plots. A schematic representation of the total N and organic C proportions is presented in Figure 4.8. The C:N ratio varied between 3.27:1 in plot E3 and 7.46:1 in plot B3 (Table 4.2). Row E and plot D2 had the narrowest ratios. The C:N ratio was relatively narrow in all twenty plots. Plots A3 and B3 had a ratio closest to that of soil organic matter (1:10).

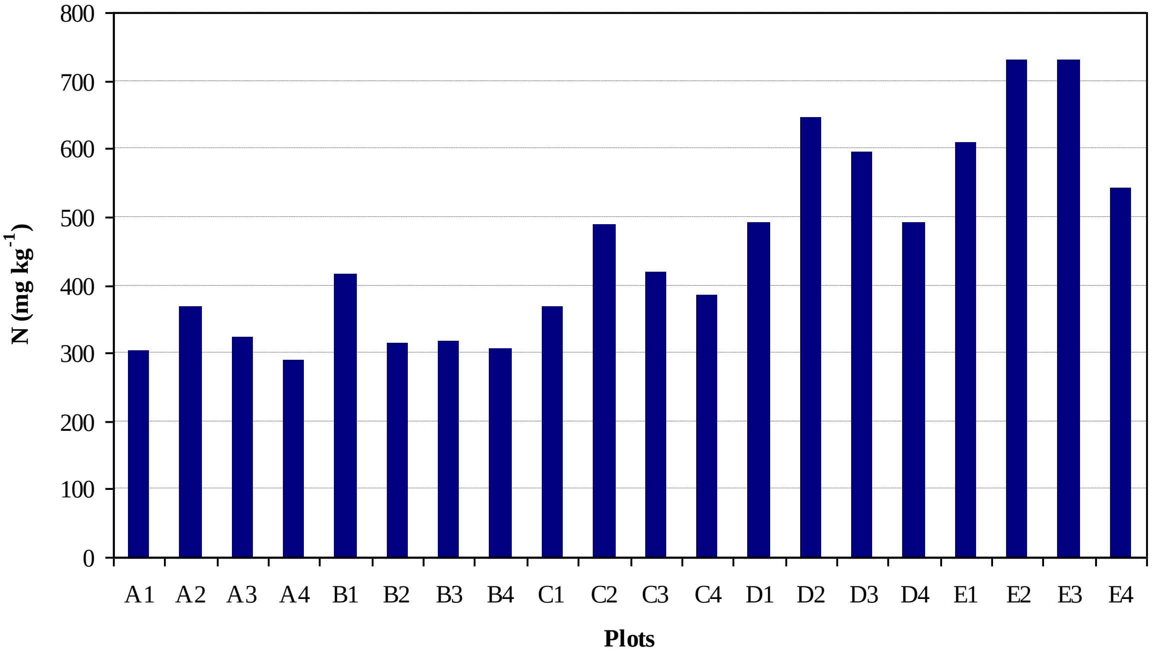


Figure 4.6: Total nitrogen (N) content of topsoil samples taken in each experimental plot.

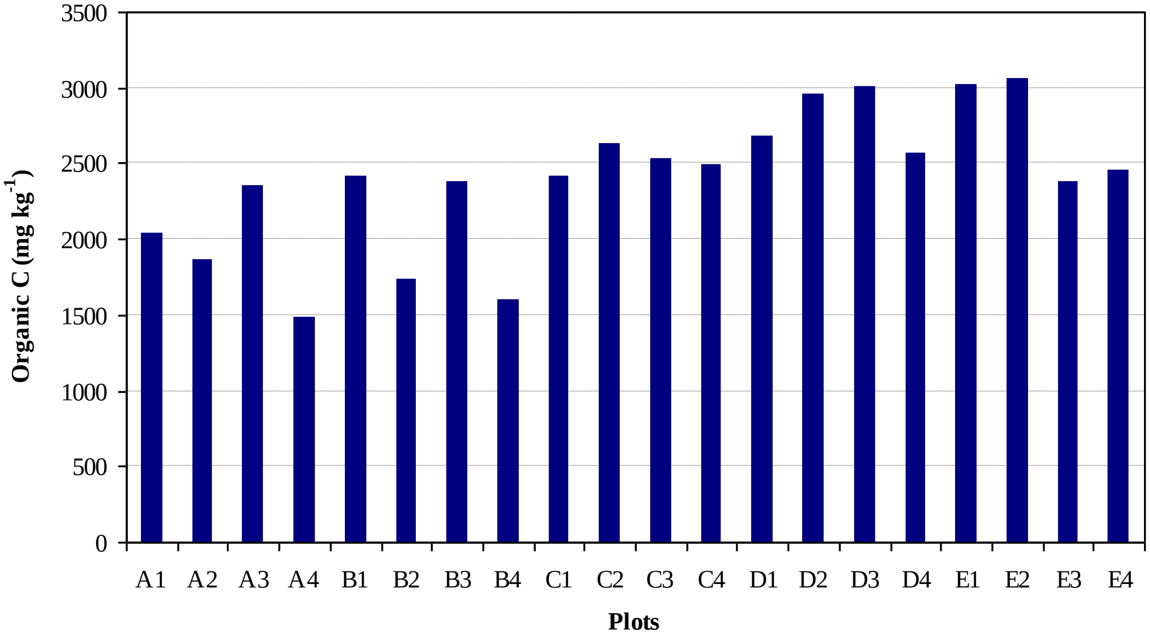


Figure 4.7: Organic carbon (C) content of topsoil samples taken in each experimental plot.

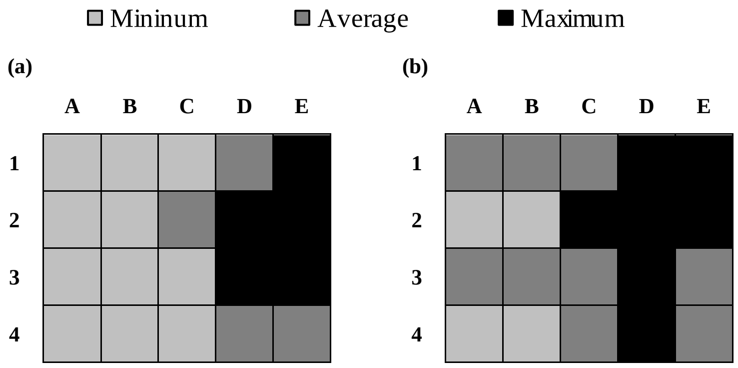


Figure 4.8: Schematic representation of the proportion (mg kg^{-1}) of (**a**) total nitrogen (N) (min = 289-436, ave = 436-583, max = 583-730) and (**b**) organic carbon (C) (min = 1 485-2 010, ave = 2 010-2 535, max = 2 535-3 060) within the twenty plot grid.

Table 4.2: Organic carbon (C) and total percentage nitrogen (N) ratio (C:N) of topsoil samples taken in each experimental plot.

Plot	C:N ratio
A1	6.75:1
A2	5.07:1
A3	7.31:1
A4	5.14:1
B1	5.82:1
B2	5.54:1
B3	7.46:1
B4	5.21:1
C1	6.57:1
C2	5.37:1
C3	6.06:1
C4	6.45:1
D1	5.46:1
D2	4.60:1
D3	5.04:1
D4	5.23:1
E1	4.97:1
E2	4.19:1
E3	3.27:1
E4	4.55:1

4.3.4 Phosphorus (P)

Phosphorus content varied greatly between the plots (Figure 4.9). Plot C2, followed by B1 and C3, had the highest P contents (≥ 30 mg kg^{-1}). The P contents of plots A4, B2, D1, D3 and E3 were above 15 mg kg^{-1} and that of plot E4 less than 5 mg kg^{-1}, representing the lowest value. A schematic representation of the proportion of P within the twenty plot grid is presented in Figure 4.10.

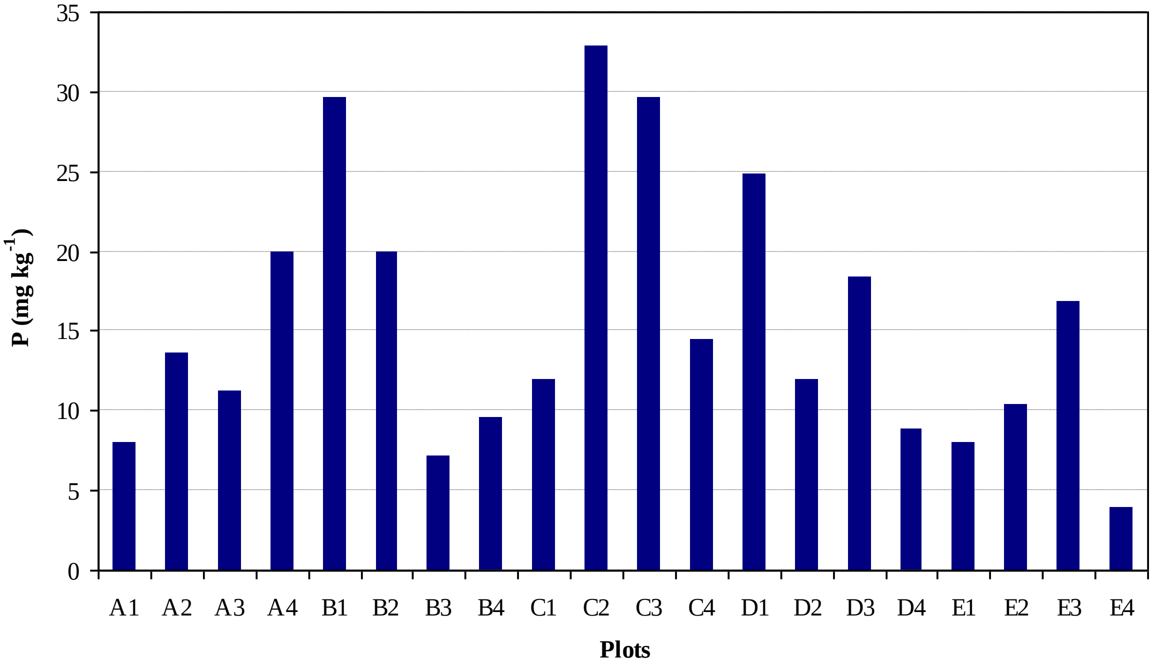
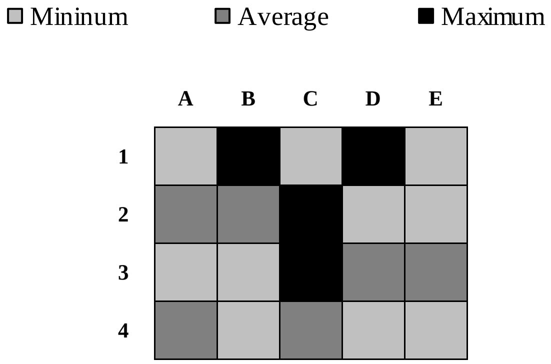


Figure 4.9: Total phosphorus (P) content of topsoil samples taken in each experimental plot.



░ Mininum ▒ Average █ Maximum

	A	B	C	D	E
1	░	█	░	█	░
2	▒	▒	█	░	░
3	░	░	█	▒	▒
4	▒	░	▒	░	░

Figure 4.10: Schematic representation of the proportion phosphorus (P) (mg kg^{-1}) (min = 4-14, ave = 14-23, max = 23-33) within the twenty plot grid.

4.3.5 Cation Concentrations

4.3.5.1 Calcium (Ca)

The Ca contents were, except for plots C2 and D3, the highest of all the cations tested (Figure 4.11). The variation in the Ca contents between the plots was relatively large. The Ca contents of plots A3&4, B4 and D1 were much higher than in the other plots (Figure 4.11). The lowest Ca contents were found in plots B1&2, C3 and E1. A schematic representation of the Ca content is presented in Figure 4.12.

4.3.5.2 Potassium (K)

With the exception of plots B1&2, C3, D4 and E1, all the plots had a K content of above 350 mg kg^{-1} (Figure 4.11). Plot B1 had the lowest K content (230 mg kg^{-1}). A schematic representation of the K content is presented in Figure 4.12.

4.3.5.3 Magnesium (Mg)

Magnesium was the cation with the second highest concentration. It is evident from Figure 4.11 that the Mg contents were lower in plots B1&2, C3 and E1-4 compared to the other plots, which had Mg contents of higher than 1 800 mg kg^{-1}. A schematic representation of the Mg content is presented in Figure 4.12.

4.3.5.4 Sodium (Na)

The Na contents were the lowest in plots on the southern side (row C to E) (Figure 4.11). The differences in the Na contents between these plots were not considerable. Plot B2, followed by B1, had the highest Na contents. A schematic representation of the Na content is presented in Figure 4.12.

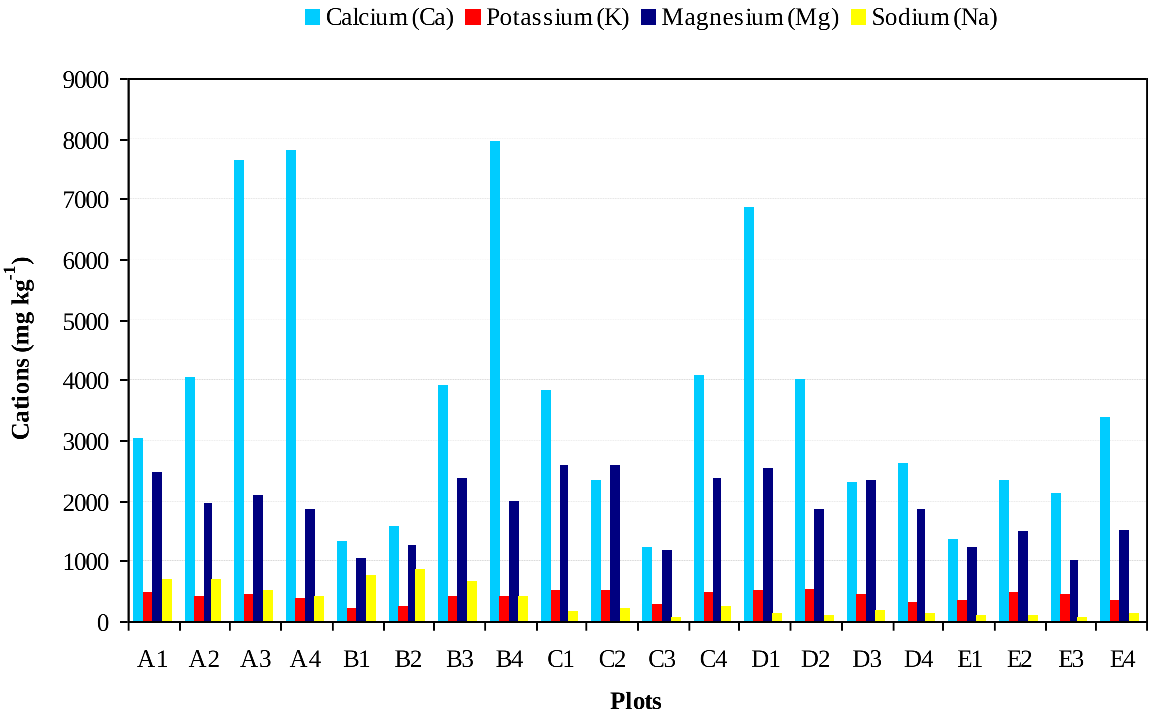


Figure 4.11: Exchangeable cation contents of topsoil samples taken in each experimental plot.

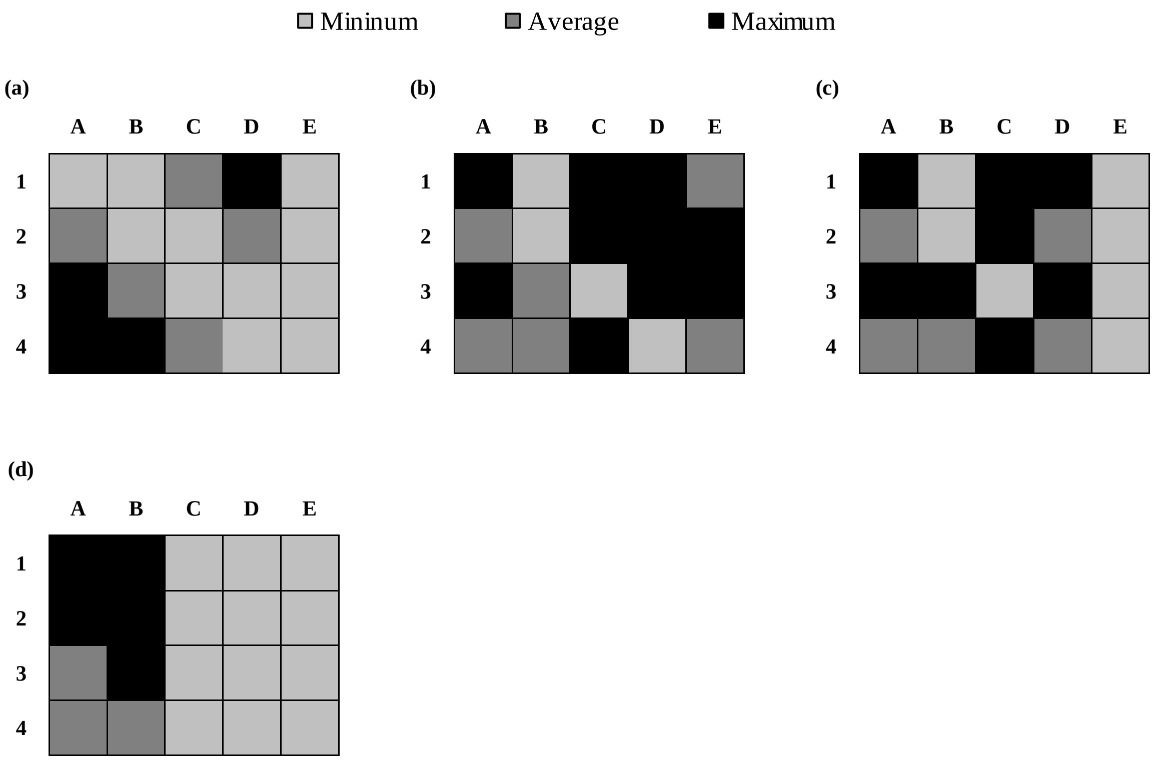


Figure 4.12: Schematic representation of the proportion (mg kg^{-1}) of (**a**) calcium (Ca) (min = 1 218-3 462, ave = 3 462-5 706, max = 5 706-7 950), (**b**) potassium (K) (min = 230-329, ave = 329-428, max = 428-528), (**c**) magnesium (Mg) (min = 1 025-1 550, ave = 1 550-2 075, max = 2 075-2 600) and (**d**) sodium (Na) (min = 68-327, ave = 327-586, max = 586-845) within the twenty plot grid.

4.3.6 Cation ratios

The cation ratios, calculated from the equivalent values, are presented in Table 4.3. When the values of the Ca and Mg ratio were compared to the normal values (Table 4.3) expected for this cation ratio (Fertilizer Handbook 2003), it was found that all the plots, except A3&4, B4 and D1, had values lower than normal. The Mg and K ratios were much higher than the normal range in all the plots. When values of the (Ca + Mg)/K ratio were compared to the normal range, it was evident that all the plots, except E1-3, again had ratios higher than the normal. The ordinary cation ratio (Ca:Mg:K:Na) of the different plots differed considerably from the normal expected ratio (Table 4.3).

4.3.7 Cation Exchange Capacity (CEC), Exchangeable Sodium Percentage (ESP) and Exchangeable Potassium Percentage (EPP)

The CEC, ESP and EPP of each plot are given in Table 4.3. It is clear that the CEC values of plots A3&4, B4 and D1 were the highest and those of plots B1, C3 and E1 the lowest. The ESP values of all the plots, except B1&2, were well below the level at which dispersion will normally occur, and consequently had sodic soil. When the EPP values were compared to the expected normal values, it was found that plots A1, B1, C2&3, D2&3 and E1-3 had values within the normal range. Plots A2, B2, C1&4, D4 and E4 were only 0.5% less than the normal range, and plots A3&4 and B4 had much higher values than the normal range.

Table 4.3: Summary of the tested cation ratios (values were calculated from the equivalent values cmol$_c$ kg^{-1}). * indicates the range of normal expected values according to the Fertilizer Handbook (F.S.S.A. 2003).

Plots	**CEC (cmol$_c$ kg^{-1})**	**Ca ÷ Mg 1.5 – 4.5***	**Mg ÷ K 3 – 4***	**(Ca + Mg) ÷ K 10 – 20***	**Ca:Mg:K:Na 65:25:8:2***	**EPP (%) 3 – 7***	**ESP(%)**
A1	39.7	0.8	16.2	28.4	38:51:3:7	3.1	7.5
A2	40.3	1.3	15.7	35.6	50:40:6:8	2.5	7.6
A3	58.5	2.3	15.3	49.8	65:29:2:4	1.9	3.6
A4	57.2	2.5	15.5	54.9	68:27:2:3	1.7	3.1
B1	19.1	0.8	14.6	25.9	34:45:3:16	3.1	16.9
B2	22.5	0.8	15.8	28.0	35:46:3:16	2.9	16.3
B3	43.1	1.0	18.5	37.2	46:45:2:7	2.4	6.8
B4	58.8	2.5	15.6	53.8	68:28:2:3	1.8	3.1
C1	42.5	0.9	17.1	32.4	45:50:3:2	2.9	1.8
C2	35.3	0.6	16.1	25.0	33:60:4:3	3.7	2.8
C3	17.8	0.7	12.8	22.3	40:54:4:2	4.2	1.6
C4	42.2	1.1	15.8	32.4	48:46:3:3	2.9	2.7
D1	56.7	1.7	16.3	43.3	60:36:2:1	2.2	0.9
D2	37.0	1.3	11.2	26.1	54:41:4:1	3.6	1.2
D3	32.5	0.6	16.4	26.3	35:59:4:2	3.6	2.4
D4	29.9	0.9	19.0	35.2	44:51:3:2	2.7	1.8
E1	18.1	0.7	11.7	19.6	37:55:5:2	4.7	2.4
E2	25.4	1.0	10.3	20.2	46:48:5:6	4.6	1.6
E3	20.4	1.3	7.4	16.7	52:41:6:1	5.6	1.4
E4	30.9	1.4	13.7	32.4	55:40:3:2	2.9	1.7

*CEC normal range

Sands (1 – 5), Fine sandy loams (5 -10), Loams and silt loams (5 – 15), Clay loams (15 – 30), Clays (> 30)

4.3.8 Zinc (Zn)

The Zn contents generally increased in plots on the southern side (Figure 4.13). Plot E2 had the highest Zn content followed by D1&2 and E1. Plot A4 had the lowest Zn content. A schematic representation of the proportion Zn within the twenty plot grid is presented in Figure 4.14.

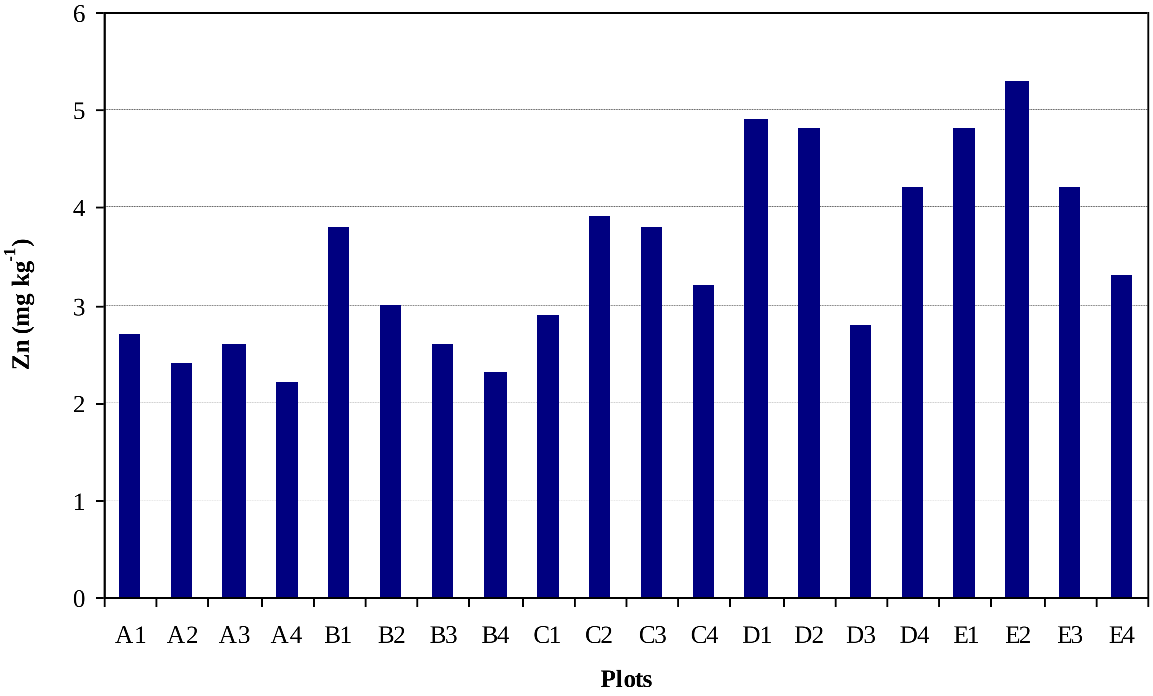
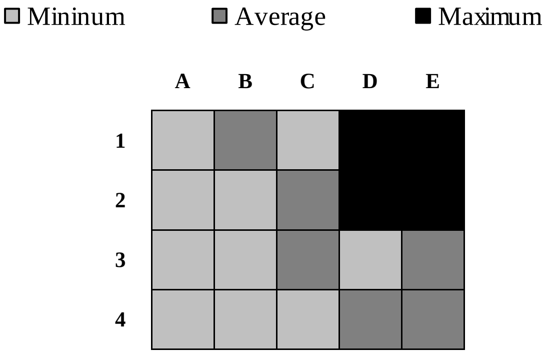


Figure 4.13: The Zinc (Zn) content of topsoil samples taken in each experimental plot.



	A	B	C	D	E
1	□	▨	□	■	■
2	□	□	▨	■	■
3	□	□	▨	□	▨
4	□	□	□	▨	▨

Figure 4.14: Schematic representation of the proportion zinc (Zn) (mg kg^{-1}) (min = 2.2-3.2, ave = 3.2-4.3, max = 4.3-5.3) within the twenty plot grid.

4.3.9 Electrical resistance

There was a larger variation in electrical resistance in plots on the southern side (Figure 4.15). Plot C3 had a much higher electrical resistance than the other plots. The electrical resistance of all the plots was relatively low. A schematic representation of the electrical resistance of the twenty plot grid is presented in Figure 4.16.

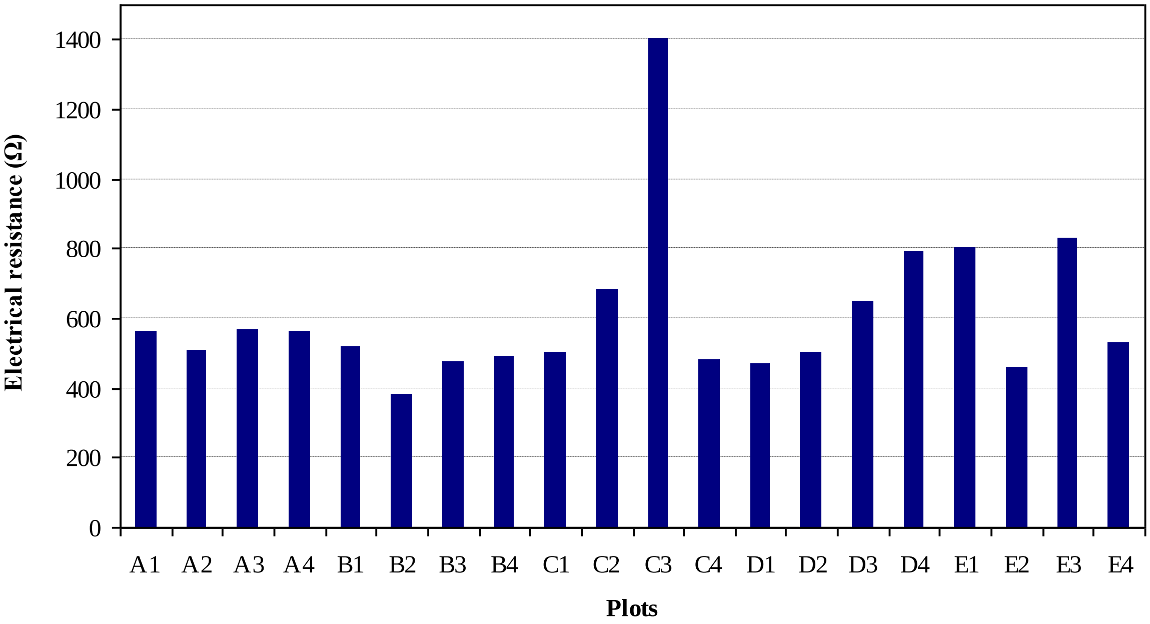


Figure 4.15: Electrical resistance of topsoil samples taken in each experimental plot.

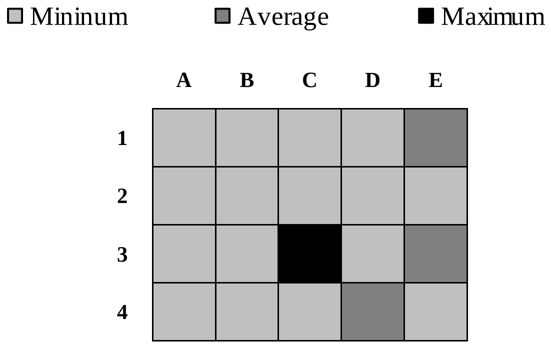


Figure 4.16: Schematic representation of the electrical resistance (Ω) (min = 380-728, ave = 728-1 060, max 1 060-1 400) within the twenty plot grid.

4.4 DISCUSSION

4.4.1 Soil texture

Natural soils are composed of soil particles of varying sizes. The soil particle-size groups, called soil separates, are sands (the largest), silts, and clays (the smallest). The relative weight percentage of soil separates in a particular soil determines the soil texture. Texture is an important soil characteristic because it greatly affects permeability and infiltration, water storage (available water holding capacity), the ease of tillage, the amount of aeration and soil fertility (Buckman & Brady 1967; Miller & Donahue 1995; Miller & Gardiner 1998). Sandy soils are easy to till, have plenty of aeration and are easily wetted, but dry rapidly and lose plant nutrients easily through leaching. High-clay soils (more than 30% clay) have very small particles that fit closely together with few large pores. This makes them difficult to wet, drain and till (Miller & Gardiner 1998).

In the study area 90% of the plots had a clay content of 30% and higher. A soil that does not exhibit the dominant physical properties of sand, silt or clay is called loam. Subsequently 60% of the plots had clay soil, 15% clay loam soil, 20% sandy clay loam and 5% sandy clay soil (Table 4.1). The texture of the topsoil from the plots was generally similar, indicating that the soils are not derived from different parent materials

(Le Roux personal communication[†]). The variation in the soil texture of the plots can play a role in determining which plant species will grow in a certain plot (as will be discussed in Chapter 8).

4.4.2 Soil pH

Soil reaction (pH) is an indication of the acidity or alkalinity, which is caused by a particular chemical, mineralogical and/or biological environment, of the soil, and is measured in pH units (Foth & Ellis 1997; Miller & Gardiner 1998). The degree of acidity or alkalinity is determined by the hydrogen ion (H^+) concentration in the soil solution (Tan 1994). The most universal effect of pH on plant growth is nutritional. The soil pH influences the rate of plant nutrient release by weathering, the solubility of all materials in the soil and the amounts of nutrient ions stored on the cation exchange sites (Foth & Ellis 1997).

The pH of the soil of the study area was determined in potassium chloride (KCl) and water (H_2O). The soluble salt content of soil can affect the pH value and this was overcome by using a salt solution (KCl) instead of distilled water. The pH (H_2O) refers to the acidity of the soil solution and the pH (KCl) refers to the acidity of the soil solution plus the reserve acidity in the colloids. The pH (KCl) values are especially important when determining if the alkali or acid contents of the soil must be altered to balance the soil pH in order to improve plant growth and production. These values are of greater value to agriculture, especially when crop planting is involved (Miller *et al*. 1990). Unless stated otherwise the pH usually refers to the pH (H_2O).

The pH (KCl) is more acidic (1 - 2 pH units lower) than pH (H_2O) (Figures 4.3 & 4.4), but both are neutral at 7. This was found in the soil of all the plots, which indicates that

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microbial decomposition is taking place in the soil. The soil pH can influence plant growth through the effect on the activity of beneficial micro-organisms (Miller & Gardiner 1998). Most nitrogen-fixing bacteria are not very active in strongly acidic soil. Bacteria that decompose the organic matter of soil are also hindered by strong acidity. Fungi, however, usually tolerate strong acidity better than other micro-organisms (Miller & Gardiner 1998).

When the soil solution has a pH below 5.5, it means that the amount of active hydrogen ions (H^+) is too high, which causes soil to be overly acidic and to have a negative effect on root growth (Miller *et al*. 1990). In the study area none of the plots had a pH below 5.5 (Figures 4.3 & 4.5a). The lowest pH was 6.2, which indicated a slightly acidic soil. By using the pH ranges described by Foth & Ellis (1997), it was found that 65% of the plots had an alkaline (7.4 – 8.5), 30% a neutral (6.6 - 7.3) and 5% a slightly acidic (6.1 - 6.5) soil. According to Miller *et al*. (1990), plants normally grow well between a pH of about 5 and 8.5. A high soil alkalinity, although more difficult to alter than soil acidity, may be just as undesirable for plants. Plants on soil of pH greater than 9 usually have reduced growth, or may even suffer mortality. In excessively alkaline soils, common in arid regions, many of the nutrient metals such as Fe, Zn and Mn will form insoluble carbonate and hydroxide compounds, and so will be unavailable to plants (Miller *et al*. 1990). None of the plots, however, had a pH greater than 8.1 (Figure 4.3).

Soil pH can be influenced by, among others, the season of the year, soil management practices, sludge and manure applications, soil organic matter, biological activity and buffering capacity (Smith & Doran 1996). Vegetation influences soil pH in complex ways because it produces organic matter and influences leaching. The addition of decomposable organic matter to soil results in the formation of organic acids (Troeh & Thompson 1993). According to Troeh & Thompson (1993), these acids add to the CEC, but the percentage base saturation and pH are lowered. They further stated that soil under grass is usually less acidic, since grasses produce new growth each year, utilising more bases and therefore depositing more bases on the soil surface. Grasses thus help to keep the soil from becoming strongly acidic. Since the pH did not differ much between the plots, no apparent influence of the herbaceous species composition on the soil pH could be detected.

4.4.3 Nitrogen (N), Organic Carbon (C) and Carbon : Nitrogen ratio

Nitrogen is a part of all living cells and is the most critical element in plant growth (Foth & Ellis 1997). It is a constituent of all proteins including enzymes, chlorophyll, nucleic acids and other plant substances (Miller & Gardiner 1998). Sufficient N produces thinner cell walls resulting in more tender and succulent forage plants. A deficiency of N causes plants to grow poorly, spindly and stunted. Cilliers *et al*. (1997) found that N fertilization resulted in veld herbage with a higher nutritive value. It would, therefore, be expected that more grazing time will be spent in the plots on the southern side were the N contents were higher (Figures 4.6 & 4.8a). According to Snyman (1999), grazing intensity influences both the organic matter and nitrogen content of soils. Mills & Fey (2002) showed that the removal of dense matrix of succulent shrubs in the Eastern Cape by goats resulted in a decline of soil carbon from 5.6% to 3% in the 0 – 10 cm layer. Plant species composition, therefore, indirectly affects nutrient contents in soil. Augustine (2003) studied the effect of livestock on the distribution and availability of soil nutrients, and found that large quantities of nutrients are concentrated into small areas, potentially altering the landscape distribution of N in soils and plants. Since the study area was previously used for grazing by cattle this could have had an influence on the N content distribution. Vinton & Burke (1995) found that soils under plants had consistently higher C and N mineralization rates and, in some cases, higher total and microbial C and N levels than soils without plant cover. They further found that plant cover patterns had larger effects on ecosystem scale estimates of soil properties than the attributes of a particular plant species. Snyman (1997) concluded on a study done in the Free State that N was more limiting during years of above average rainfall. This is because much of the N is lost through leaching. However, due to the high clay content in the soil of the study area (see section 4.4.1) N loss due to leaching is unlikely.

Soil quality has been typically associated with soil organic matter or its associated indicator elements, C and N. Soil organic matter is a source of plant nutrients in soils and is important in maintaining soil tilth, aiding infiltration of air and water, promoting water retention and reducing erosion (Gregorich *et al*. 1993). Organic matter is also involved in adsorption of cations, such as calcium, magnesium and sodium, which are important in plant nutrition, and can influence the soil water holding capacity. The organic matter content of soils in semi-arid rangeland areas of southern Africa is normally below 2.5% (Snyman 1999). In a broad sense it consists of diverse components such as living micro-organisms, slightly altered plant and animal organic residues, and well decomposed organic residues that vary considerably in their stability and susceptibility to further decomposition (Magdoff 1992).

The level of organic matter in the soil is a broad indicator of soil condition, and its concentration in the soil is largely determined by the addition of surface litter (fallen leaves, manure and dead organisms) and root material, as well as the rate at which micro-organisms break down organic compounds. Soil texture and soil environmental conditions affect soil organic matter decomposition rates (Sikora & Stott 1996). Roots are the most important source of organic matter in grassland ecosystems (Foth & Ellis 1997). The C is supplied largely, but not exclusively, by dying root material, but in the absence of adequate N it may be rapidly lost from the soil (Snyman 1999). This is essential for plant growth, due to its effects on other soil properties. The preponderance of roots and the concentration of soluble salts in the subsoils may also have an influence on the organic C content (Anderson & Talbot 1965). Organic C makes up approximately 58% of soil organic matter by weight (Sikora & Stott 1996).

According to Snyman (1999) there is a complex interaction between grazing and the organic matter content of the soil. The most important factors that can contribute to a change in organic matter content, with or without grazing, include: (i) veld condition, as organic matter content decreases considerably with veld degradation (Du Preez &

Snyman 1993); (ii) environmental factors like soil water and soil temperature (Snyman 1997); (iii) soil cultivation (Du Toit *et al*. 1994; Mills & Fey 2003); (iv) increased aridity (Le Houérou 1984) and (v) the grazing history of the veld, i.e. intensity and frequency of grazing (Dormaar *et al*. 1990; Manley *et al*. 1995; Lavado *et al*. 1996), type of animals (McNaughton *et al*. 1988) and fire (Mills & Fey 2003).

The tendency of a higher organic C content in the soil of the plots on the southern side of the grid (Figures 4.7 & 4.8b) can be attributed to various factors such as previously mentioned. According to Snyman (1999), grazing intensity influences both the organic C and N content of soils, but results have generally been inconsistent in other studies. The low occurrence of organic C in the plots on the northern side might be due to low levels of soil organic matter. However, the transformation of organic soil material is a slow process and the changes in C found in the plots are most likely the result of processes that took place long before the study was conducted. Spain (1990) and Feller *et al*. (1991) also found significant positive correlations between soil textures and soil organic C content. The soil texture could, however, not have had a strong influence in such a small area since other plots with the same soil texture had a higher organic C content. Monitoring levels of soil organic C provides good measure of the impact of land management on soil health. Exploitative, environmentally damaging land management practices tend to reduce soil C levels. The level of organic matter in the soil is thus affected by land management history, however, climate, drainage, soil type and landform also influence the level of soil C. Further investigation is required to obtain more precise explanatory reasons.

An important factor influencing plant growth is the ratio of organic carbon:total nitrogen (Miller & Gardiner 1998). The C:N ratio of the substrate provides an indication of the adequacy of N for the mineralizers and the amount of N that will appear as an excess, which accumulates and can be used by roots (Foth & Ellis 1997). Humus or soil organic matter has a C:N ratio of approximately 10:1 (Sikora & Stott 1996; Foth & Ellis 1997). A wide C:N ratio indicates a material relatively low in N content. According to Sikora &

Stott (1996) higher ratios may indicate recent additions of manure or plant residues. It would, therefore, be expected that the plots with a high level of occupation will have a higher ratio. The values found in all the plots indicate that the soil has sufficient N to supply the decomposing microorganisms, and also to release nitrogen for plant use (Table 4.2). The differences between the plots were relatively small. The narrow ratio found in row E and plot D2 indicates that these plots had the most N for C, which might be due to the higher presence of bacteria and fungi in the soil. When these micro-organisms die, their bodies, which have a high N content, are decomposed by other living micro-organisms, breaking down C and releasing CO_2 to the atmosphere and some N to the soil (Miller & Gardiner 1998).

4.4.4 Phosphorus

Phosphorus is the second most critical and most limiting plant nutrient and is classified as a macronutrient because of the relatively large amounts of P required by plants (Foth & Ellis 1997; Miller & Gardiner 1998). The nucleus of each plant cell contains P, so cell division and growth are dependent upon adequate amounts of this element. Organic compounds that contain P are used to transfer energy from one chemical reaction to drive another reaction within cells. Phosphorus nutrition is especially critical because the total supply of P in most soils is low and the P is not readily accessible for plant use. Much of the P used by plants is believed to come from organic phosphates released by decomposition of organic matter (Miller & Gardiner 1998).

The P content varied extremely between the plots from as low as 4 mg kg^{-1} to as high as 33 mg kg^{-1} (Figures 4.9 & 4.10). This variation could be due to inherent soil differences between the plots. Soil P is fixed, or made less available by the formation of less soluble phosphates or iron aluminium (from clays) and Ca. At a soil pH below 5.5 (acidic), both iron and aluminium will fix P. At a pH above 7.0 (alkaline), Ca will fix P. Maximum P availability is at a pH of 5.5 for organic soil (Miller *et al*. 1990). The variation in the pH values of the plots was marginal, and plots with a less suitable pH had a higher P content than plots with a more appropriate pH. The variations in the P contents can therefore not entirely be explained in terms of the pH. The higher P contents in plots B1, C2&3 and D1 can possibly be attributed to manure deposits, especially in plot B1 (pers. obs.). According to Withers *et al*. (2001), manure increases the P content of soil. Augustine (2003) and Tolsma *et al*. (1987) found that the soil in areas where cattle gathered, was significantly nutrient enriched in comparison to surrounding areas. This is due to the significant quantities of plant nutrients in manure. According to Augustine (2003) these areas have persisted as nutrient-enriched patches for at least four decades. The centripetal dung transport may therefore diminish the P content of topsoil in the areas where the animals forage, increasing concentrations elsewhere. Tolsma *et al*. (1987) further states that trampling and the hoof activity of the animals will also contribute to the movement of P. This relative change in distribution of soil nutrients is of significance for plant growth. The resultant P contents of the plots are thus most likely due to land use prior to its conversion to a game lodge.

4.4.5 Exchangeable cation concentrations

Cations are positively charged ions. Soil colloids have various surface locations that have negative charges. The cations are absorbed at these negatively charged sites by electrostatic attraction (positive to negative). The absorbed cations resist removal by leaching water but can be replaced by other cations in solution by mass action (competition for the negative site because of the large number of ions present). This exchange of one positive ion by another is called cation exchange (Miller & Gardiner 1998).

Cations perform many important functions, but are especially important to vegetation growth because plants absorb nutrients from the soil mostly in the form of ions. Calcium (Ca), magnesium (Mg), sulphur (S) and chlorine (Cl), along with nitrogen (N), phosphorus (P), potassium (K) and sodium (Na), are the eight most-abundant elements taken up by plants from soils (Foth & Ellis 1997). Calcium, Mg, K and Na are taken up as cations and N, P, S and Cl are taken up as anions, except for the uptake of some N as NH_4^+. Calcium, Mg, S, and Cl are generally taken up in lesser amounts than N, P, and K, but in much greater amounts than the micronutrients (Foth & Ellis 1997).

Calcium plays an important role in plant nutrition. It tends to make plant cells more selective in their absorption and is a constituent of the middle lamella of each cell wall (Miller *et al*. 1990). Calcium deficiency shows first as a reduction in the growth of meristematic tissues, such as the growing tips and youngest leaves. Variations in Ca content of different soil types can be great, because many Ca minerals are fairly soluble. Calcium normally dominates the cation exchange capacity because of the large amounts of Ca that are found in soil solution (Le Roux personal communication[‡]). The large variations in the Ca contents of the different plots can, however, not be explained entirely in terms of the soil types, since variations also occurred within plots with the same soil type. Calcium minerals are so abundant that they are seldom deficient, except in sandy soil (which contains none or only a few Ca minerals) and in strongly acidic mineral soil (Foth & Ellis 1997), which has usually resulted from prior leaching of Ca minerals. It was also clear from this trial that the Ca content declined in plots with a higher percentage contribution of sand. It was generally higher in plots where clay contributed 50% or more to the soil texture. Soil tests for Ca content have shown that extractable levels increase with clay content and also increase as the soil drainage changes from well drained to poorly drained (Foth & Ellis 1997). Texture and leaching therefore plays an important role in the Ca content in soil. Since the differences in the pH were so small between the plots, it could not have had a big influence on the Ca contents of the plots.

Potassium plays a role in water relationships and osmotic pressure in cells (Cihacek *et al*. 1996). A deficiency in K appears on the oldest leaves as a chlorotic marginal firing. In

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advanced stages, the entire leaf turns yellow and is necrotic. The deficiency symptoms are mostly yellowing and eventually the death of cells near leaf margins. Potassium is needed in large amounts and is closely related to N nutrition (Kayser & Isselstein 2005). The amount of available K in unfertilized soils depends on the amount and kinds of K minerals that were in the parent material and the kinds and degree of changes during soil genesis (Foth & Ellis 1997). It was clear that soil texture played a role in the K content of the soil in the study area, as it was generally higher in plots with a predominantly clay texture. According to Malavolta (1985) and Foth & Ellis (1997), soil type affects K leaching because the final amount of K lost depends on the available soil K, which is related to texture, and the amount of water that leaches through the soil. Leaching losses and extent of K movement tend to increase as soils become sandier (Foth & Ellis 1997). Pal *et al*. (1999) showed that soluble K is negatively related to the proportion of coarse sand and positively related to the amounts of clay and silt. Soil texture therefore plays a role in K analysis, partly because K is leached very quickly out of sandy soils, otherwise because clay mineralogy plays an important role in K-binding (Malavolta 1985). According to Kayser & Isselstein (2005), the leaching of K from grassland is usually low, but high levels of available soil K and high K inputs at urine patches lead to increasing losses. They further state that high K inputs have a negative influence on Mg and Ca uptake by plants and can cause accelerated leaching of these ions.

Alfaro *et al*. (2004) found that soil type affected K losses because of differences in hydrological properties. He also stated that where macropore flow is an important pathway, large differences in K losses can be expected between similar soils. The macropores are usually the spaces between the soil structural units and as such, they are the main channels for air movement (Tan 1994). Soil with a well-defined structure, particularly in arid and semi-arid areas, will contain a large number of macropores as well as many cracks and fissures. These macropores, cracks, and fissures allow for a relatively rapid flow of water through the soil profile (Miller & Donahue 1995; Buckman & Brady 1967). According to Foth & Ellis (1997) K has its percentage composition and uptake reduced by poor aeration to a greater degree than some other nutrients. Potassium leaching losses in grazed areas can occur by preferential flow after urination (Williams &

Haynes 1992) or by percolation after rainfall (Warren & Johnston 1962). Since the variation in pH was minor, it could not have had an influence on the K content. Due to the lack of previous soil analysis data, with which the results could have been compared, the reason for variation in the K content is not entirely clear.

Magnesium is essential for chlorophyll production and enzyme functions in plants (Cihacek *et al*. 1996). When a Mg deficiency occurs, the oldest or lower leaves will show a progressive yellowing leaf discoloration, necrosis and defoliation (Chapman 1966). Magnesium deficiency is more common than Ca deficiency, but much less common than K deficiency. In most soils the amount of exchangeable Mg is usually less than the quantity of exchangeable Ca (Miller *et al*. 1990). The same was found to be true for all the plots, except C2 and D3 (Figure 4.11). Although the Mg content was relatively high in all the plots, it appears that texture also had an influence on the Mg content. Plots with a clay loam and sandy clay loam texture had the lowest Mg content. According to Foth & Ellis (1997), Mg deficiencies most often occur on coarse-textured, acidic soils that have a low clay content, low CEC and high leaching potential. They also state that K represses Mg uptake. Therefore, Mg deficiency is also likely when exchangeable K exceeds exchangeable Mg on a material exchange basis. This was, however, not the case in this study since the Mg content in all the plots was a lot higher than the K content. Various other factors, such as the manganese (Mn) content, high cation application and low soil temperatures can influence the availability of Mg to plants (Foth & Ellis 1997).

The quantity of Na in the soil influences the permeability of the soil and thus the efficiency with which plant species will emerge from the soil. In the Serengeti short-grass plains Hamilton *et al*. (2001) found that the concentration of soil Na is an important factor influencing plant species composition. It appears that more favourable species occur on soils with a lower Na content, hence less sodic soils. If the latter is taken into consideration, it would be expected that more favourable plant species would occur in the plots on the southern side of the grid where the Na content was lower (Figures 4.11 & 4.12d). Hamilton *et al*. (2001) further found that photosynthetic rates and water relations were positively correlated with field soil Na concentrations. In many fully-saturated soils exchangeable sodium is bound to vary with the moisture status of the soil at any given time, because the degree of its adsorption depends on the concentrations of sodium and other ions in the soil solution (Kelley 1962). Sodium salts are the most soluble and their preferential accumulation in time may result in a sodium adsorption ratio of 13 or more, or 15% or more exchangeable Na and the formation of sodic soils (Foth & Ellis 1997). Exchangeable Na in concentrations above about 15% exerts its greatest effect on plant growth by dispersing soil (Miller *et al*. 1990).

In arid and semi-arid regions the presence of crusted salt and sodium-affected soil is a recognized occurrence (Bauder & Brock, 1992). Although some degree of crusting may be caused naturally by the physical impact of incoming water, especially rainfall, the dispersive effects of sodium may be greater than the effects of rainfall or irrigation (Hardy *et al*. 1983). Colloid dispersal makes the soil partially permeable or impermeable and causes it to form hard surface crusts when dry (Miller *et al*. 1990). Agassi *et al*. (1981) found that crust formation due to rainfall is greatly enhanced by clay dispersion and movement in the soil. Crusting was mostly apparent in plots with large bare patches and low basal cover (see Chapter 5). It was also more prominent during the dry season and in plots with high clay contents, which were the plots with the higher Na content (Figures 4.11 & 4.12d). Crust formation can lead to reduced soil infiltration and substantial rainwater runoff losses. This sequentially leads to reduced plant coverage and soil erosion, which is not desirable.

Due to the number of cation exchange sites, clay soils have the greatest risk for excess sodium binding and dispersion (Buckman & Brady 1967; Miller & Donahue 1995). Sodium reduces the permeability more in soils predominated with montmorillonite clays than in soils with illite-vermiculite clays, and much more than in soils with kaolinite-sesquioxide clays, which are the least affected. This is due to the structure of the crystal lattices of the respective clay types (Miller & Donahue 1995). Differences in the cation exchange capacities of various clay mineralogies explain much of this difference as well.

4.4.6 Cation ratios

The fact that the ratios between Ca and Mg were lower than the normal values expected of the soil in most of the plots, indicates that an imbalance may be present in the cation contents (Table 4.3). According to Schulze & Kelling (1993), a low Ca:Mg ratio reflects one of the following: (i) a soil with low exchangeable Ca and normal Mg, or (ii) a soil with normal exchangeable Ca and high Mg. It is, however, impossible to distinguish between these two cases using only ratios, therefore further research is necessary. The Ca content of soil in relation to its Mg also influences the formation of crusts on the soil surface (Agassi *et al*. 1981). The higher the Mg in relation to the Ca, the more susceptible the soil will be to the formation of crusts (Smit 1994). Norton & Dontsova, cited by Dontsova & Norton (2001) reported that in the USA mid-western soils, a high percentage of Mg had deteriorated soil structural properties and lowered infiltration rates during simulated rainfall, compared to similar soils high in Ca. Dontsova & Norton (2001) found that Mg has a specific effect on soil clay flocculation and surface sealing due to hydration behaviour differing from Ca.

The Mg and K ratio also showed an imbalance in all the plots (Table 4.3). As a result of the high Mg and low K status, Mg:K ratios were particularly wide in comparison to the normal expected ratios (Table 4.3). The same was found for the (Ca + Mg)/K ratio in most of the plots. There was, therefore, more Mg in relation to K and more Ca + Mg in relation to K. Since the history of the study area prior to the conversion to a game lodge is not known, various factors, such as fertilizers and many others, could have affected these ratios. According to Loide (2004), for example, incorrect use of lime fertilisers may result in a change in both the Ca:Mg and K:Mg ratios in soil, which is detrimental to plants and will lead to lower production.

The reason why the Ca:Mg:Na ratios of all the plots were out of proportion can be attributed to a variety of factors. Further research is needed to determine the exact mechanism by which these imbalances were established.

4.4.7 Cation Exchange Capacity (CEC), Exchangeable Sodium Percentage (ESP) and Exchangeable Potassium Percentage (EPP)

The CEC is the amount of exchangeable cations per unit weight of soil (dry basis) (Miller *et al*. 1990). Foth & Ellis (1997) describe it as the capacity of a soil for nonspecific adsorption and exchange of cations. The CEC is produced from the amount and type of negative charge. According to Foth & Ellis (1997), it is mainly a function of the amount and kind of clay and organic matter and soil pH. The exchange takes place on the surfaces of clay and humus colloids as well as on the surfaces of plant root cell walls (Miller & Gardiner 1998). Cation exchange is an important reaction that influences soil fertility, fertilizer applications, nutrient uptake and environmental quality (Tan 1994). It contributes to the correction of soil acidity and alkalinity, assists in the alteration of some soil physical properties and acts as a percolation mechanism whereby water is purified or altered (Miller *et al*. 1990).

When the CEC values of the plots were compared to the range of normal values for different soil textures, it was concluded that all the plots occurred on clay loam to clay soil (Table 4.3). This concurs to a great extent with the results found in the soil texture analysis (see section 4.4.1). Since sandy clay loam and sandy clay texture classes were absent in the range of normal expected values according to Miller & Gardiner (1998), plots with the latter mentioned textures fell into the range with a clay loam texture. The CEC of soils remain relatively constant for a given soil if the soil pH, humus, clay content and types of clays remain the same. However, it will change if the soil properties change (Tan 1994). An important aspect of soil texture is the fact that clays generally comprise the majority of cation exchange sites in soils. This is because clays, by virtue of their small particle size, have the most surface area, and therefore the most exchange sites (Buckman & Brady 1967; Miller & Donahue 1995). Montmorillonite clays have the highest cation exchange capacities, followed by illite and kaolinite, respectively (Miller & Donahue 1995). According to Tan (1994), the higher the clay content, the larger the CEC of the soil will be. The latter was also true for this trial. Plots with a sandy clay loam to sandy clay texture had a lower CEC than plots with a clay texture. The same principle applies for organic matter content.

Soil alkalinity (or sodicity) is characterized by the ESP, the content of exchangeable Na ions as a percentage of the total soil cation exchange capacity (Hillel 2004). Soil through which salty water flows frequently, adsorbs too much Na on the soil particle exchange site. This effect can take place in both saline (brackish) and non-saline soil. According to Cook & Muller (1997), sensitivity to levels of ESP varies across soil types. If a high proportion of the exchange sites are occupied by Na ions, soil can become very alkaline with pH values ranging between 8.5 and 10.5, and the soil aggregates disintegrate and disperse. These soils can become resistant to water infiltration because small soil particles that are dispersed by the Na, are lodged in the pores and seal them (Miller *et al*. 1990). Not only does dispersion and subsequent resolidifying of soil material cause a reduction in the amount of water entering the soil, it also affects the rate at which water flows through the soil, hence the hydraulic conductivity (McNeal 1968; Ayers & Westcot 1976; Frenkel *et al*. 1978; Hardy *et al*. 1983). According to Agassi *et al*. (1981), the degree of dispersion differs among clay mineralogy and soil type. Because of the high ESP, dispersion was more likely in plots B1&2 and will therefore reduce the permeability and tilth in these plots (Table 4.3). The ESP values of the remaining plots were well below the level at which dispersion will normally occur. The sodicity of plot B1 can possibly be attributed to the occurrence of mineral licks in this plot. The high ESP of plot B2 cannot be entirely explained, although, runoff water could have had an influence. A similar reasoning might also be applicable to other plots with a high Na content, depending on the slope.

The ESP value is used extensively to indicate the likelihood of soil dispersal whereby its hydraulic conductivity (rate of water flow through it) will be reduced. The disruption of soil hydraulic properties has two main consequences. Firstly, less water infiltrates into the soil, therefore less water is available to plants, particularly at deeper depths (Barbour *et al*. 1998; Miller & Donahue 1995; Bauder & Brock 2001). Secondly, runoff, and therefore water loss and soil erosion, may be enhanced (Hardy *et al*. 1983; Miller & Donahue 1995). When high concentrations of sodium affect a soil, the subsequent loss of structure reduces the hydraulic conductivity, or rate at which water moves through a soil (Shainberg & Letey 1984; Hardy *et al*. 1983; Levy *et al*. 1999). Soils with a low clay content can tolerate greater exchangeable Na percentages because they are more permeable (Miller *et al*. 1990). An ESP value equal to or greater than 15 indicates a sodic soil (Miller & Gardiner 1998). Agassi *et al*. (1981) also stated that the ESP is an important determinant of exposed soil surfaces crusting.

The exchangeable K maintains an equilibrium with the K in solution, and together the exchangeable and solution K make up the available K. The K in solution is equal to 1 to 3% of the exchangeable K in most soils (Foth & Ellis 1997). The EPP of most of the plots fell within the range of normal values or differed marginally from the normal values (Table 4.3). The highest K imbalance was found in plots A3&4 and B4, which differed on average 1.8% from the normal range.

4.4.8 Zinc (Zn)

Zinc is essential for numerous enzyme systems and is capable of forming many stable bonds with nitrogen and sulphur ligands. It plays an important role in plant growth, nutrition, seed and stalk maturation, and enables the plant to withstand lower air temperatures. Zinc deficiency is perhaps one of the easiest to recognize under field conditions. Low Zn mobility in plants causes some interveinal chlorosis in both young and older leaves, and yellowing between the veins of the leaf tissues is a typical symptom

(Miller & Gardiner 1998). It most often occurs on calcareous soils and soils that have high levels of phosphate. Soil Zn availability is diminished by high soil phosphorous levels and soil pH greater than 6.5. In general the Zn deficiency appears early in the growing season and is caused by either cool weather or by the restricted rooting zone of plants (Foth & Ellis 1997). Warmer, drier weather may result in the deficiency symptoms disappearing. The Zn content was generally higher in plots with a clay soil texture and a higher soil pH (Figures 4.13 & 4.14). Since a range of factors could have had an influence on the Z content, the exact reason for the variation between the plots is not known.

4.4.9 Electrical resistance

Electrical resistance, measured in ohms, is reciprocal to conductivity (mS m^{-1}). It is an indication of the amount of dissolved salts in the soil. Salts, e.g. calcium and sodium, conduct electricity and reduce the resistance of the soil solution. A low resistance in the soil thus indicates the presence of large quantities of salts in the soil, i.e. the soil is saline (Miller *et al*. 1990). This corresponds with the results of some plots, but the opposite occurred in the other plots, which indicates that other factors could have had an influence. These salts act osmotically to lower the water potential, making it more strenuous for plants to absorb water from the soil solution (Miller & Gardiner 1998). Soil tension or suction indicates the energy required by plant roots to extract water from soil particles. As soil water is removed its soil tension increases (Foth & Ellis 1997). Tension relates directly to soil water content. Electrical resistance can therefore also be used to determine the soil moisture content.

Various kinds of brackishness are encountered in soils. Both the ESP and the specific resistance serve as criteria for classifying the type of soil brackishness. If the resistance is below 300 Ω and the ESP more than 15%, it means that there is an excess of sodium brackishness in the soil (Hillel 2004). This, however, did not occur in any of the plots since the lowest resistance found was 380 Ω (Figure 4.15).

4.5 CONCLUSION

The following conclusions can be drawn from the results of this study:

(i) Differences in the tested soil variables were found within the twenty plot grid. These differences are likely to have an influence on the herbaceous layer, which will be discussed later in Chapter 8.

(ii) It appears that soil texture played an important role in the chemical properties of the soil, since it had an influence on most of the tested soil variables.

(iii) Due to the lack of previous soil analysis data, with which the results could have been compared, the exact reasons for variations in the nutrient contents are not entirely clear.

(iv) It is also important to keep in mind that soil enrichment is a slow process. Therefore, the variability of the tested soil variables is most likely due to land use practices prior to the conversion to a game lodge, as well as natural small scale variability that exists in most ecosystems.

CHAPTER 5

AN ASSESSMENT OF THE HERBACEOUS LAYER

5.1 INTRODUCTION

Tainton (1999) stated that plants are a measure of the environment, as every plant is the product of the conditions under which it grows. Mostert *et al*. (1971) suggested that plants could be regarded as the symptom of veld condition. There is great concern for the retrogression of veld in the arid and semi-arid areas of South Africa. Pasture scientists identified poor veld management and over-grazing as the main causes of veld degradation (Snyman 1993a).

Stocking rate is probably one of the most important elements in determining the sustainability of any game ranching enterprise. The need for veld condition assessment and simultaneous determination of grazing capacity cannot be overemphasized for the sustained use and management of the vegetation of South Africa. Veld condition is the condition of vegetation in relation to, amongst others, sustained forage production and resistance to soil erosion, for sustained optimum animal production (Trollope *et al*. 1990). An assessment of the condition of plant communities provides a means of comparing them, a way to determine quantity and quality, and observe spatial and temporal changes within a plant community or vegetation type (Hardy *et al*. 1999). Because vegetation is a more sensitive indicator of ecosystem changes, it is usually used to quantify veld condition and is easier to measure than changes in the soil properties (Teague & Danckwerts 1989). According to Van der Westhuizen (1994), vegetation is constantly changing, and these changes can be progressive or retrogressive. If an assessment of the veld condition is repeated over time, changes in the vegetation can be monitored and the direction or tendency of change can be determined.

Various methods of quantifying veld condition have been suggested during recent decades (Roberts 1970; Foran 1976; Foran *et al*. 1978; Tainton *et al*. 1980; Vorster 1982; Barnes *et al*. 1984; 1985; Heard *et al*. 1986; Bosch *et al*. 1989; Hurt & Hardy 1989; Bosch & Gauch 1991; Bosch & Kellner 1991). Tainton (1988) and Smith (1989) regard the veld condition score as the most important factor in any management system. Friedel (1991), however, points out that this concept is still under debate.

The objectives of this study were to determine:

(i) the botanical composition,

(ii) the dry matter production,

(iii) the veld condition, and

(iv) the grazing capacity of the herbaceous layer in each experimental plot for the 2003/04 and 2004/05 growing season.

The results from this will be used to determine the interaction between the vegetation, soil properties (see Chapter 4), and grazing by herbivore game species namely springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*) and black wildebeest (*Connochaetes gnou*) (see also Chapter 8).

5.2 PROCEDURE

5.2.1 Botanical composition of the herbaceous layer

The botanical composition of the herbaceous layer was determined using a wheel point apparatus according to the nearest plant method (Tidmarsh & Havenga 1955). Surveys were done at the end of each growing season (2003/04 & 2004/05), normally during April or May. Two hundred point-observations were randomly recorded in each experimental plot (see Chapter 3). According to Hardy & Walker (1991), a 200 point survey is usually sufficient for homogenous grassland. At every point-observation the nearest live herbaceous plant was identified on species level and recorded. The abundance of each species was expressed as a percentage of the total number of point-observations in each experimental plot. A "bare patch" was recorded when no plants occurred in a radius of 30 cm of the point.

5.2.2 Dry matter production of the herbaceous layer

Above-ground dry matter (DM) production of the herbaceous plants (grasses, Karoo bushes and forbs) in the 20 experimental plots was determined at the end of each growing season (2003/04 & 2004/05), normally April or May. A harvesting technique as proposed by Grunow *et al*. (1980) was employed. In each of the twenty experimental plots, all plants in randomly placed quadrates of 0.5 m x 0.5 m (0.25 m^2) were harvested. A total of 20 quadrates per plot were harvested. Using hand clippers, rooted herbaceous plants within each quadrate were clipped to stubble height. Stubble height varied from 0.1 - 3.0 cm, depending whether the species was tufted or not. The clipped material was placed in paper bags, dried to a constant mass at 70ºC and then weighed.

5.2.3 Veld condition assessment

The Ecological Index Method (for grassland), described by Vorster (1982) as revised by Tainton *et al*. (undated), was used to determine the veld condition. This method classifies veld condition according to the response of vegetation to abiotic and biotic environmental impacts and is most commonly used in grasslands (Hardy *et al*. 1999). The species are classified into ecological classes in a similar manner to that described by Dyksterhuis (1949), Foran (1976) and Tainton *et al*. (1980). Species were placed into the following ecological classes (relative index values indicated in parenthesis): Decreaser species (10); Increaser Ia species (7); Increaser IIa species (7); Increaser IIb species (4);

Increaser IIc species (1) and Invader species (1). A detailed description of each group is given in Appendix B_1. Although the ecological status of many species is constant, this is not always the case. There is often a considerable genetic variation in widespread species, and these species respond as ecotypes (Van Oudtshoorn 1999; Van Rooyen *et al*. 2000). Different ecotypes of the same species that occur in different areas react in different ways to grazing and can potentially be classified into different ecological classes. The ecological status of a species can also be influenced by the variation in environmental and habitat conditions.

By taking the above mentioned variables into consideration, grouping of the grass species and non-grasses into different ecological classes was done by means of correlation analysis. This comprises the identification of well represented species that are typical of each group. The occurrence of the other grass species within the different plots was tested against the representative species of each ecological class. Species were placed in the group that gave the highest correlation value. The non-grasses (Karoo bushes and forbs) were combined as a group. The identification of the species representing each ecological class was done according to the classification of Fourie & Du Toit (1983) and Smit (2005, personal communication[§]). The following grass species were selected as representative of each group: Decreaser - *Themeda triandra*; Increaser Ia - *Cymbopogon pospischilii* (synonym *C. plurinodis*); Increaser IIa - *Eragrostis chloromelas*; Increaser IIb - *Aristida bipartita* and Increaser IIc - *Brachiaria eruciformis*.

A Veld Condition Score (VCS) for each experimental plot was calculated by totalling the percentage occurrence of the plant species in the relevant ecological classes and multiplying it with the relative index values (given in parenthesis). By summing these class values the VCS was attained.

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5.2.4 Grazing capacity

Estimates of the grazing capacity were made from the above-ground DM production, using the formula proposed by Moore *et al*. (1985), and again described by Moore & Odendaal (1987) and Moore (1989):

$$Y = d \div \frac{[DM \times f]}{r}$$

where Y = grazing capacity (ha GU^{-1})

d = number of days in a year (365)

DM = total herbaceous DM production (kg ha^{-1})

f = utilisation factor [0.2; 0.3; 0.4 – depending on the grazing value of the particular plant species (Smit undated)

(see Appendix B_1)

r = daily grass DM required per GU (2.5% of body mass = 4.5 kg day^{-1}) (Owen-Smith 1999)

A Grazer Unit (GU) is defined as the metabolic equivalent of a blue wildebeest (*Connochaetes taurinus*), a 100% grazer with a mean body mass of 180 kg (Dekker 1997).

5.2.5 Data analysis

The qualitative Sörensen's Quotient of similarity, $QS=2j/(a+b)$, where a and b are the total number of plant species sampled in two adjacent experimental plots respectively, and j is the number of species common to both plots, was used to determine the similarity of the flora between adjoining plots (Magurran 1988). A high value (closer to 1) indicates a more homogenous botanical composition in the two plots, while a lower value (closer to 0) indicates a more heterogeneous botanical composition in each plot.

In order to create a 5 x 4 grid schematic representation of the relevant tested parameter, four intervals were established for each parameter. The minimum and maximum values were used for the first and last interval, and by using the formulas below the third (Y) and fourth (X) intervals were calculated. The third interval represented ⅓ of the difference between the maximum and minimum value and the fourth interval ⅔ of the difference.

$$Y = Min + \left(\frac{Max - Min}{3} \right)$$

$$X = Min + 2\left(\frac{Max - Min}{3} \right)$$

Additional statistical analysis included Regression and Correlation analysis (Draper & Smith 1981; Graph Pad InStat 3.0 1997; Microsoft Excel 2003).

5.3 RESULTS

5.3.1 Botanical composition of the herbaceous layer

The percentage contribution of the three dominant grass species to the species composition of each experimental plot for both seasons is provided in Figures 5.1 & 5.2. The remaining grass species are grouped as “other” species. The contribution of the non-grasses (Karoo bushes and forbs) is also indicated. A detailed table of the occurrence of all the plant species in the herbaceous layer of each experimental plot for the 2003/04 and 2004/05 growing seasons is presented in Appendix $B_{2\text{-}6}$.

It is clear from Figures 5.1 & 5.2 that *Aristida bipartita* and *Eragrostis chloromelas* were the dominant grass species in plots A1-4. Over the two seasons combined, these species together contributed an average of 72.3% to the species composition of plot A1, 87.8% to plot A2, 89.5% to plot A3 and 83.5% to plot A4. The other grass species and none grasses contributed less than 10% to the species composition.

In plot B1, *E. chloromelas* and *Setaria incrassata* were the dominant species during 2003/04 and had a combined contribution of 33% (Figure 5.1). The non-grasses contributed 28.5% (Figure 5.1). During 2004/05 the occurrence of *Tragus berteronianus* increased drastically and became the dominant species (Figure 5.2). *Eragrostis chloromelas* and *Brachiaria eruciformis* were second and third in abundance, respectively (Figure 5.2). The contribution of forbs also increased by 7%. *Eragrostis chloromelas*, *E. obtusa* and *Themeda triandra* were dominant in plot B2 during 2003/04, but during 2004/05 the abundance of *E. obtusa* decreased (Figures 5.1 & 5.2). The forbs increased by 15.5%. *Aristida bipartita* and *E. chloromelas* were dominant in plots B3&4. Over the two seasons, they contributed 59.5% and 76.8% (combined average) to the species composition of these plots, respectively (Figures 5.1 & 5.2).

It is clear from Figures 5.1 & 5.2 that *S. incrassata* and *A. bipartita*, and to a lesser extent *E. chloromelas*, were the dominant grass species in plot C1 during 2003/04 and 2004/05. During both growing seasons, *E. chloromelas* and *S. incrassata* were the dominant species in plot C2, and *T. triandra* and *S. incrassata* in plot C3 (Figures 5.1 & 5.2). *Aristida bipartita* and *E. chloromelas* were the dominant grasses in plot C4 during both seasons. Over the two seasons they contributed an average of 47% to the species composition. Due to an increase in the occurrence of *B. eruciformis* it became the third most abundant species in this plot during 2004/05 (Figures 5.1 & 5.2). The occurrence of forbs increased in all four plots (Figures 5.1 & 5.2).

Setaria incrassata and *T. triandra* were the dominant grass species in plot D1 (Figure 5.1). During 2004/05, *A. bipartita* became slightly more abundant than *T. triandra* (Figure 5.2). In plot D2, *S. incrassata* contributed 54% and 50% to the species composition of 2003/04 and 2004/05, respectively (Figures 5.1 & 5.2). The second most abundant grass species contributed less than 10% to the species composition. *Setaria incrassata* and *T. triandra* were also dominant in plot D3 (Figures 5.1 & 5.2). Due to an increase of *Eragrostis plana* it replaced *Panicum stapfianum* as the third most abundant grass species during 2004/05. *Aristida bipartita, E. chloromelas*, and to a lesser extent *T. triandra*, were the dominant species in plot D4 during both 2003/04 and 2004/05 (Figures 5.1 & 5.2).

During 2003/04 and 2004/05 the dominant grass species in plots E1 and E2 were *T. triandra* and to a lesser extent *E. chloromelas* (Figures 5.1 & 5.2). *Eragrostis plana* was the third most abundant species in plot E1 during both seasons and *S. incrassata* in plot E2, but was replaced by *E. plana* during 2004/05. *Themeda triandra* and *S. incrassata* were the dominant species in plot E3 during 2003/04 and 2004/05 (Figures 5.1 & 5.2). *Eragrostis plana* had a higher occurrence during 2004/05 than *P. stapfianum*, which was the third most abundant species during 2003/04. *Aristida bipartita* and *T. triandra* were the dominant grass species in plot E4 during both seasons (Figures 5.1 & 5.2). Due to an increase in occurrence of *E. obtusa*, it replaced *P. stapfianum* as the third most abundant species during 2004/05 (Figure 5.1 & 5.2).

It is clear from Figures 5.1 & 5.2 that *E. chloromelas* and *A. bipartita* were more abundant in plots situated on the northern and western side of the grid. The occurrence of *S. incrassata* generally increased further to the south. *Themeda triandra* and other grass species increased drastically in the plots situated in the southern side. There was also a general increase in Karoo bushes and forbs towards the southern plots.

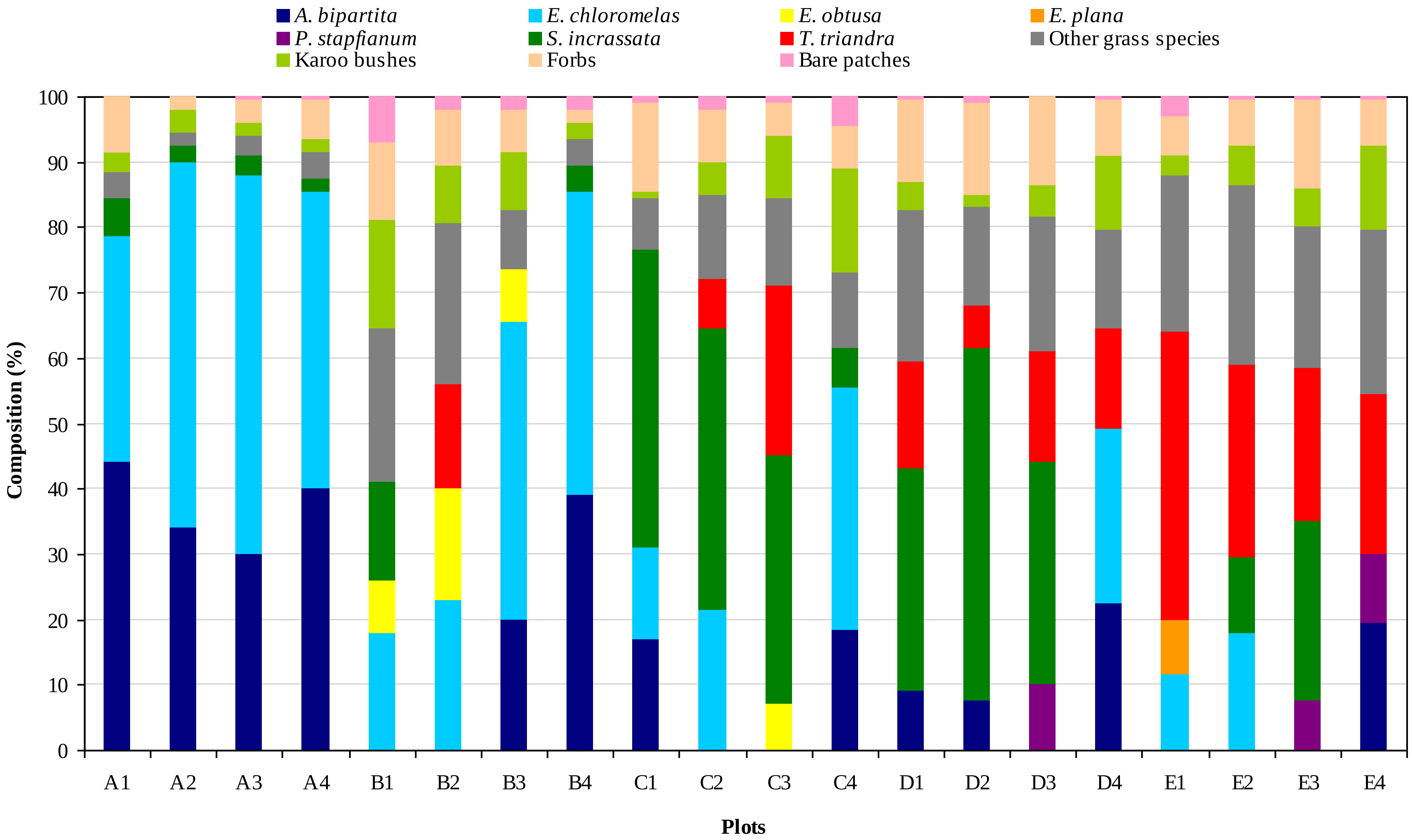

Figure 5.1: Percentage contribution by the most abundant grass and non-grass (Karoo bushes and forbs) species to the species composition of the herbaceous layer of the experimental plots during the 2003/04 growing season.

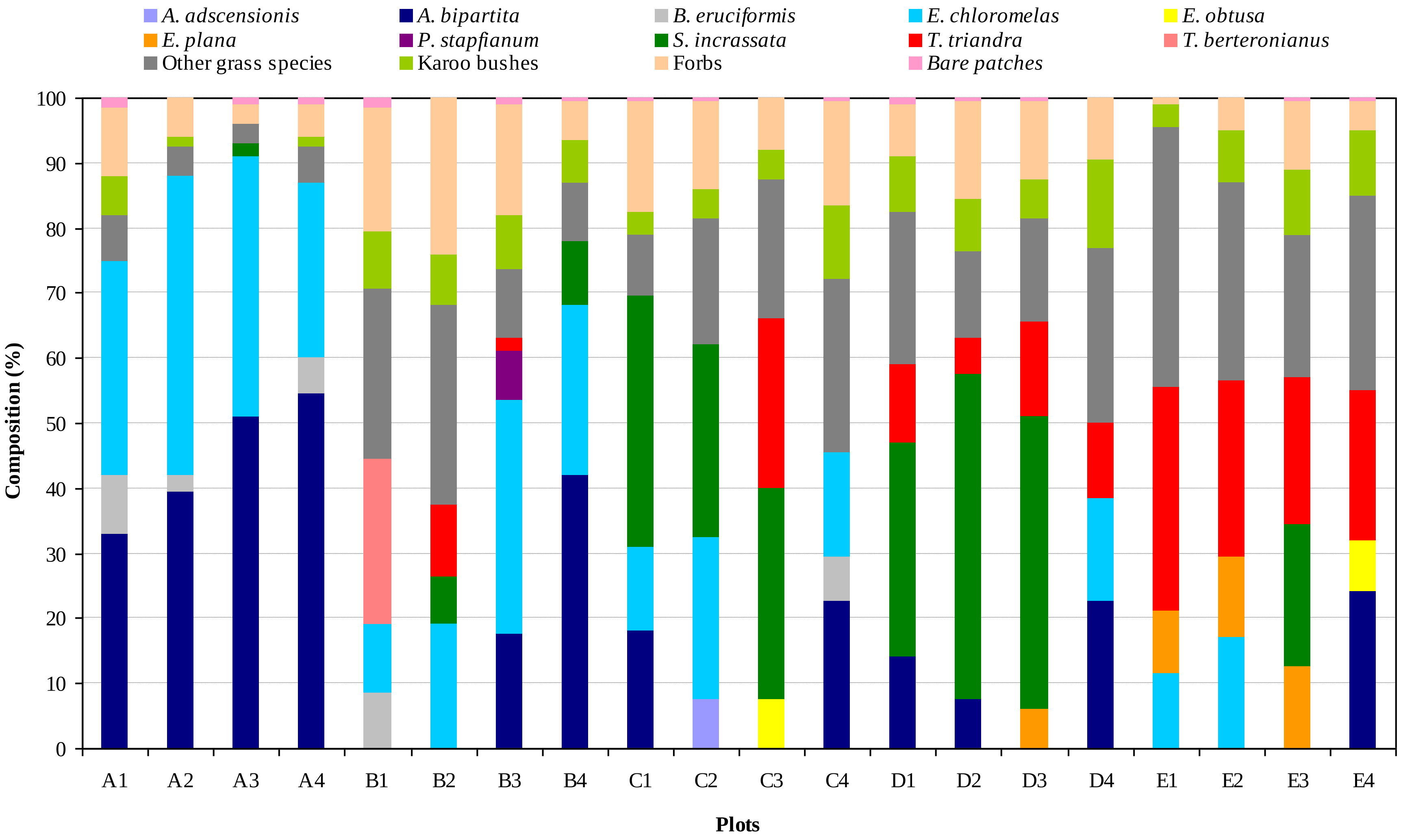

Figure 5.2: Percentage contribution by the most abundant grass and non-grass (Karoo bushes and forbs) species to the species composition of the herbaceous layer of the experimental plots during the 2004/05 growing season.

The percentage contribution of grasses in different succession classes, as well as non-grass (Karoo bushes and forbs) in each experimental plot during the 2003/04 and 2004/05 growing seasons is presented in Table 5.1. The classification of the grass species into the different succession classes is presented in Appendix B$_7$. It is clear that climax grasses dominated in all the plots. There was a moderate increase in the occurrence of pioneer grass species and a corresponding decrease in climax grass species from 2003/04 to 2004/05 (Table 5.1). The occurrence of bare patches decreased slightly. The increase in the occurrence of Karoo bushes was minor, while forbs increased on average by 2.3%.

The plant species diversity was the lowest in Row A (Figure 5.3). Plant species diversity generally increased from the north-west (A4) to the south-east (E1), although several intermediate plots had a higher or lower diversity. Sörensen's quotient values were mostly between 0.6 and 0.9 (Figure 5.3). The highest botanical similarity was found between plots D1 and D2 (0.905). Plots with values greater than 0.8 have a high similarity, providing the herbivores with a more uniform and continuous forage resource in adjacent plots.

Table 5.1: Percentage contribution of grasses in different succession classes, as well as non-grasses (Karoo bushes and forbs) in each experimental plot during the 2003/04 and 2004/05 growing season.

	Contribution (%)											
	2003/04						2004/05					
Plot	**Climax Grasses**	**Sub-climax Grasses**	**Pioneer Grasses**	**Karoo bushes**	**Forbs**	**Bare patches**	**Climax Grasses**	**Sub-climax Grasses**	**Pioneer Grasses**	**Karoo bushes**	**Forbs**	**Bare patches**
A1	85.5	-	3.0	3.0	8.5	0.0	71.0	-	11.0	6.0	10.5	1.5
A2	94.5	-	0.0	3.5	2.0	0.0	89.5	-	3.0	1.5	6.0	0.0
A3	92.0	-	2.0	2.0	3.5	0.5	94.0	-	2.0	0.0	3.0	1.0
A4	89.5	-	2.0	2.0	6.0	0.5	86.0	-	6.5	1.5	5.0	1.0
B1	43.5	9.0	12.0	16.5	12.0	7.0	27.0	5.5	38.0	9.0	19.0	1.5
B2	59.0	18.0	3.5	9.0	8.5	2.0	47.0	6.5	20.5	8.0	18.0	0.0
B3	72.5	8.0	2.0	9.0	6.5	2.0	64.5	1.5	7.5	8.5	17.0	1.0
B4	91.5	-	2.0	2.5	2.0	2.0	79.0	-	8.0	6.5	6.0	0.5
C1	80.0	2.0	2.5	1.0	13.5	1.0	72.0	-	7.0	3.5	17.0	0.5
C2	81.0	2.0	2.0	5.0	8.0	2.0	73.0	1.0	7.5	4.5	13.5	0.5
C3	73.5	8.0	3.0	9.5	5.0	1.0	69.0	9.0	9.5	4.5	8.0	0.0
C4	68.0	1.0	4.0	16.0	6.5	4.5	55.0	2.5	14.5	11.5	16.0	0.5
D1	71.5	4.0	7.0	4.5	12.5	0.5	65.0	6.0	11.5	8.5	7.5	1.5
D2	78.0	2.5	2.5	2.0	14.0	1.0	71.5	2.5	2.5	8.0	15.0	0.5
D3	71.5	7.0	3.0	5.0	13.5	0.0	67.5	7.5	6.5	6.0	12.0	0.5
D4	74.0	3.0	2.5	11.5	8.5	0.5	61.5	4.5	11.0	13.5	9.5	0.0
E1	67.0	11.0	10.0	3.0	6.0	3.0	66.5	14.0	15.0	3.5	1.0	0.0
E2	74.5	9.0	3.0	6.0	7.0	0.5	68.0	14.0	5.0	8.0	5.0	0.0
E3	73.0	4.5	2.5	6.0	13.5	0.5	61.5	12.5	5.0	10.0	10.5	0.5
E4	69.0	8.5	2.0	13.0	7.0	0.5	66.5	9.5	9.0	10.0	4.5	0.5
Average	75.5	6.5	3.5	6.5	8.2	1.5	67.8	6.9	9.7	6.6	10.5	0.6

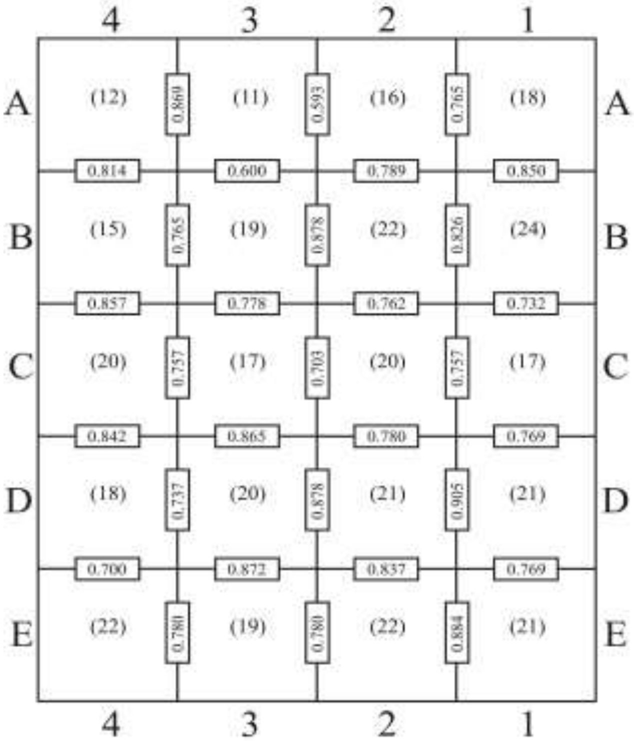

Figure 5.3: Qualitative Sörensen's Quotient of similarity values indicating the similarity of the botanical composition between the experimental plots. The species diversity (number of species) of each experimental plot is given in parenthesis.

5.3.2 Dry matter production of the herbaceous layer

The total above-ground DM production of grasses in different succession classes, as well as of Karoo bushes and forbs of each experimental plot for 2003/04 and 2004/05 is presented in Table 5.2. The individual contribution of plant species to the total DM production of each plot is presented in Appendix B_{8-12}.

In most plots, the average DM production of the climax and sub-climax grass species declined between 2003/04 and 2004/05 (Table 5.2), while the pioneer grass species increased in DM production. The opposite was, however, found in plot E4. In plots A4, B1, C1&4 and D1 the DM production of climax grasses increased. During 2003/04, DM production of the climax grasses was the highest in plot A1, followed by A3 and A2, and the lowest in B1 (Table 5.2). In 2004/05 production was the highest in A4 followed by E4 and D1, and the lowest in E1. The production of the sub-climax grasses was the highest in plots E1&2 during both seasons. DM production of pioneer species increased considerably in all the plots, except in plots A4 and E3&4. Karoo bushes had a lower DM production in 2004/05 than in 2003/04, while the forbs had a higher production during 2004/05 (Table 5.2).

It is clear from Figure 5.4a that the percentage species composition on basis of above-ground DM production (percentage contribution of each species to the DM production) and species composition on basis of occurrence (percentage contribution of each species to the species composition) curves follow the same trend. There was a highly significant ($P < 0.001$) positive correlation between these two curves (Figure 5.4b). The trends of dominant grass species are graphically illustrated in Figures 5.5 – 5.12. There were highly significant ($P < 0.001$) positive correlations between the percentage species composition on basis of DM-production and species composition based on occurrence of *A. bipartita*, *E. chloromelas*, *S. incrassata* and *T. triandra* during both seasons (Figures 5.5 – 5.12). The two curves of these grass species generally showed a similar trend in most of the plots. During 2004/05 the curves of *E. chloromelas* showed a slight deviation (Figure 5.8).

Table 5.2: Above-ground DM production (kg ha^{-1}) of grasses in different succession classes, as well as non-grasses (Karoo bushes and forbs) in the 2003/04 and 2004/05 growing seasons.

	Above-ground DM production (kg ha^{-1})											
	2003/04						2004/05					
Plot	**Climax**	**Sub-climax**	**Pioneer**	**Karoo bushes**	**Forbs**	**Total**	**Climax**	**Sub-climax**	**Pioneer**	**Karoo bushes**	**Forbs**	**Total**
A1	783.2	2.4	1.6	13.6	24.8	825.6	383.8	1.1	90.2	76.0	41.2	592.3
A2	536.2	0.0	2.6	19.6	16.6	575.0	482.4	0.0	11.9	0.0	16.1	510.4
A3	639.8	0.0	0.2	4.6	2.8	647.4	407.7	0.0	49.8	6.4	9.3	473.2
A4	452.8	0.0	3.2	32.8	63.0	551.8	575.1	0.0	5.0	12.4	17.9	610.4
B1	15.6	1.2	5.2	107.6	88.2	217.8	243.6	6.7	62.1	67.8	193.5	573.7
B2	286.2	2.8	3.6	79.6	71.8	444.0	248.5	17.1	27.5	67.8	69.9	430.8
B3	279.2	0.0	4.8	35.2	11.4	330.6	280.3	0.0	37.7	88.4	54.1	460.5
B4	423.0	0.0	1.0	29.6	16.0	469.6	247.2	0.0	61.0	9.7	4.8	322.7
C1	372.8	0.6	16.0	12.6	36.1	438.1	421.8	0.0	27.4	10.1	58.9	518.2
C2	358.0	0.0	3.6	36.8	34.0	432.4	347.6	0.0	35.0	23.3	41.5	447.4
C3	351.1	0.0	2.4	56.0	0.0	409.5	332.3	7.2	27.9	21.1	20.6	409.1
C4	233.2	0.0	0.0	79.8	28.4	341.4	326.2	0.0	106.2	30.0	48.8	511.2
D1	288.4	0.8	15.8	49.4	30.0	384.4	486.1	0.0	72.0	15.8	46.6	620.5
D2	476.8	0.0	2.2	10.0	7.2	496.2	359.5	12.1	61.8	16.2	74.2	523.8
D3	509.0	6.2	9.2	44.8	40.6	609.8	366.6	8.1	24.0	24.2	80.7	503.6
D4	317.8	3.8	1.0	58.4	63.2	444.2	273.1	0.0	70.9	7.4	15.6	367.0
E1	359.0	9.0	52.4	41.0	4.0	465.4	198.1	47.9	92.2	40.1	4.2	382.5
E2	322.6	38.2	0.0	70.2	31.8	462.8	303.9	42.2	18.8	49.3	24.3	438.5
E3	309.0	8.6	23.8	40.8	70.0	452.2	240.4	21.9	3.9	104.1	81.9	452.2
E4	365.6	1.2	3.4	65.2	30.0	465.4	538.0	20.3	0.7	33.9	28.8	621.7
Average	384.0	3.7	7.6	44.4	33.5	473.2	353.1	9.2	44.3	35.2	46.6	488.5

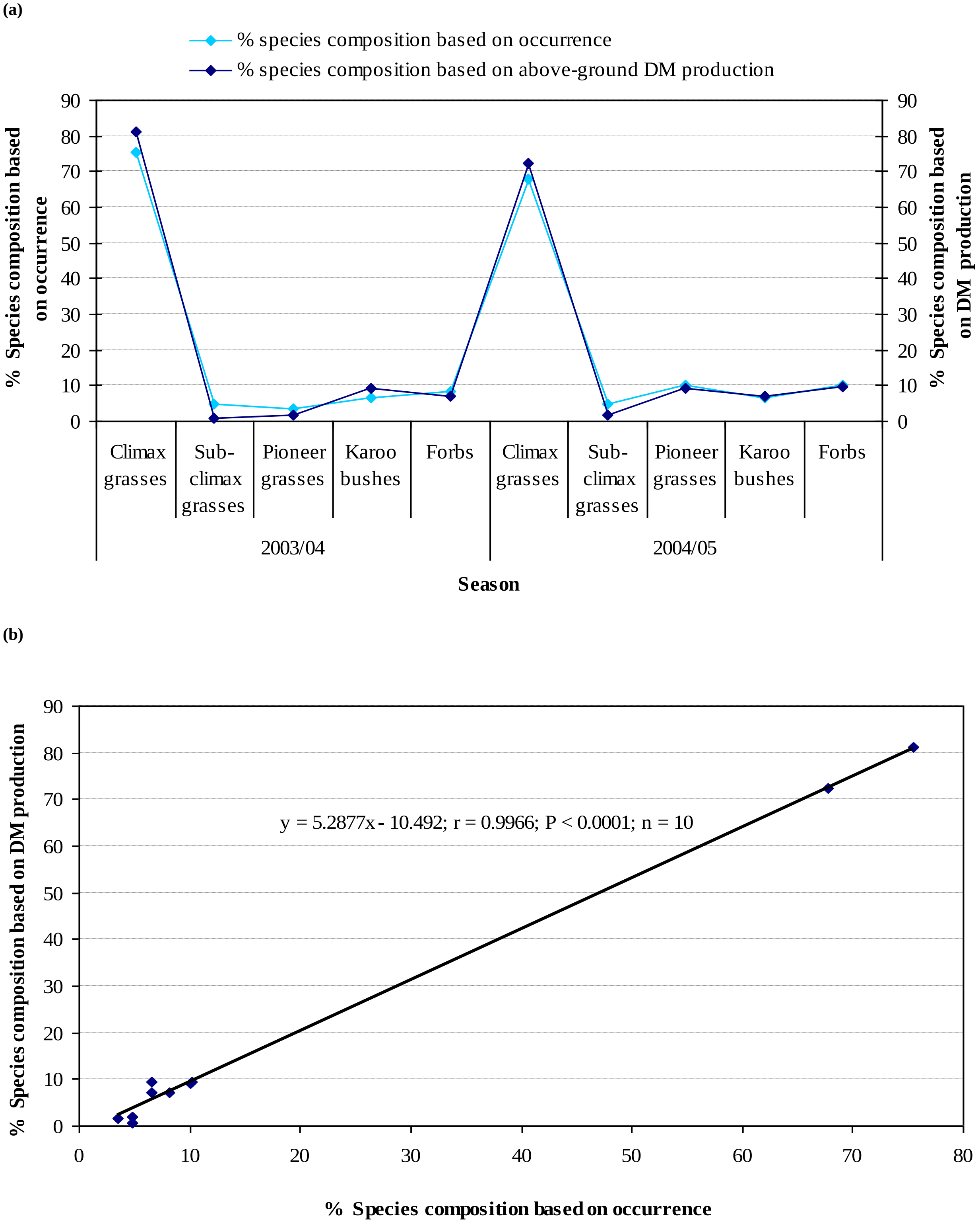

Figure 5.4: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of grass species in different succession classes, as well as non-grasses (Karoo bushes and forbs) during the 2003/04 and 2004/05 growing season and (**b**) the regression analysis.

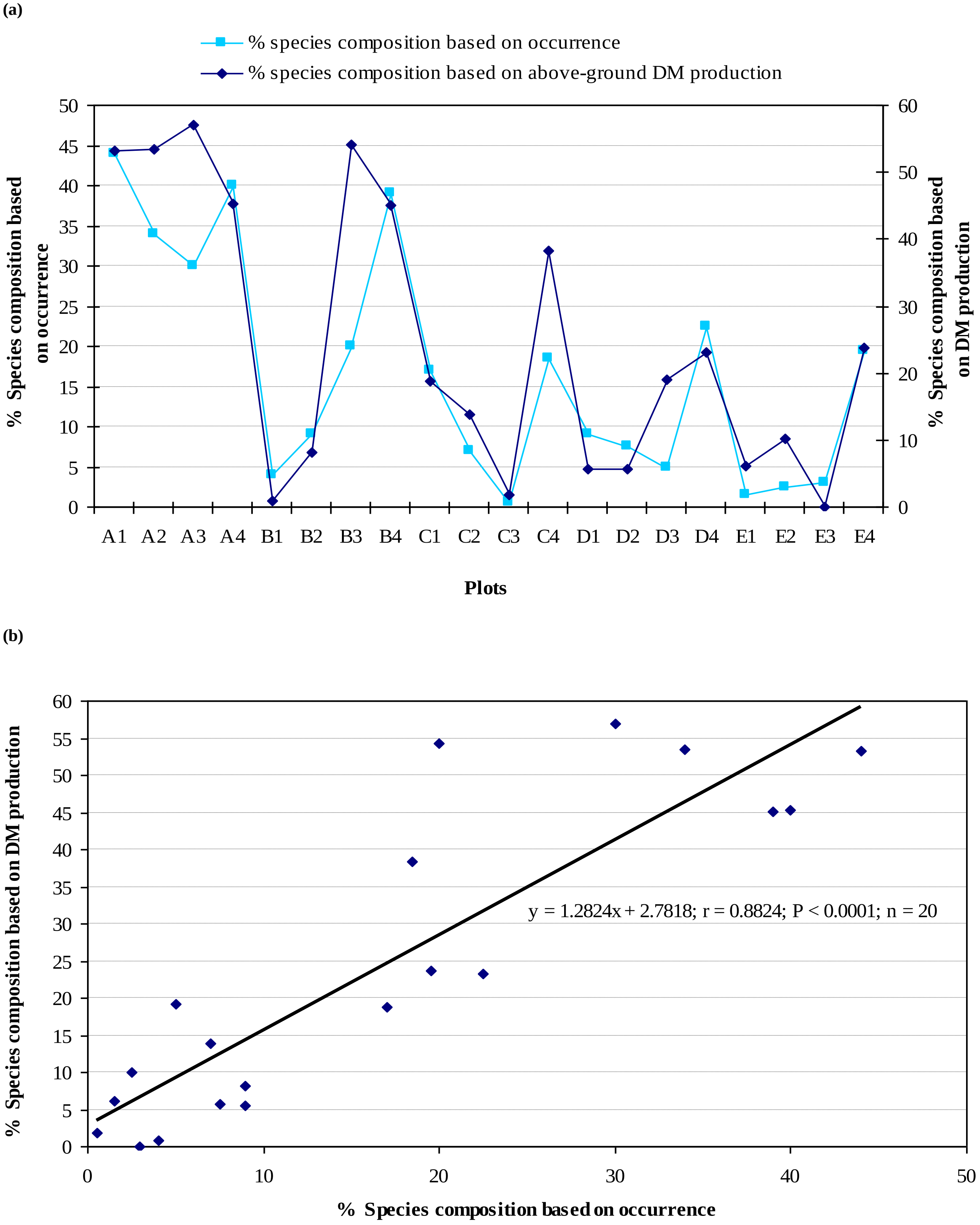

Figure 5.5: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Aristida bipartita* during the 2003/04 growing season and (**b**) the regression analysis.

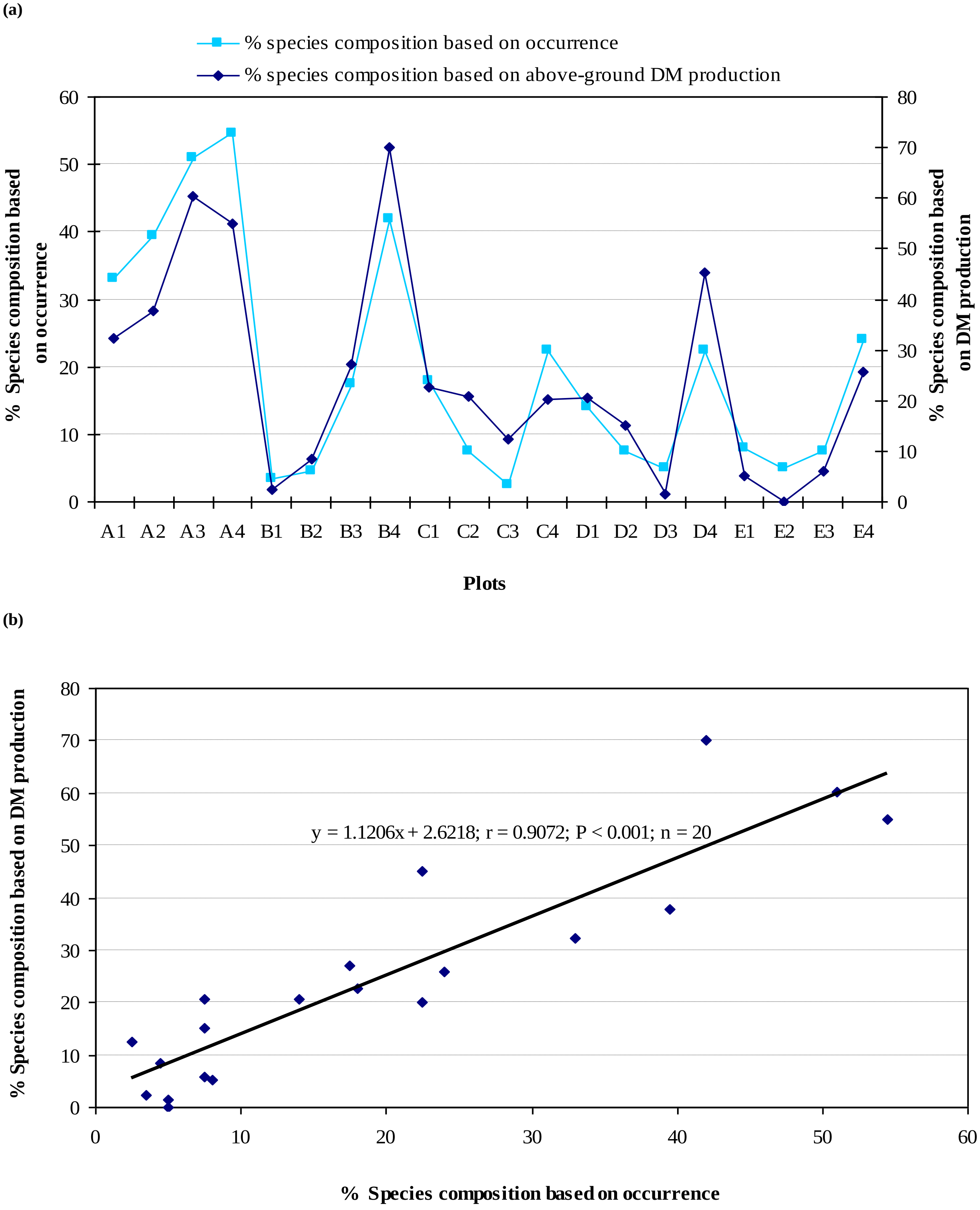

Figure 5.6: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Aristida bipartita* during the 2004/05 growing season and (**b**) the regression analysis.

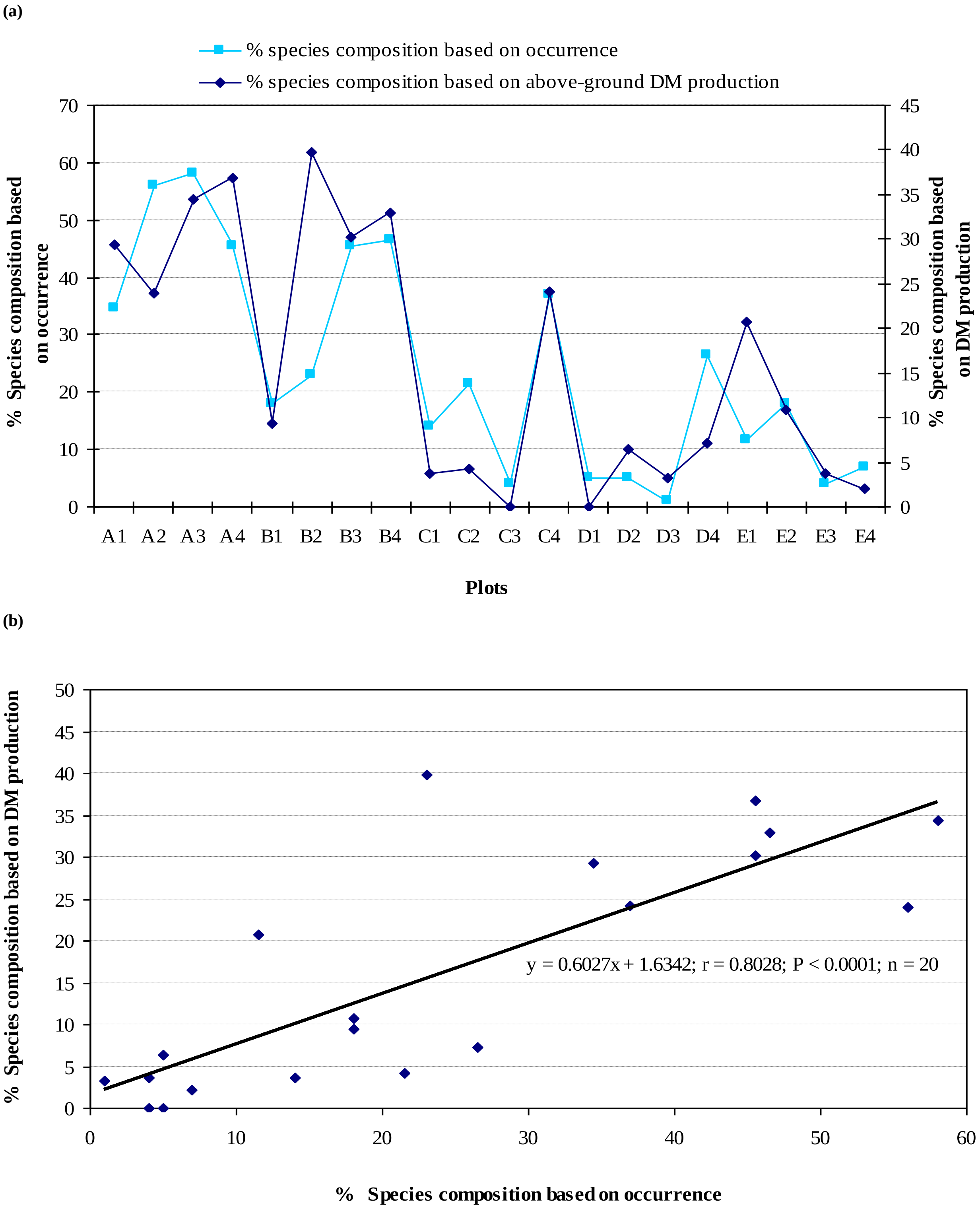

Figure 5.7: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Eragrostis chloromelas* during the 2003/04 growing season and (**b**) the regression analysis.

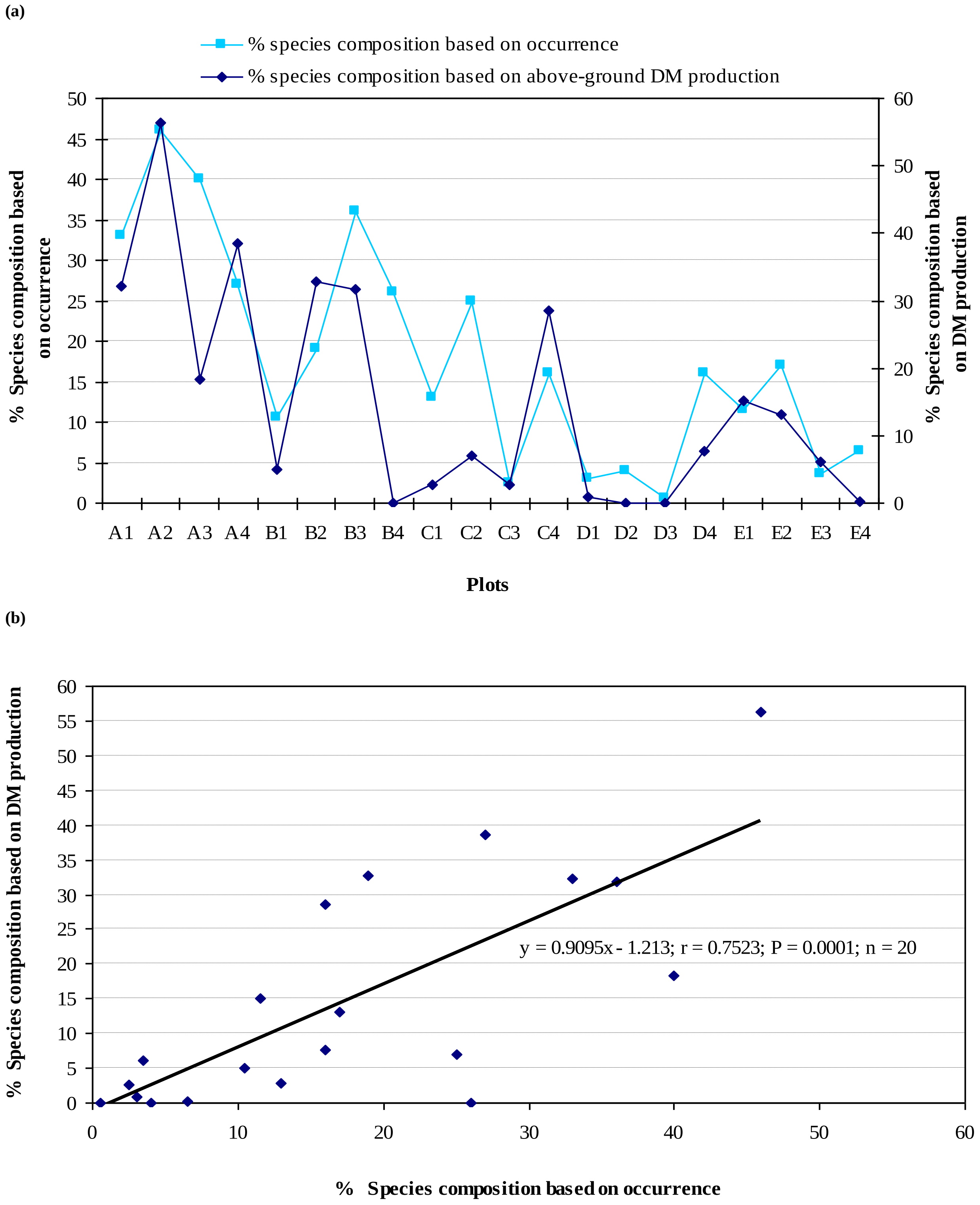

Figure 5.8: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Eragrostis chloromelas* during the 2004/05 growing season and (**b**) the regression analysis.

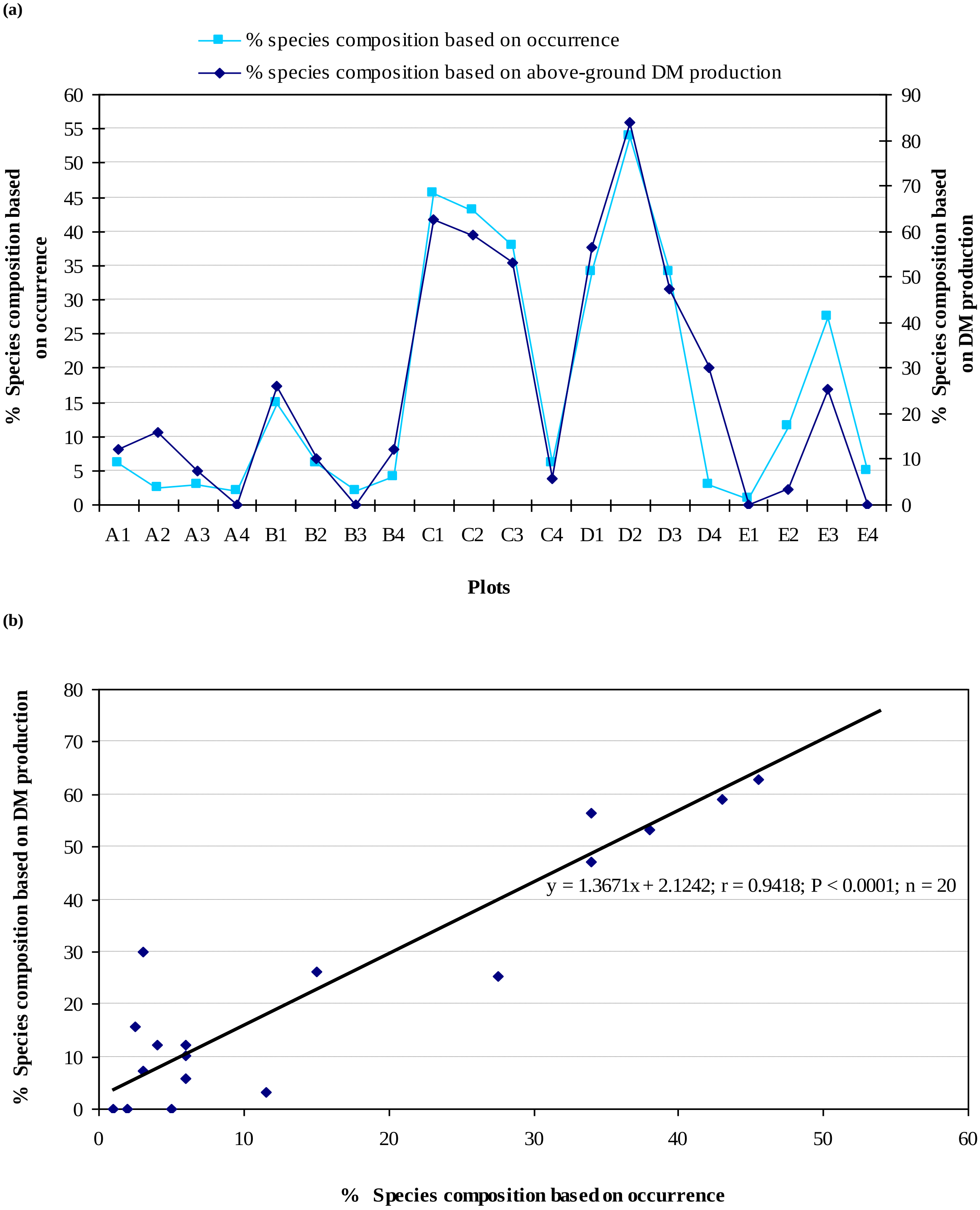

Figure 5.9: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Setaria incrassata* during the 2003/04 growing season and (**b**) the regression analysis.

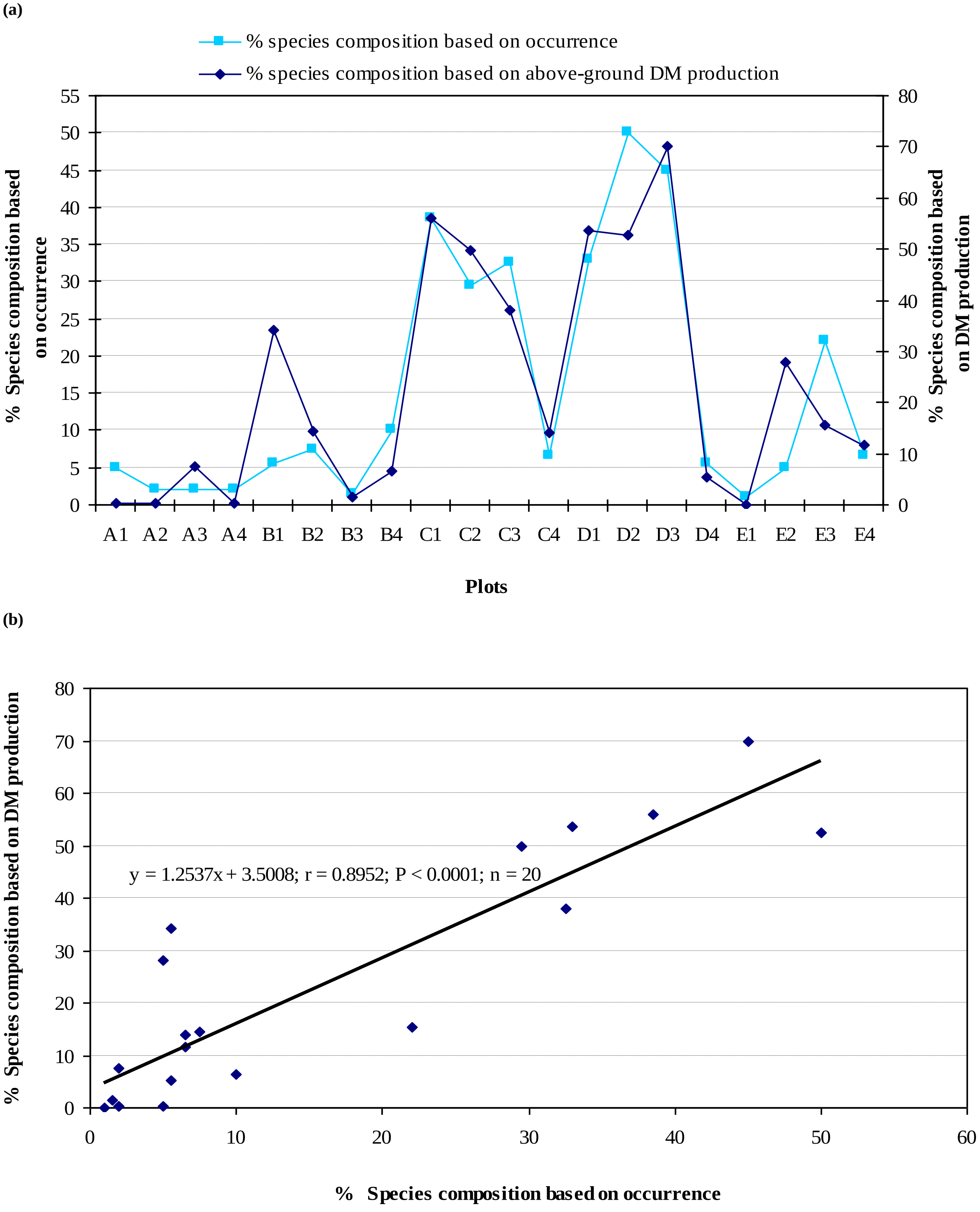

Figure 5.10: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Setaria incrassata* during the 2004/05 growing season and (**b**) the regression analysis.

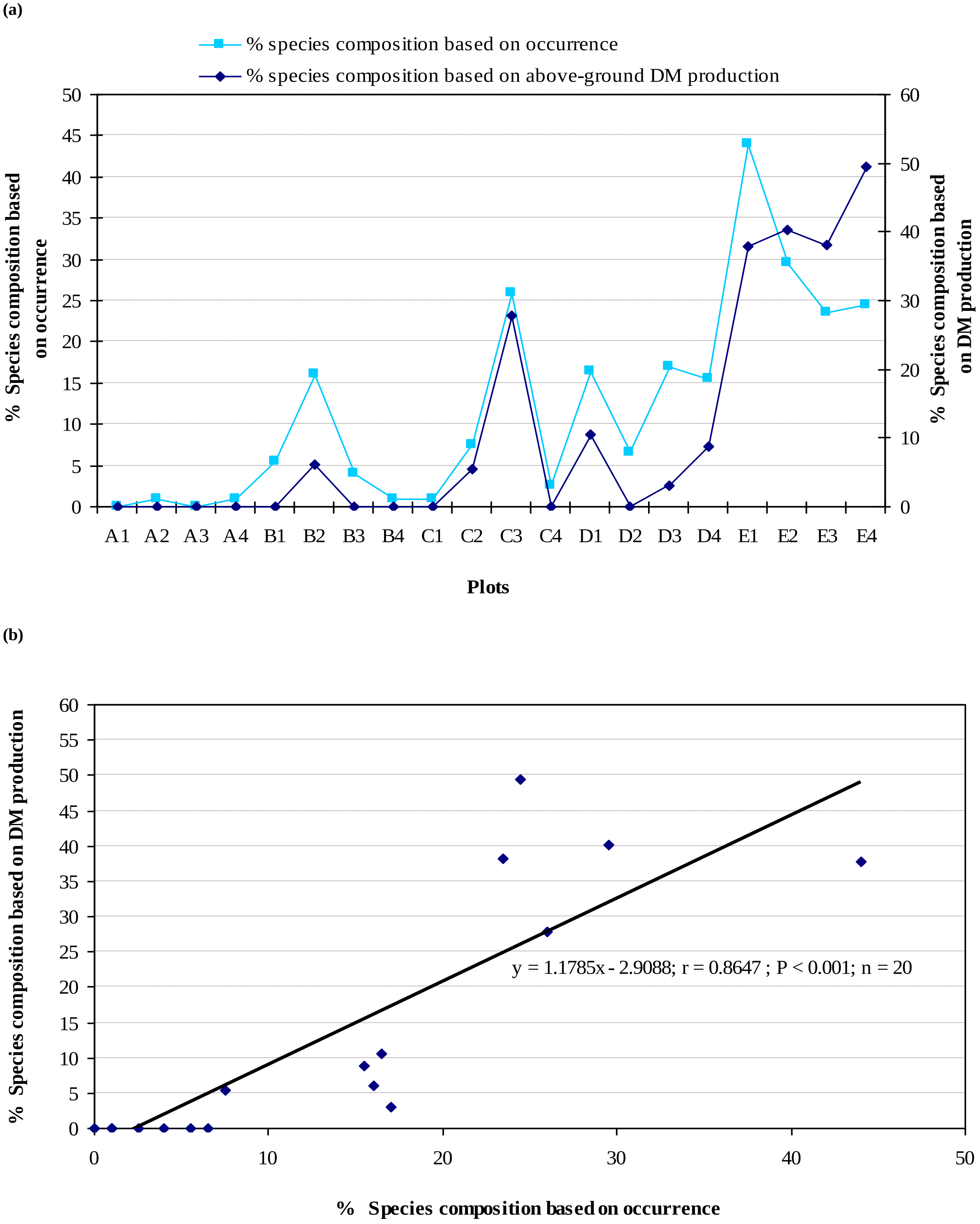

Figure 5.11: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Themeda triandra* during the 2003/04 growing season and (**b**) the regression analysis.

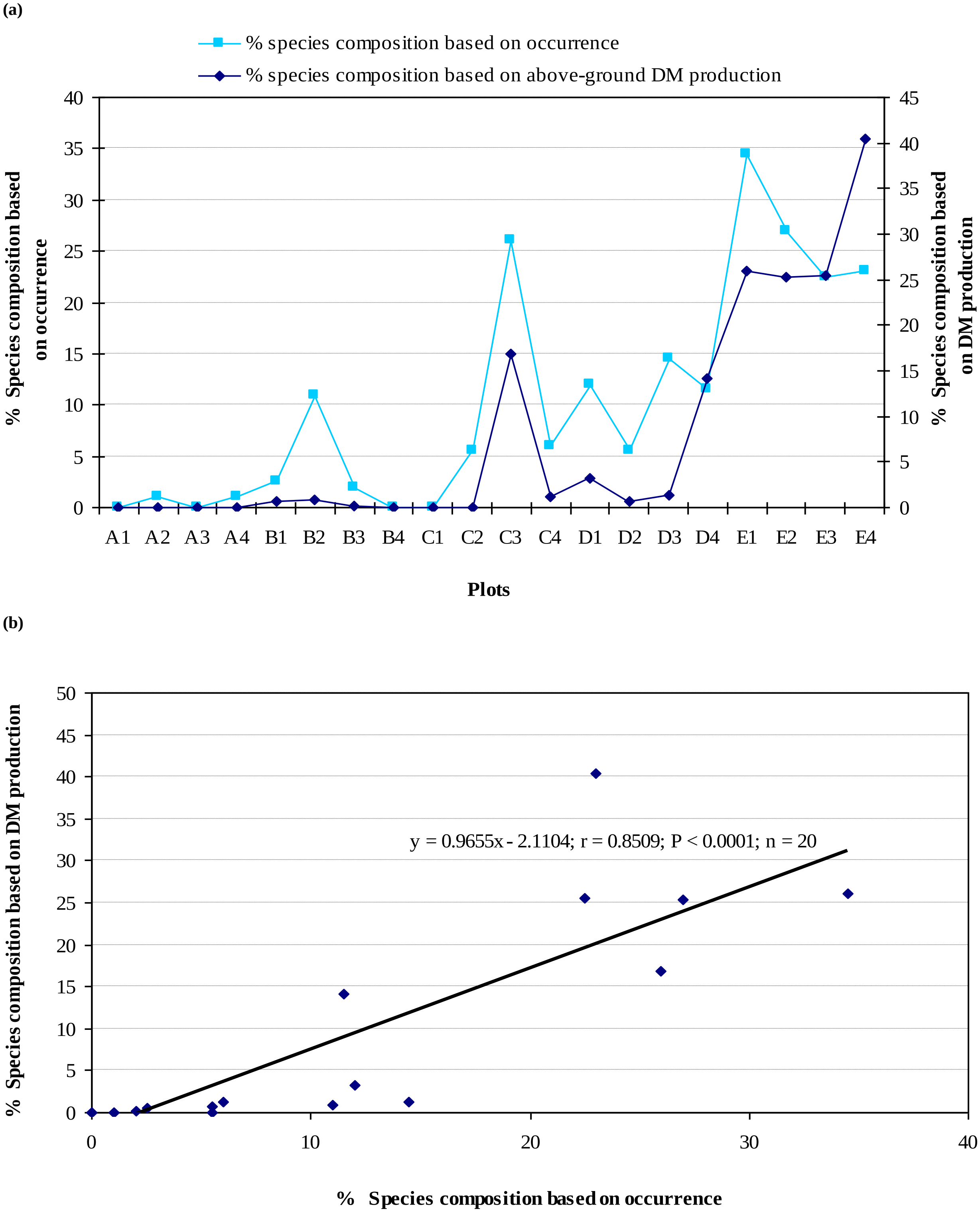

Figure 5.12: (**a**) Percentage species composition based on occurrence and percentage species composition based on above-ground DM production of *Themeda triandra* during the 2004/05 growing season and (**b**) the regression analysis.

5.3.3 Veld condition assessment

The five correlation coefficients (r), one for each correlation analysis between the species representing each of the five ecological classes (see section 5.2.3) and the remaining grass species, Karoo bushes and forbs (grouped), are presented in Appendix B_{13}. The final grouping of grass species into the various ecological classes are given in Table 5.3.

Table 5.3: Ecological classes of the grass species, Karoo bushes and forbs. * indicates that the species was grouped according to personal observations. † indicates species typical to that specific group.

Species	Group
Poaceae	
Digitaria eriantha†	Decreaser
Panicum stapfianum†	Decreaser
Setaria incrassata†	Decreaser
Themeda triandra†	Decreaser
Cymbopogon pospischilii†	Increaser Ia
Cynodon dactylon	Increaser Ia
Eragrostis plana†	Increaser Ia
Eragrostis chloromelas†	Increaser IIa
*Heteropogon contortus**†	Increaser IIa
Aristida bipartita†	Increaser IIb
*Eragrostis obtusa**†	Increaser IIb
*Aristida adscensionis**†	Increaser IIc
Brachiaria eruciformis†	Increaser IIc
Chloris virgata†	Increaser IIc
Tragus berteronianus†	Increaser IIc
Karoo bushes	Increaser IIc
Forbs	Increaser IIc

The occurrence of species of the different ecological classes in the experimental plots during 2003/04 and 2004/05 is presented in Figures 5.13 & 5.15. A schematic representation can be seen in Figures 5.14 & 5.16. The occurrence of Decreaser species increased from north (row A) to south (row E) (Figures 5.14a & 5.16a). The Decreaser grass species dominated plots C1-

3, D1-3 and E1-4 (Figures 5.13 & 5.15). Decreaser species were practically absent in plots A1-4 and B3&4 (Figures 5.13 & 5.15). *Setaria incrassata* and *T. triandra* contributed most to the Decreaser group (Figures 5.17 & 5.18).

The occurrence of Increaser Ia species was higher in the plots on the south-eastern side during 2003/04, but increased in the south-western side during 2004/05 (Figures 5.14b & 5.16b). An increase of 4% was found in plot D3, 8% in E2 and 3% in E3 (Figures 5.13 & 5.15). *Eragrostis plana*, followed by *C. dactylon*, contributed most to the Increaser Ia group (Figures 5.19 & 5.20). The overall occurrence of this ecological class was low.

The Increaser IIa group had the highest occurrence in the plots on the northern and north-western side (row A) of the grid (Figures 5.14c & 5.16c). The occurrence of this group decreased in all the plots except E1 (Figures 5.13 & 5.15). The occurrence of *H. contortus* in the Increaser IIa group was low (less than 5% in plot E2 during 2003/04) (Figures 5.21). This group was mostly dominated by *E. chloromelas* (Figures 5.21 & 5.22).

The occurrence of Increaser IIb species were the highest in plots in the northern side and increased in the western side during 2004/05 (Figures 5.14d & 5.16d). This ecological class was dominated by *A. bipartita* (Figures 5.23 & 5.24). *Eragrostis obtusa* contributed less than 10% in all the plots, except plot B2 during 2003/04 (Figure 5.23).

In plots A1-4, B2-4, C4 and D4 Increaser IIa and IIb species dominated during 2003/04 (Figure 5.13). During 2004/05 the Increaser IIc species were more abundant in plots B2 and C4 (Figure 5.15). In plot D4 the Increaser IIa and IIb contributed relatively the same than the Increaser IIc species to the species composition (Figure 5.15). It is clear that an increase in Increaser IIb species caused a decline in the Increaser IIa species. Correlation analysis showed a highly significant ($P < 0.001$) correlation between these two ecological classes. A significant ($P < 0.01$) negative linear correlation was found between the occurrence of the Decreaser group and the Increaser IIa ($r = -0.8450$) and IIb ($r = -0.8017$) groups, which implies that species of the Increaser IIa and IIb groups were abundant in areas where the percentage occurrence of Decreaser species was low.

The occurrence of Increaser IIc plant species was generally low, with the highest occurrence in plots B1, followed by C4 during 2003/04 (Figures 5.13 & 5.14e). The occurrence of Increaser IIc grass species increased in all the plots (Figure 5.15). This group, which includes Karoo bushes and forbs, increased with 8.79% from 2003/04 to 2004/05. This increase was mostly the result of the increase in occurrence of *Tragus berteronianus*, *B. eruciformis* and forbs (Figures 5.25 - 5.28).

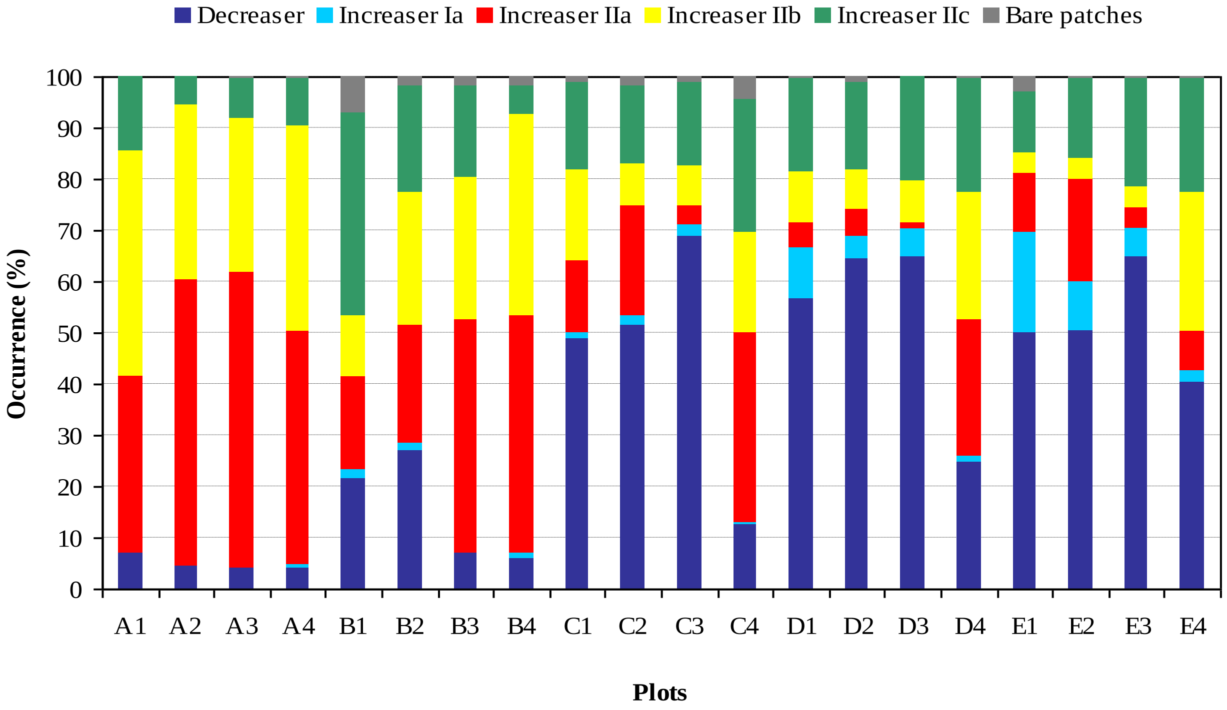

Figure 5.13: The percentage contribution of the Decreaser and Increaser groups to the species composition of the herbaceous layer of the experimental plots during the 2003/04 growing season.

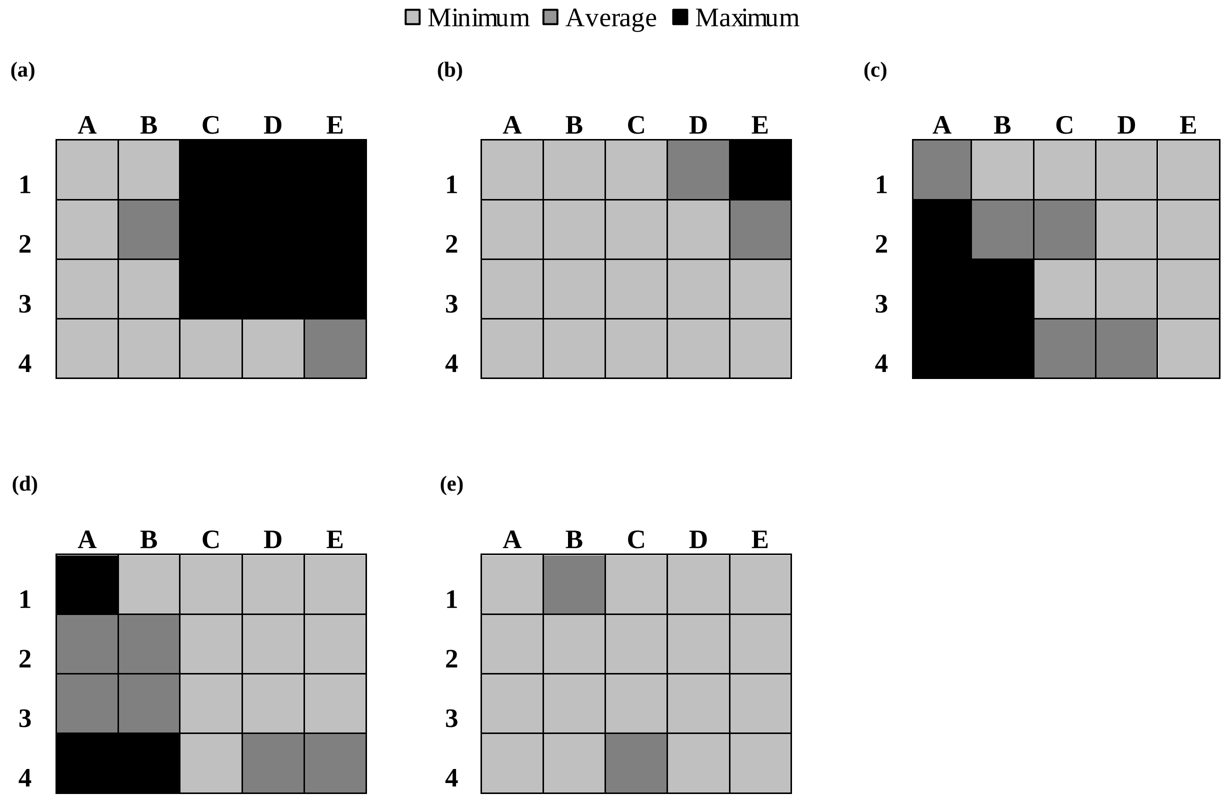

Figure 5.14: Schematic representation of the percentage contribution of the (**a**) Decreaser (min = 3-25, ave = 25-47, max = 47-69), (**b**) Increaser Ia (min = 0-7.33, ave = 7.33-14.67, max = 14.67-22), (**c**) Increaser IIa (min = 0.5-19.67, ave = 19.67-38.83, max = 38.83-58), (**d**) Increaser IIb (min = 4-20.83, ave = 20.83-37.67, max =37.67-54.5) and (**e**) Increaser IIc (min = 4-24.67, ave = 24.67-45.33, max = 45.33-66) ecological classes to the species composition of the herbaceous layer in the twenty plot grid during the 2003/04 growing season.

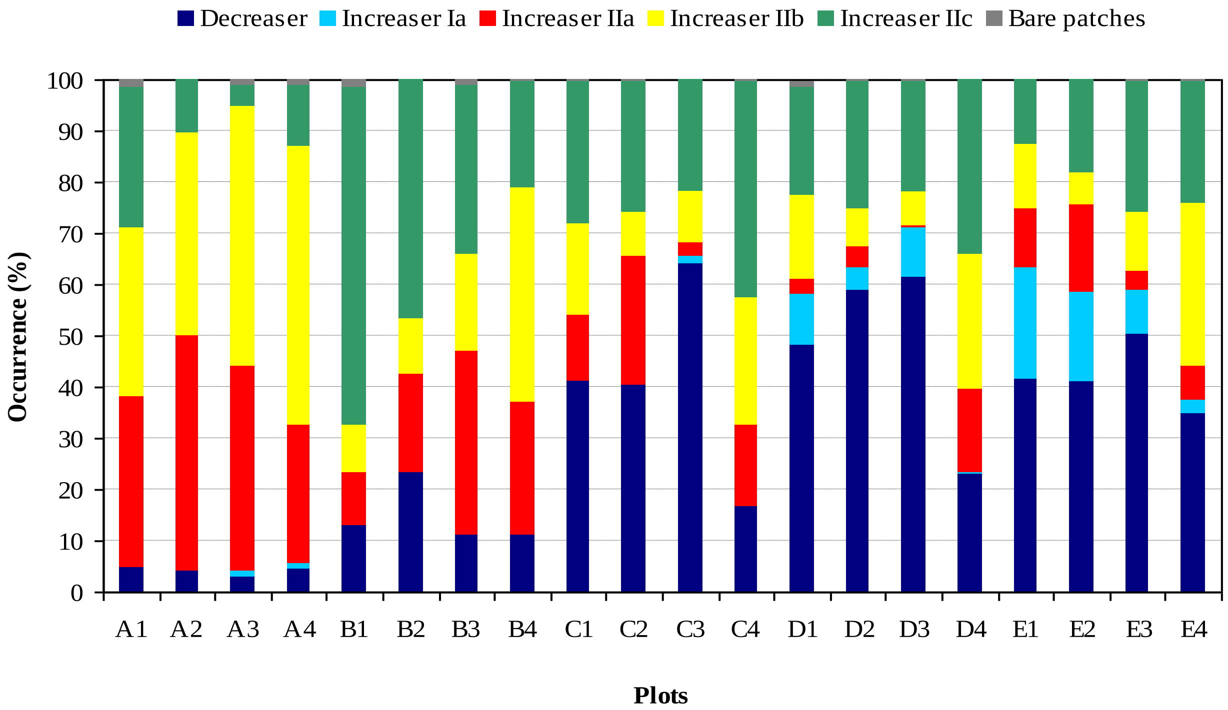

Figure 5.15: The percentage contribution of the Decreaser and Increaser groups to the species composition of the herbaceous layer of the experimental plots during the 2004/05 growing season.

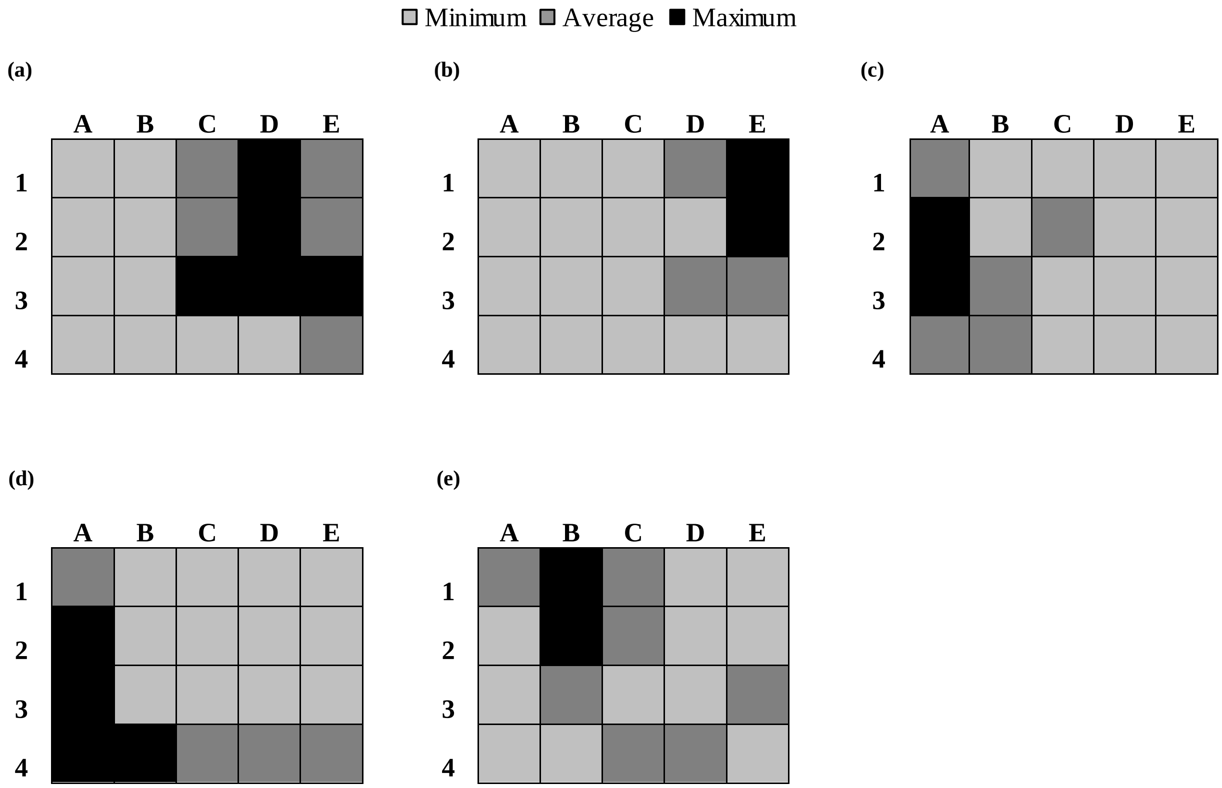

Figure 5.16: Schematic representation of the percentage contribution of the (**a**) Decreaser (min = 3-25, ave = 25-47, max = 47-69), (**b**) Increaser Ia (min = 0-7.33, ave = 7.33-14.67, max = 14.67-22), (**c**) Increaser IIa (min = 0.5-19.67, ave = 19.67-38.83, max = 38.83-58), (**d**) Increaser IIb (min = 4-20.83, ave = 20.83-37.67, max =37.67-54.5) and (**e**) Increaser IIc (min = 4-24.67, ave = 24.67-45.33, max = 45.33-66) ecological classes to the species composition of the herbaceous layer in the twenty plot grid during the 2004/05 growing season.

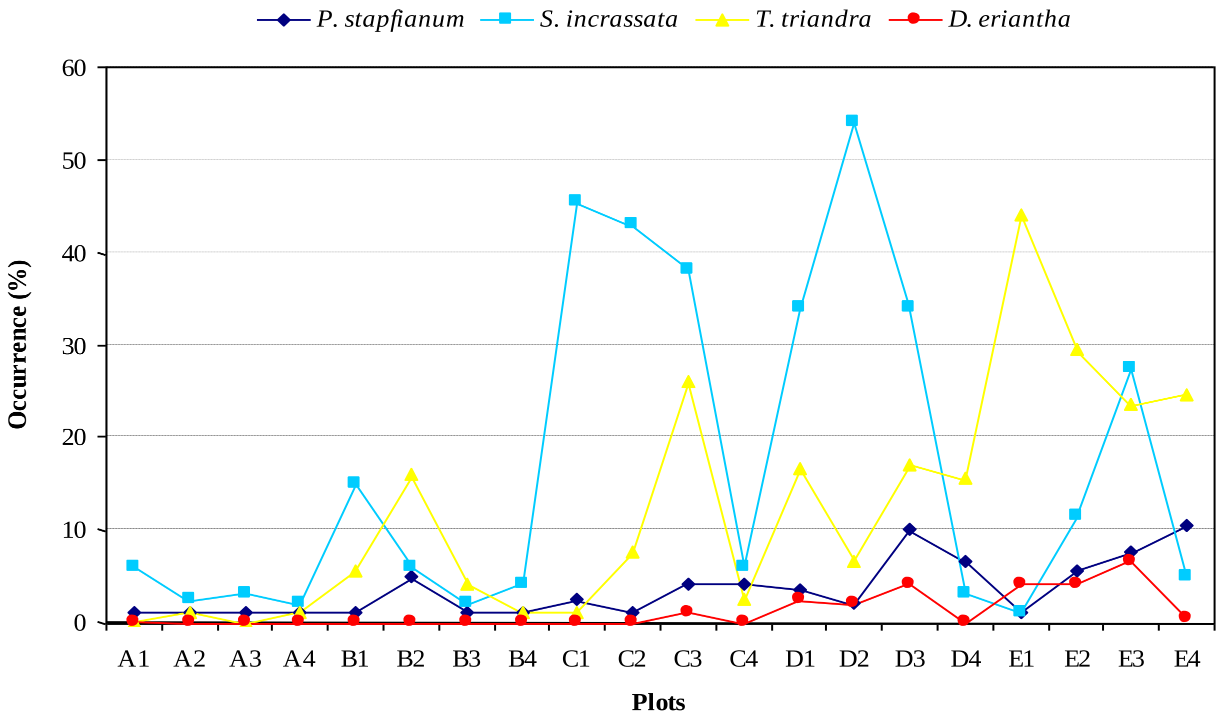

Figure 5.17: Occurrence of Decreaser grass species in the experimental plots during 2003/04.

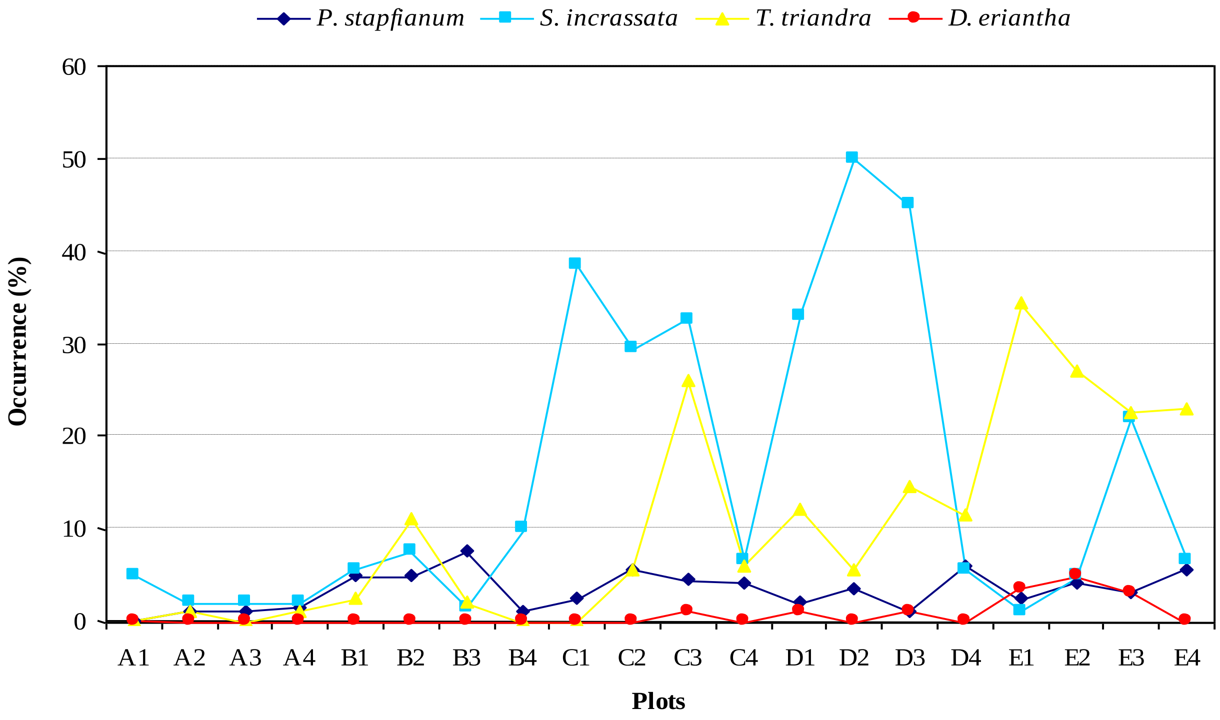

Figure 5.18: Occurrence of Decreaser grass species in the experimental plots during 2004/05.

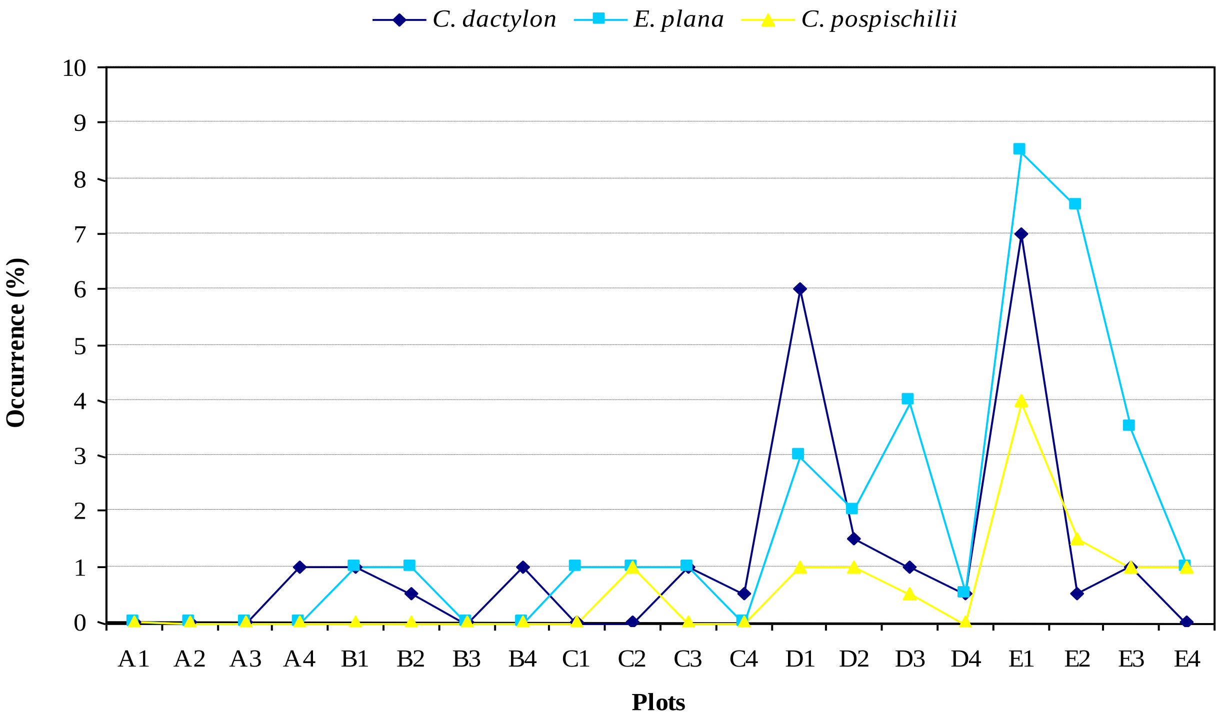

Figure 5.19: Occurrence of Increaser Ia grass species in the experimental plots during 2003/04.

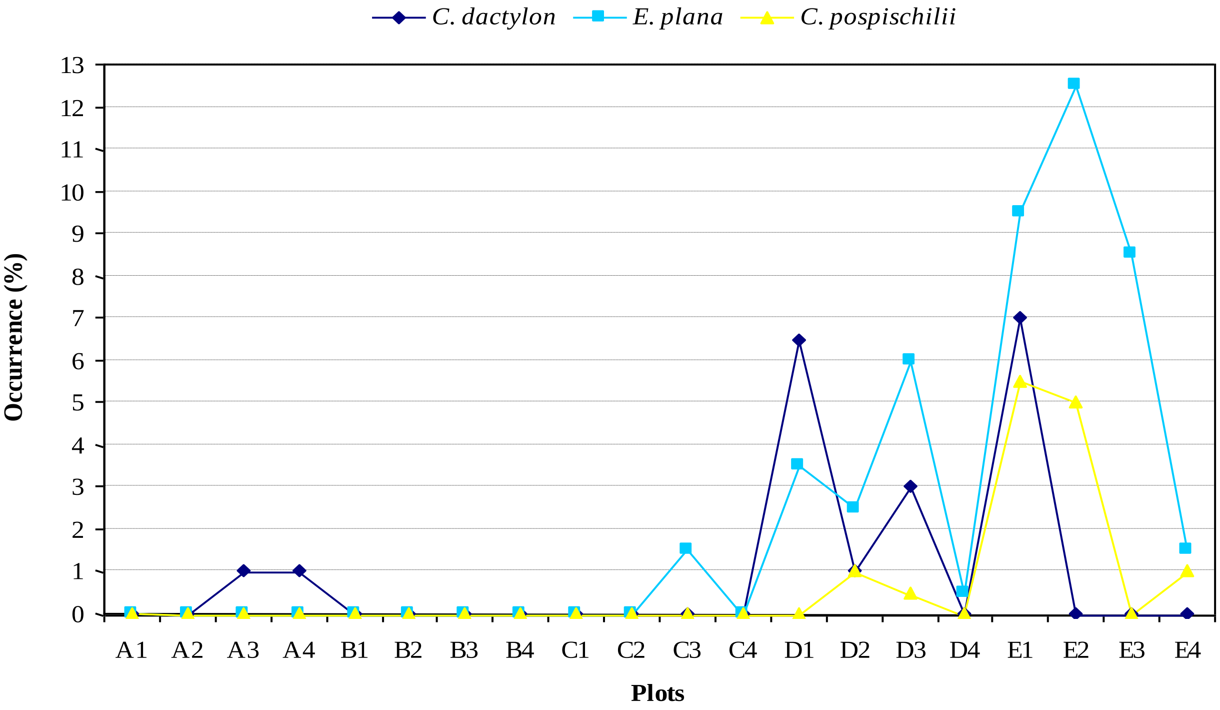

Figure 5.20: Occurrence of Increaser Ia grass species in the experimental plots during 2004/05.

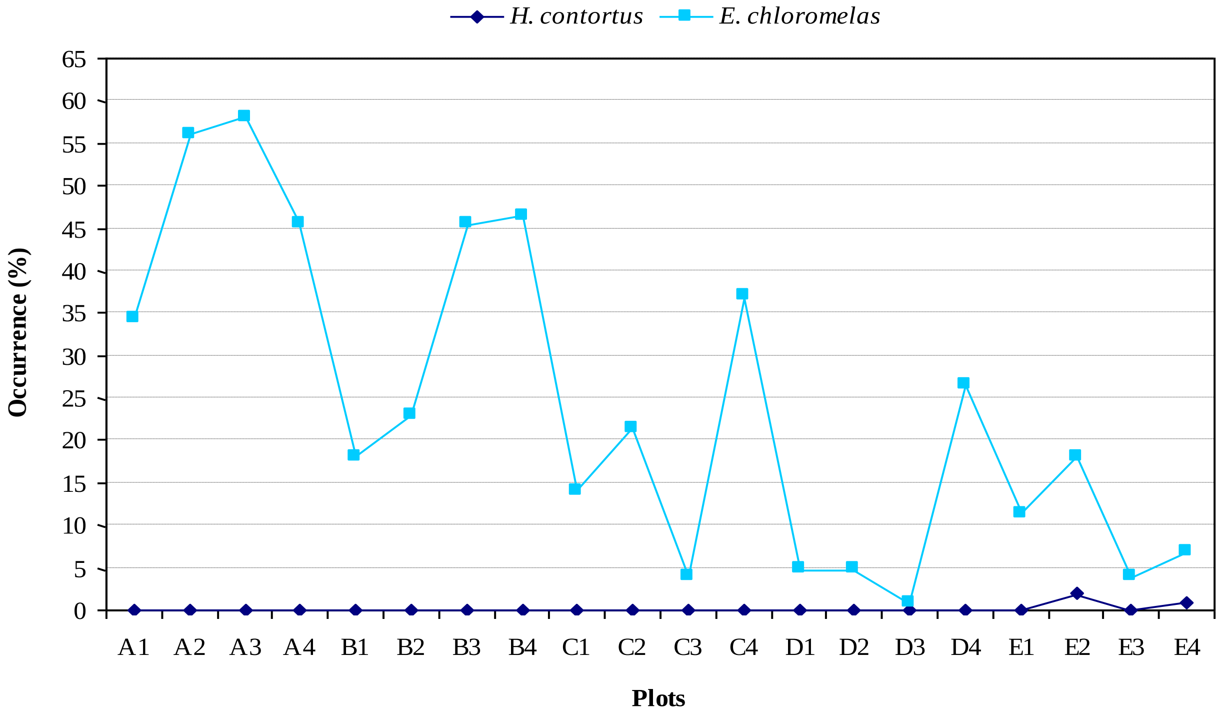

Figure 5.21: Occurrence of Increaser IIa grass species in the experimental plots during 2003/04.

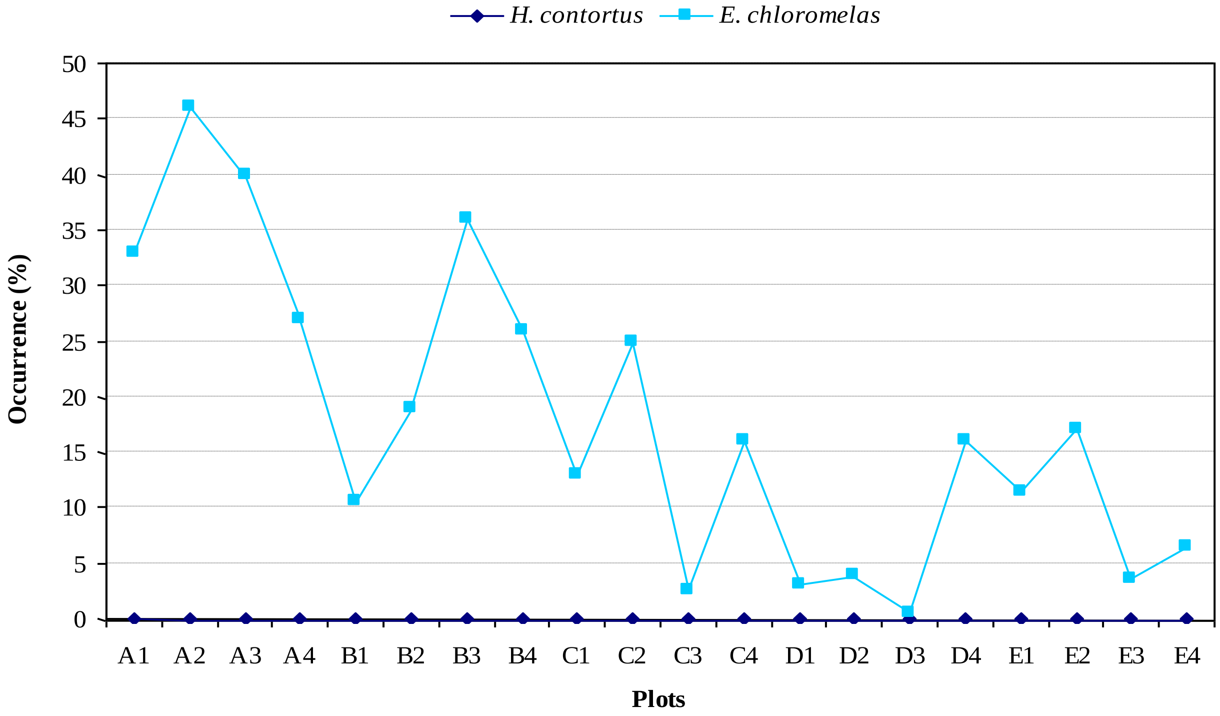

Figure 5.22: Occurrence of Increaser IIa grass species in the experimental plots during 2004/05.

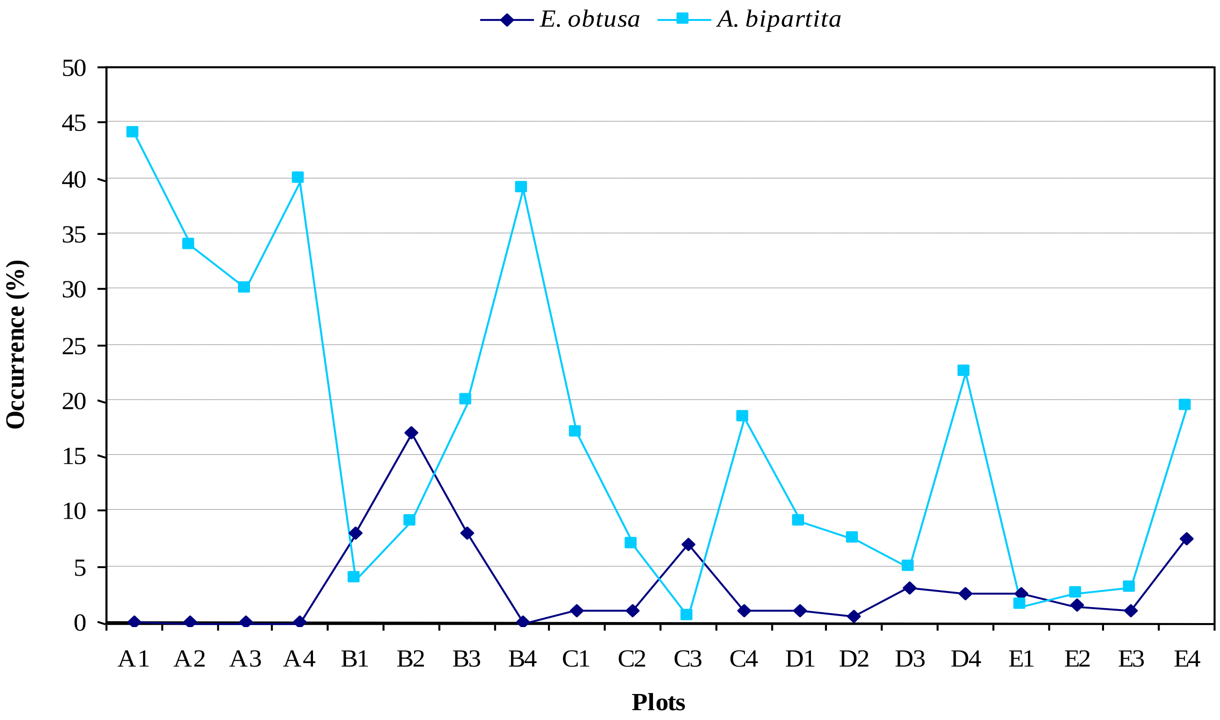

Figure 5.23: Occurrence of Increaser IIb grass species in the experimental plots during 2003/04.

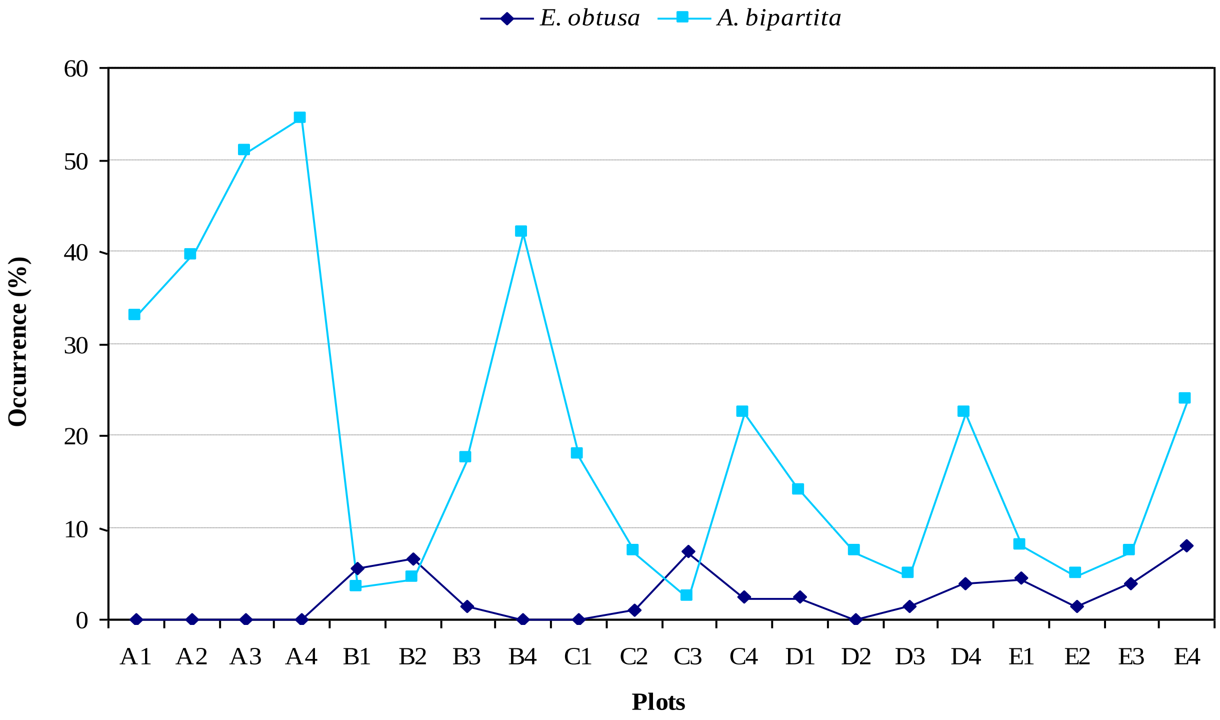

Figure 5.24: Occurrence of Increaser IIb grass species in the experimental plots during 2004/05.

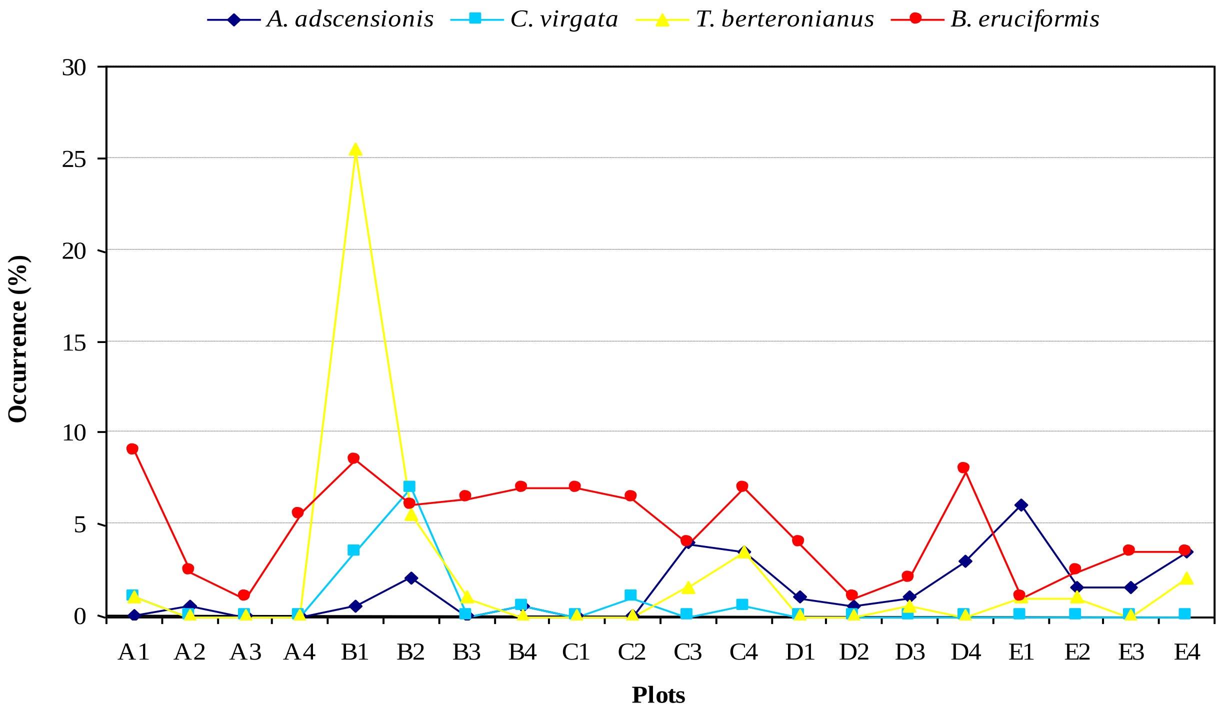

Figure 5.25: Occurrence of Increaser IIc grass species in the experimental plots during 2003/04.

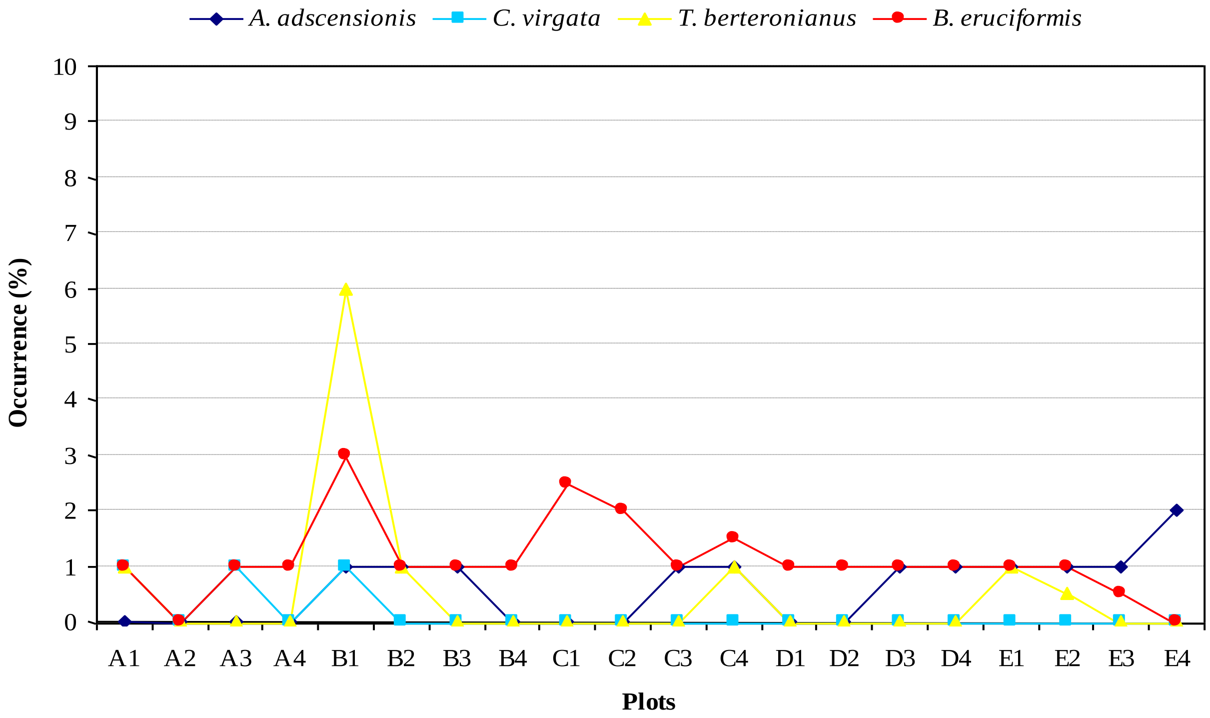

Figure 5.26: Occurrence of Increaser IIc grass species in the experimental plots during 2004/05.

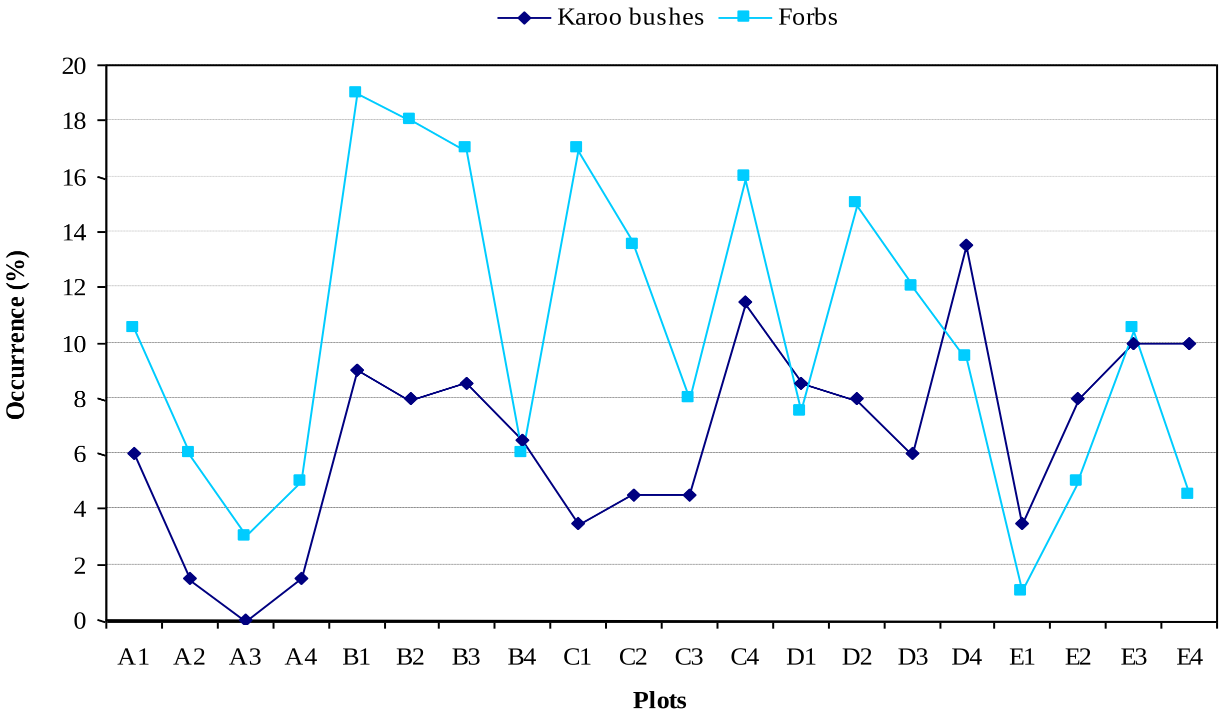

Figure 5.27: Occurrence of Increaser IIc non-grasses (Karoo bushes and forbs) in the experimental plots during 2003/04.

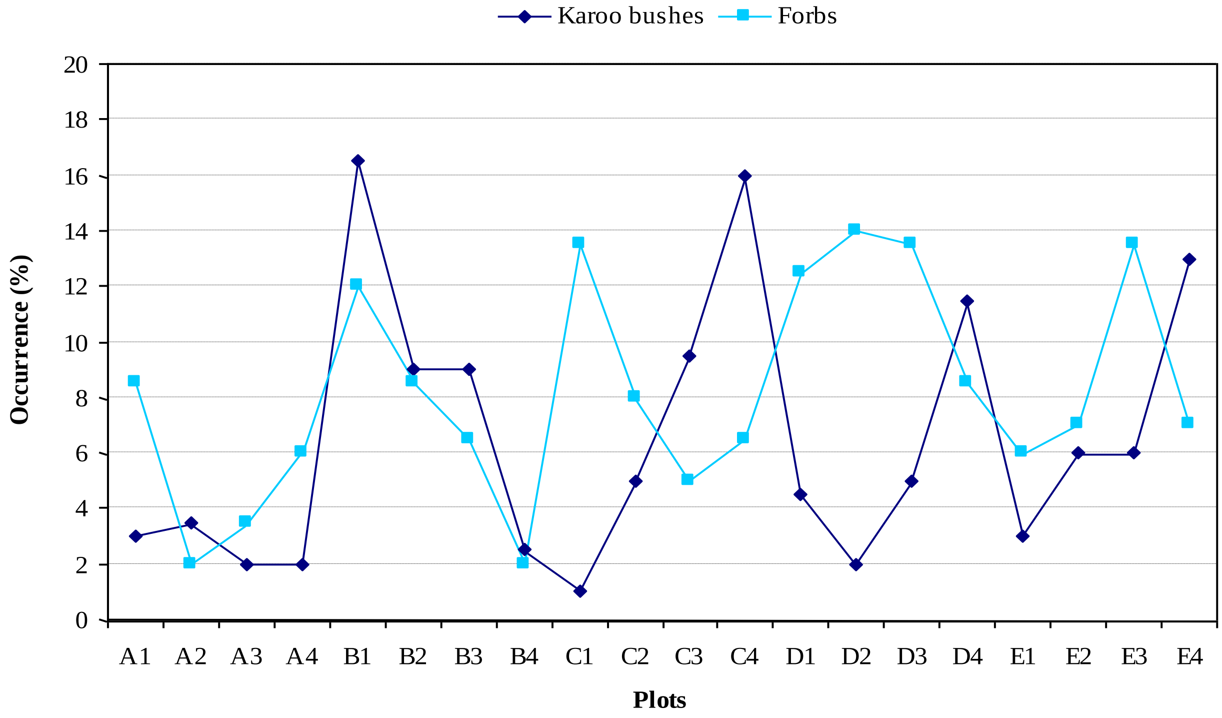

Figure 5.28: Occurrence of Increaser IIc non-grasses (Karoo bushes and forbs) in the experimental plots during 2004/05.

The veld condition scores (VCS) of the twenty experimental plots are presented in Table 5.4. The VCS of each plot was substantially influenced by the dominant ecological class of species in each plot. This is clear from plots A1-4, B3, B4, C4 and D4, where the dominant grass species were Increaser IIa (*E. chloromelas*) and IIb (*A. bipartita*) species, which had a lower VCS (average 509.6) than the other plots with a Decreaser as the dominant species (Table 5.4). Plots C3, D1, D3 and E3, where Decreaser species were dominant, had a higher VCS (average 721.4). The Decreaser and Increaser Ia groups were significantly ($P < 0.001$) positively correlated with the VCS, whereas the Increaser IIa, IIb and IIc (excluding Karoo bushes and forbs) groups were significantly ($P < 0.001$) negatively correlated with the VCS (Figures 5.29 –5.33). Therefore, it is clear that the VCS declined with an increase in grass species of the Increaser IIa, IIb and IIc groups. Plot C3 had the highest score during 2003/04, whereas plot D3 followed by C3 during 2004/05. In both seasons plot B1 had the lowest VCS. There was a general decline in the condition of the veld from 2003/04 to 2004/05.

Table 5.4: Veld condition score (VCS) of each of the twenty experimental plots during the 2003/04 and 2004/05 growing season, respectively.

Plot	**Veld conditon score (VCS)**		
	2003/04	**2004/05**	**Increase (+)/Decrease (-)**
A1	503.0	440.5	-62.5
A2	585.5	530.5	-55.0
A3	573.5	526.0	-47.5
A4	534.5	476.5	-58.0
B1	435.5	305.1	-130.4
B2	559.0	458.5	-100.5
B3	518.0	471.0	-47.0
B4	554.0	480.5	-73.5
C1	684.0	600.5	- 83.5
C2	726.5	639.5	-87.0
C3	778.5	730.0	-48.5
C4	490.5	419.0	-71.5
D1	728.0	658.0	-70.0
D2	760.5	704.0	-56.5
D3	730.0	732.5	+2.5
D4	564.5	485.5	-79.0
E1	745.0	712.0	-33.0
E2	738.5	695.5	-43.0
E3	753.5	660.8	-92.7
E4	605.0	564.5	-40.5

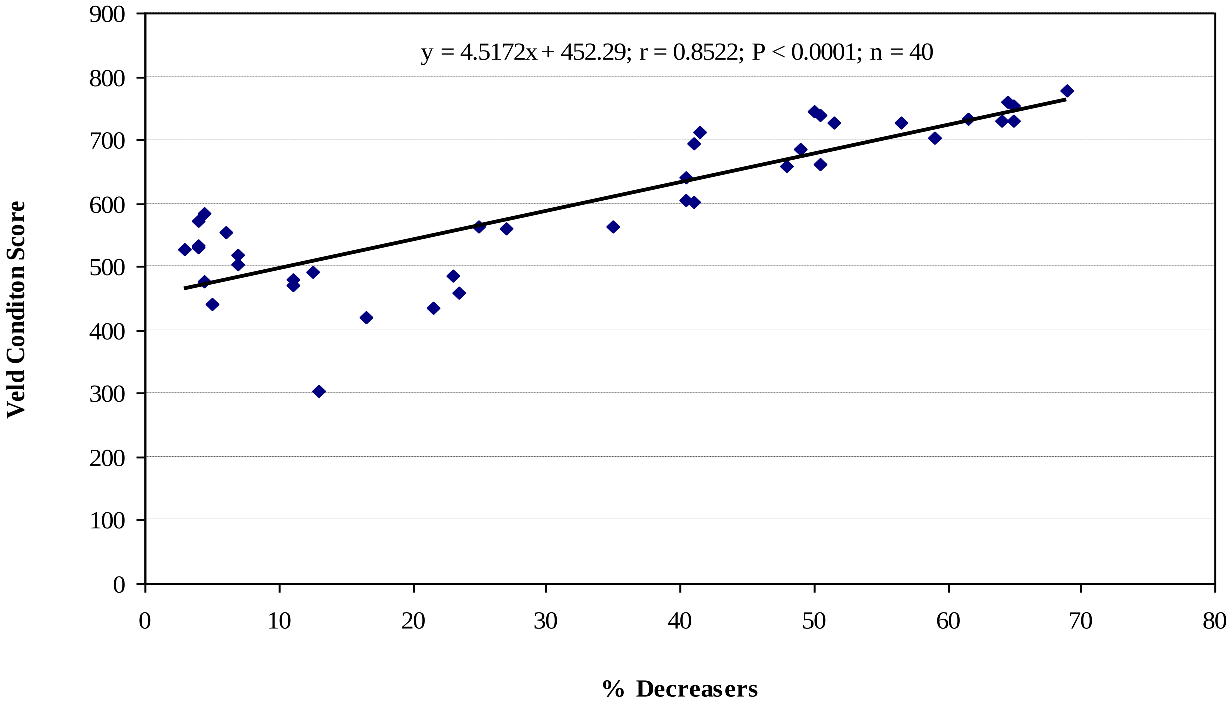

Figure 5.29: Regression analysis of the relationship between % Decreasers (independent variable) and Veld Condition Score (dependant variable).

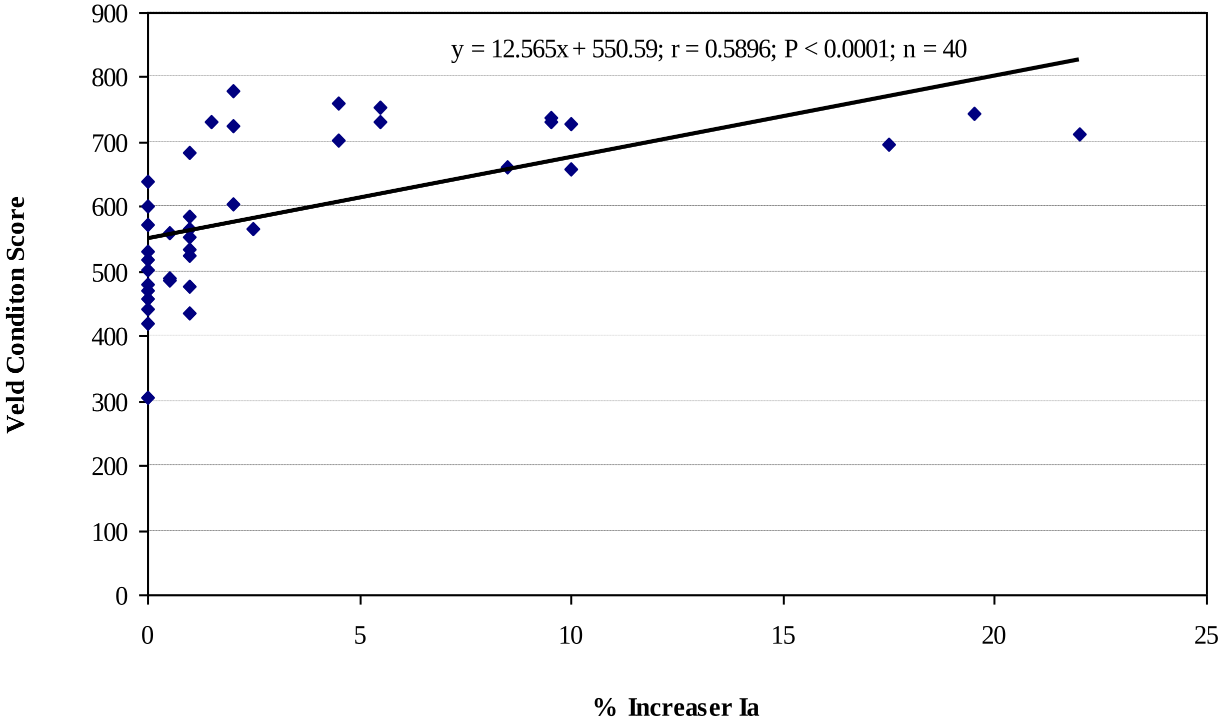

Figure 5.30: Regression analysis of the relationship between % Increaser Ia (independent variable) and Veld Condition Score (dependant variable).

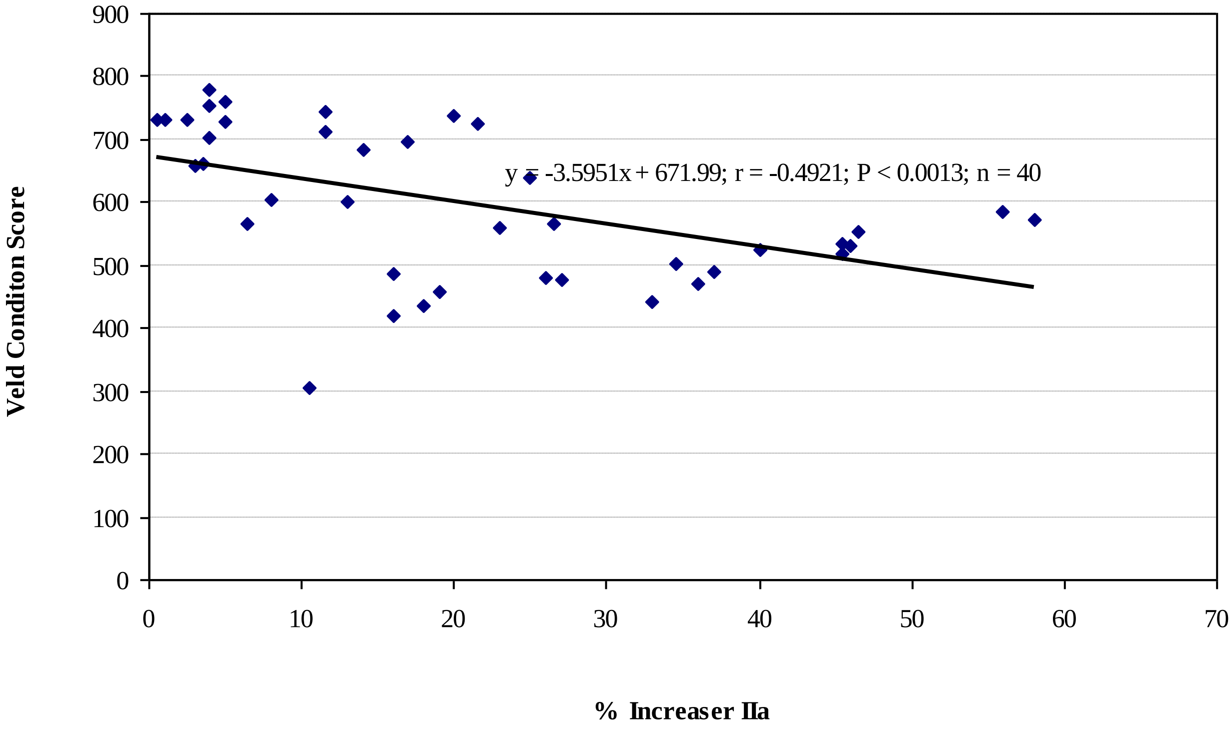

Figure 5.31: Regression analysis of the relationship between % Increaser IIa (independent variable) and Veld Condition Score (dependant variable).

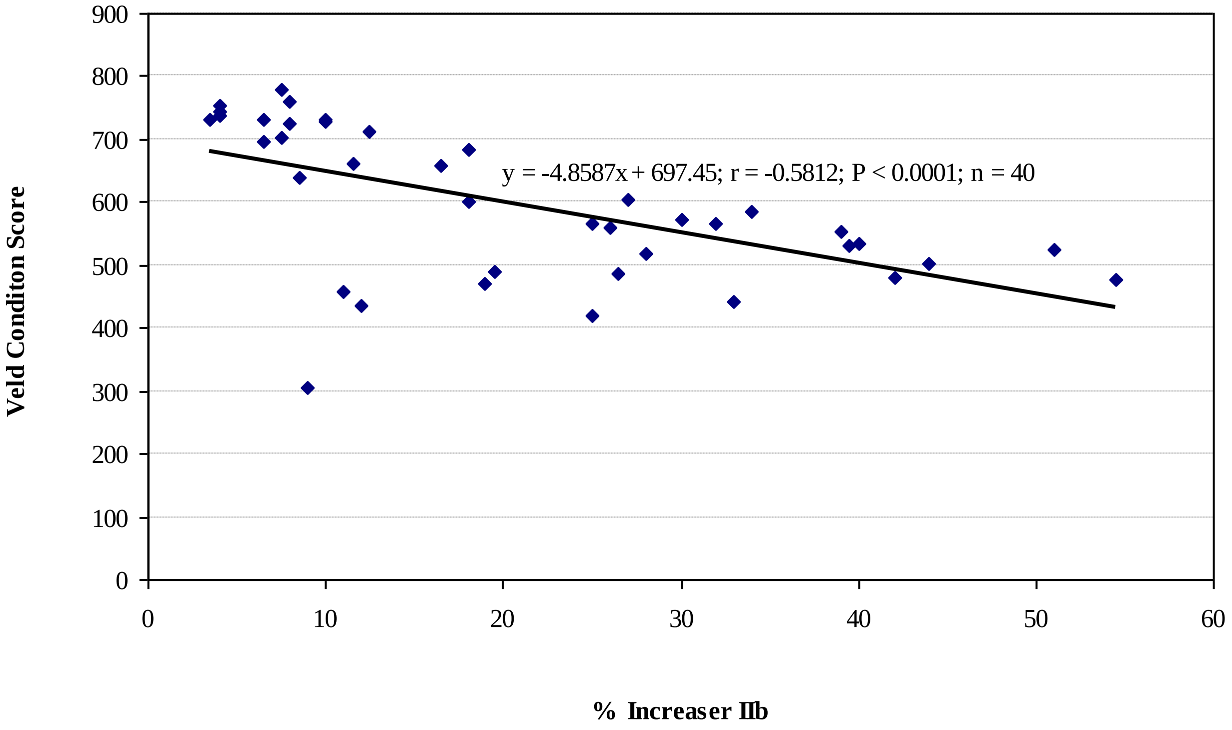

Figure 5.32: Regression analysis of the relationship between % Increaser IIb (independent variable) and Veld Condition Score (dependant variable).

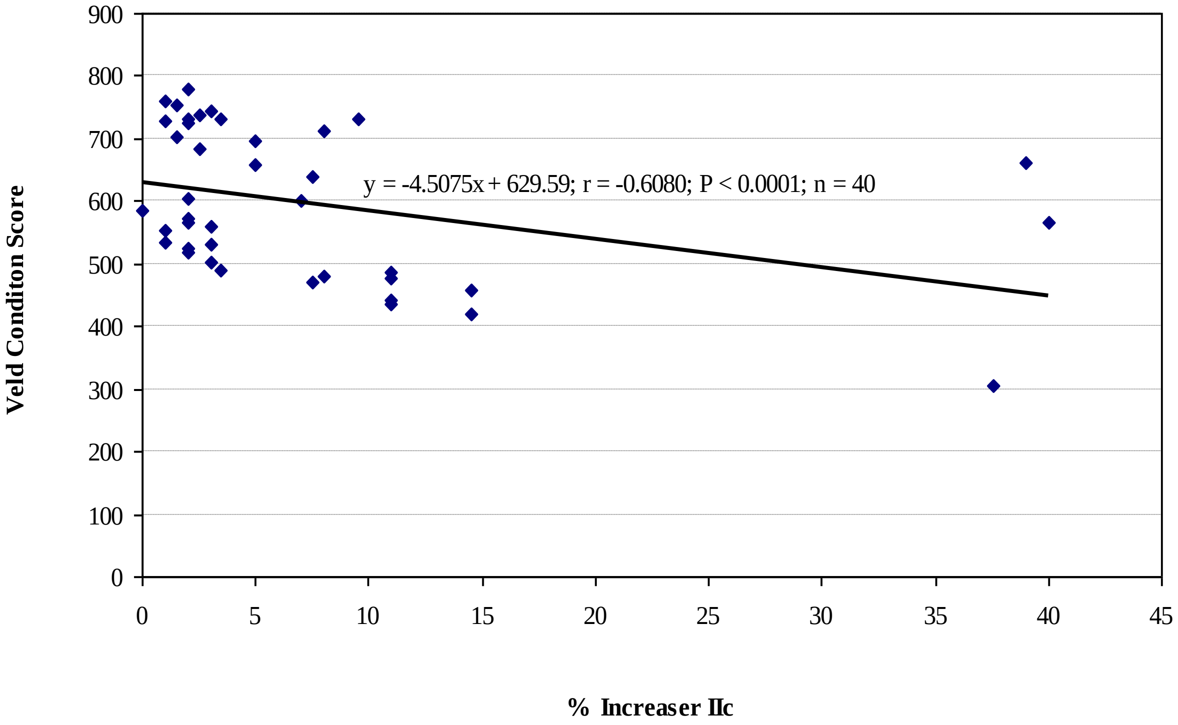

Figure 5.33: Regression analysis of the relationship between % Increaser IIc (independent variable) and Veld Condition Score (dependant variable).

5.3.4 Grazing capacity

The grazing capacity of each plot is presented in Table 5.5 and a schematic representation in Figure 5.42. Plots B1, 3&4 had the lowest grazing capacity during 2003/04 and 2004/05 respectively. These plots also had the lowest above-ground DM production (Table 5.2). Plot A1 had the highest grazing capacity as well as DM production in 2003/04, and D1 during 2004/05. The major increase in the grazing capacity of plot B1 is due to the increase in the production of *S. incrassata* (Appendix B9). The grazing capacity, for veld in a semi-arid area, was relatively good in most of the plots (Figure 5.34). There was a highly significant ($P < 0.001$) negative correlation between the amount of hectares needed for a GU and the Decreaser ecological class, and a significant ($P < 0.01$) positive correlation with the Increaser IIa group (Table 5.6). The correlation coefficients were, however, low for all the other ecological classes.

Table 5.5: Grazing capacity of the experimental plots during the 2003/04 and 2004/05 growing season.

Plot	Grazing capacity (ha GU^{-1})		
	2003/04	2004/05	Increase (+)/Decrease (-)
A1	7.8	10.3	+2.5
A2	11.0	12.4	+1.4
A3	10.2	14.2	+4.2
A4	12.4	11.1	+1.3
B1	14.4	9.7	-4.7
B2	12.7	12.9	+0.2
B3	20.4	13.4	-7.0
B4	13.2	21.7	+8.5
C1	11.2	11.5	+0.3
C2	11.1	11.5	+0.4
C3	10.3	11.6	+1.3
C4	17.9	11.2	-6.7
D1	11.6	7.9	-3.7
D2	8.8	9.7	+0.9
D3	8.1	9.1	+1.0
D4	12.0	15.0	+3.0
E1	10.2	13.6	+3.4
E2	11.0	11.4	+0.4
E3	10.4	11.1	+0.7
E4	10.7	8.1	-2.6

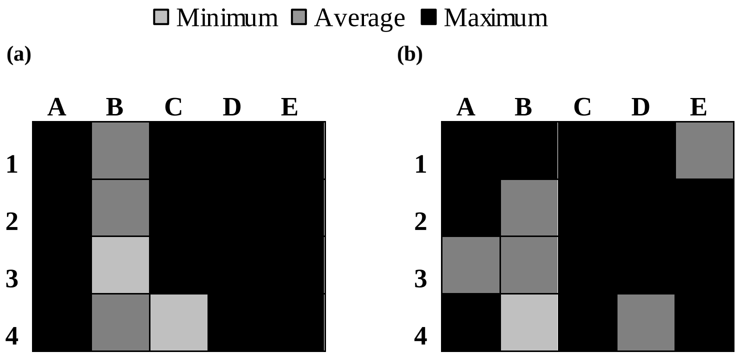

Figure 5.34: Schematic representation of the grazing capacity (ha GU^{-1}) (min = 7.8-12.43, ave = 12.43-17.07, max = 17.07-21.7) of the experimental plots during (**a**) 2003/04 and (**b**) 2004/05.

Table 5.6: Results from the Correlation analysis between the amount of hectares needed for a GU (dependant variable) and the different ecological classes, and above-ground DM production (independent variable). [ns = not significant; * = significant; ** = very significant; *** = highly significant]

Variables	**Correlation coefficient (r)**	**P value**
Decreaser	-0.4362	0.005^{**}
Increaser Ia	-0.2144	0.184^{ns}
Increaser IIa	0.4010	0.010^{*}
Increaser IIb	0.2863	0.073^{ns}
Increaser IIc	-0.0022	0.989^{ns}
Dry matter production	-0.6923	$< 0.0001^{***}$

5.4 DISCUSSION

The vegetation of the study area is the result of a series of developmental and physiological processes within individual plants. The developmental morphology of plants defines their architectural organisation. It influences the plant's palatability and accessibility to herbivores, and affects its ability to grow following defoliation. Physiological processes establish the capacity for the capture of solar energy and the synthesis of the products necessary to sustain structural development (Briske 1991). Biotic factors influencing the developmental morphology and physiological processes of plants include humans, animals, insects, plants (competition) and micro-organisms, and abiotic factors include topography, soil, climate and fire. The biotic conditions that exist or are imposed on any plant community will determine the composition of that community. The botanical species composition indicates the relationship between the desirable and undesirable grazing plants. The occurrence of the former group mainly determines the availability of suitable forage for the herbivore game species and is, therefore, important in determining the grazing capacity.

The Sörensen's quotient values (Figure 5.3) indicate that the botanical composition between adjacent experimental plots was generally similar, although each plot contained unique species within each comparison. The plots on the northern side of the grid had lower values than plots on the southern side, which indicates a larger degree of variation in the botanical composition between the northern plots. Fifth teen grass species were recorded in the study area but four made up the bulk of the herbaceous layer, namely *A. bipartita*, *E. chloromelas*, *S. incrassata* and *T. triandra*. Because the leaf blades of *A. bipartita* (a weak perennial tufted grass) are usually rolled, curled and rough to touch, it is relatively unpalatable and has a low grazing value (Roberts 1973; Van Oudtshoorn 1999). *Eragrostis chloromelas* is a perennial tufted grass and is reasonably palatable early in the growing season with an average grazing value (Roberts 1973; Moffett 1997; Van Oudtshoorn 1999). *Aristida bipartita* was a dominant grass species in 55% of the experimental plots, and *E. chloromelas* in 65% of the plots. Their occurrence was the highest in plots on the northern and western sides of the grid. *Setaria incrassata* is a perennial tufted grass with long round leaf blades and a high grazing value (Van Oudtshoorn 1999). It was a dominant grass species in 40% of the plots, which mostly occurred on the eastern side and in the centre of the grid layout. *Themeda triandra* is generally regarded as one of the best climax grazing grasses in the Free State (Roberts 1973; Moffett 1997; Van Oudtshoorn 1999). It is especially palatable when young, forming a very leafy tuft, but becoming less palatable as it matures. It has a high grazing value and the nutritive value is good in summer but poor in winter (Roberts 1973; Moffett 1997). *Themeda triandra* was a dominant grass species in 40% of the plots, mostly located on the southern side of the grid. Other less abundant grass species included the palatable *P. stapfianum*, the less palatable *E. obtusa* and *B. eruciformis,* and the unpalatable *E. plana*, *T. berteronianus* and *A. adscensionis* (Van Oudtshoorn 1999).

The progressive development of vegetation in any area, through a series of different plant groupings or communities, is known as plant succession (Tainton & Hardy 1999; Van Oudtshoorn 1999). Specific plant succession patterns occur under particular soil and climatic conditions, and some plants can therefore be regarded as indicator species. Plant succession is continuous until the climax plant community has been established. One can distinguish between three succession stages, namely: the pioneer, sub-climax and climax stage (Van Oudtshoorn 1999). Grasses in the pioneer stage are quick-reacting annual or tough perennial grasses that can grow under extremely unfavourable conditions. They protect the bare soil against wind, sun and flooding. The pioneer grass cover of the study area was dominated by annual grass species such as *B. eruciformis*, *T. berteronianus* and *A. adscensionis*. Sub-climax grass species are denser than pioneer species and provide more protection to the soil. These species replace the pioneer species if growing conditions are favourable. The extremely low sub-climax grass cover (Table 5.1) consisted of *E. obtusa* and *E. plana.* Climax grasses are strong perennial plants that are adapted to normal optimal growth conditions. The climax grass cover in the experimental area was dominated by *A. bipartita*, *E. chloromelas*, *S. incrassata* and *T. triandra*. These four species dominated the herbaceous layer in the study area, suggesting that the area has reached a successional climax.

The concept of stability and equilibrium of a plant community and the factors that influence this state is of great importance. From the literature it is apparent that plant communities can display both equilibrial and non-equilibrial trends (Sullivan & Rohde 2002). The increase in the occurrence of pioneer grass species, mostly *B. eruciformis* and *T. berteronianus*, and the decrease in climax grass species in all the experimental plots (Table 5.1) is an indication that the veld is deteriorating. In contrast, the general decrease in percentage bare patches can be attributed to the increase in pioneer and forb species (Table 5.1). According to Van Oudtshoorn (1999), if the plant community is disturbed, it moves back to the pioneer stage. This is clearly visible in plot B1. During 2003/04 the climax stage dominated, but during 2004/05 deteriorated and species typical of the pioneer successional stage dominated (Table 5.1).

Canfield (1957) stated that compositional changes frequently involve the replacement of higher successional species by lower successional species. The lower succesional species are frequently mid- or short grass species held in a subordinate position by competitive interaction with species possessing greater stature (Arnold 1955; Belsky 1986). Grazing reduces the competitive ability of the mid- and tall grass through the removal of leaf area and by creating the potential for differential growth rates (Briske 1991), thereby increasing the relative abundance of lower successional grasses and forbs and establishing the potential for shrub invasion. In some plots it was found that the tall grass species such as *T. triandra* and *S. incrassata* were abundant during the first season, but in the second season shorter species such as *B. eruciformis* and *E. obtusa* were more abundant. The inherent morphological and physiological characteristics of individual plant species, therefore, influence the structure and function of plant communities by determining the extent of competition among plant species. Season of grazing in relation to the progression of phenological development among species plays a major role in determining the outcome of competitive interactions. Species grazed throughout their entire growth period are placed at a competitive disadvantage in the presence of species possessing growth periods that do not coincide entirely with the grazing season (Briske 1991). Species replacement influences the quantity, quality and variability of biomass production by altering the initial harvest and subsequent flow of energy through the ecosystem (Briske 1991). In many rangeland systems, the ratio of unpalatable to palatable species increases with increasing grazing severity (Noy-Meir & Walker 1986). Although this may not decrease total productivity of the system, it reduces the proportion of energy transferred through the grazing food chain.

The utilisation of vegetation by the herbivore game species is a natural ecological factor. The influence of this factor on the vegetation depends on the game species' feeding preferences, which includes selection of plants, trampling of soil, frequency and intensity of defoliation, and the resistance of the different plant species to these effects. Although grasses are adapted to grazing, the greatest threats to the grass plant are overgrazing and non-defoliation. If grass is not grazed, burnt or defoliated, the tuft accumulates excess dead leaf material (it becomes moribund), which can suffocate the tuft and the grass can die off entirely (Van Oudtshoorn 1999; Van Rooyen *et al*. 2000).

Dyksterhuis (1949) proposed a functional (response) classification of range plants into ecological classes. The ecological status of grasses refers to the grouping of grasses on the basis of their reaction to different levels of grazing. Although grasses are adapted to grazing, continuous overgrazing and consequent re-growth will result in the exhaustion of plant reserves, and the plant will weaken and die. Generally there is an association between the grazing value of different grass species and their ecological status. Species with a low grazing value are utilised less than palatable species and they therefore increase during conditions of overgrazing. According to Bosch & Van Rensburg (1987) and Van Oudtshoorn (1999), *A. bipartita* and *E. chloromelas* are species that are associated with overgrazing and they dominate in areas where retrogression is taking place. This indicates that most of the experimental plots, mainly situated on the northern- and western-side of the grid, are overgrazed.

Roberts (1973) reported that *E. chloromelas* often dominates heavily utilised veld, is able to withstand heavy grazing and often replaces *T. triandra* on heavier soils. In this study *A. bipartita* and *E. chloromelas* belonged to the Increaser II class, which increases when veld is overgrazed (Van Oudtshoorn 1999). The Increaser II ecological classes (IIa, IIb & IIc) increased on average by 8.75% between 2003/04 and 2004/05, emphasising the fact that the plant community is over-utilised. Increaser I species mostly occurred in plots on the southern side with minor differences (0.5%) between the two seasons. Palatable species have a high grazing value are selectively utilised and decrease when exposed to overgrazing. The Decreaser class, which mainly occurred in plots on the southern and eastern side of the grid, included species such as *T. triandra*, *D. eriantha*, *P. stapfianum* and *S. incrassata* (Figures 5.17 & 5.18). This class declined on average by 4.2% between 2003/04 and 2004/05. The higher occurrence of Decreaser and Increaser Ia species in the southern side might be due to the differences in soil and/or selective grazing (see Chapter 8).

Most veld condition assessment methods applied in southern African grasslands use proportional species composition as a basis for determining the veld condition score (Hurt & Bosch 1991). It is assumed that such a score will reflect the natural ability of the grassland to provide a sustained source of feed. Eckhardt *et al*. (1993) stated that responsive key plant species provide an indication of the past grazing pressure but do not necessarily indicate the grazing potential of an area unless a direct linear relationship exists between veld condition and grazing capacity. The increase of the VCS to the southern side of the grid can be ascribed to a higher occurrence of Decreaser species (Table 5.4). The highly significant ($P < 0.0001$) positive correlation found between the Decreaser and Increaser Ia classes indicate that the VCS will increase with an increase in plant species occurring within these groups (Figures 5.29 & 5.30). The increase in the contribution of Increaser II species to the VCS resulted in lower VCS during 2004/05 (Table 5.4). The negative correlation found between the Increaser II ecological classes and the VCS indicate that the VCS will decrease if species in these classes increase (Figures 5.31 - 5.33). According to Tainton (1982), the maximum score is 1 000, i.e. 100% Decreaser species, and the minimum is 100, i.e. 100% Increaser IIc or Invader species. If the scores found in this study are compared to these values the veld on the southern side of the grid was in a good to moderate (row C to E) condition during 2003/04. However, during 2004/05 the scores declined and the condition of the veld deteriorated. The grazing pressure present in the experimental area is a possible reason for the decrease in the VCS (Table 5.4). The fact that the VCS decreased between 2003/04 and 2004/05, in spite of the slightly higher rainfall during the second season (see Chapter 3), indicates that other factors, of which herbivory is the most important, are also influencing the veld condition. This also indicates that veld degradation is clearly taking place. The condition of the veld on the northern side was moderate to poor.

The average occurrence of *O. ficus-indica*, which generally is an indicator of veld degradation, increased by 100% from 2003/04 to 2004/05 (expressed as a percentage of 2003/04 occurrence) (Appendix B_{2-6}). The cactus-like *O. ficus-indica* can be an aggressive invader, rendering heavily infested land virtually useless. The spines on the fruit and leaves are highly irritating to browsing animals. *Opuntia ficus-indica* is listed as a Category 1 weed in terms of the Conservation of Agricultural Resources Act (No. 43 of 1983), which means it may not occur on any land other than in biological control reserves. These plants must be removed and destroyed, unless measures are being taken to control them and prevent their spread, which the owner of the study area is not doing. This problem plant can be chemically or biologically controlled. Chemical control includes stem injection, usually for large plants, or foliar spray. Herbicides such as MSMA (sodium methyl oxido-arsinic acid), Roundup (isopropylamine glyphosate) and Touchdown (glyphosate-trimesium) can be used (Bromilow 2001). However, biological control with *Cactoblastis* and Cochineal (*Dactylopius opuntiae*) has been so successful that special control measures are rarely required (Bromilow 2001).

Variation in the DM production between different areas is the result of numerous determinants that can exert an influence individually, or more likely in interaction with each other. These determinants include various environmental factors, for example temperature (Christie 1981; Epstein *et al*. 1997), rainfall (Booysen 1983; Van den Berg 1983; Fouché 1984; Snyman 1999), soil texture and soil water-holding capacity (Sala *et al*. 1988; Snyman 2000), evapotranspiration (Snyman 1998a), nutrient availability (Chapin 1991; Du Preez & Snyman 1993), species composition (Milchunas & Lauenroth 1993), basal cover (Wiegand *et al*. 2004) and fire (Trollope & Tainton 1986; Trollope 1999; Oesterheld & McNaughton 2000). The effects that grazing (herbivory) and trampling can have on herbaceous DM production are also well documented (Frost *et al*. 1986; Westoby *et al*. 1989; O'Connor 1994; O'Connor & Roux 1995; Teague & Smit 1992; Moleele & Perkins 1998; Drawe 1999). The total DM production during the 2003/04 growing season, when 354.3 mm rain fell, which was 198 mm below the long-term annual average of 552.3 (see Chapter 3), was slightly lower (1.60%) than the production during the 2004/05 growing season, when 415.4 mm rain fell, which was 136.9 mm below the average (Table 5.2). The 61.1 mm difference (17.2% increase) in rainfall between the two seasons, therefore, did not have a big influence on the above-ground DM production. It is clear that there was a close relationship between the species composition based on occurrence of plant species and the species composition based on DM production (Figures 5.4 – 5.12). The DM production was apparently higher in experimental plots with a higher occurrence of species with a lower grazing value such as *A. bipartita* and *E. chloromelas* (Van Oudtshoorn 1999). Experimental plots with a high occurrence of *S. incrassata* also had a relatively high DM production. This is attributed to fact that the plots with more species with a higher grazing value were more frequently grazed, which resulted in less available plant material, or that the plant species occurring in the plot had a low production potential.

Plots with a higher species diversity generally had a lower DM production than plots with a lower species diversity due to the higher occurrence of more palatable species. The decrease in the DM production in plots dominated by grass species with a low grazing value, gives an indication of the potential production of the herbaceous layer under the current rainfall regime. However, factors other than grazing or rainfall could also have caused differences in the DM production between the two seasons. The contribution of forbs to the DM production increased by 39.3%, and the contribution of Karoo bushes decreased by 20.7%.

Grazing capacity refers to the stocking rate (ha GU^{-1}) that can be applied without the deterioration of the veld due to over utilisation or under utilisation (Van Rooyen *et al*. 2000). The stocking rate must be more conservative on game ranches since game species cannot be rotated as livestock. The grazing capacity varies regionally according to the soil, climate, vegetation composition, topography, types of animals and management (Van Rooyen *et al*. 2000). In the present study the small variation in the rainfall between the two seasons did not have a major influence on the grazing capacity (Table 5.5). It is important to keep in mind that the grazing capacity in dry areas varies annually and must be determined each year. In this study, differences were minor and none of the plots had the same grazing capacity as the previous year (Table 5.5). The changes in DM production and grazing capacity in the different plots can also be attributed to differences in plant species composition that in turn depend on various ecological factors, as previously mentioned. The effect of species composition on differences in DM production and grazing capacity of different areas has been reported worldwide (Dye & Spear 1982; Scanlan & Burrows 1990; Smit & Rethman 1992; O'Connor 1994; Moyo & Campbell 1998; Drawe 1999; Hacker *et al*. 1999; Abule *et al*. 2005; Snyman & Du Preez 2005). Since grazing capacity is dependent on vegetation DM production, it would be expected that shortly-grazed areas will have a negative effect on the grazing capacity. The DM production had a highly significant ($P < 0.0001$) negative correlation with the amount of hectares needed for a GU. This implies that when the DM production decreases the hectares needed per GU increases (Table 5.6). The negative correlation found between the percentage occurrence of Decreaser species and the hectares per GU indicates that the hectares needed per GU increase with a decrease in the occurrence of Decreaser grass species (Table 5.6). The significantly ($P < 0.01$) positive correlation found with Increaser IIa species confirms that the hectares needed per GU increases with an increase in the occurrence of Increaser IIa grass species (Table 5.6). It is important that the stocking rate must be of such a manner that the veld can still sustain the animals during the dry season. It is, therefore, important to have a basic knowledge of the grass species most commonly grazed by the herbivore game species in order to calculate a proper stocking rate.

5.5 CONCLUSION

The following conclusions can be drawn from the results:

(i) The botanical composition varied between the experimental plots situated on the northern and southern side of the experimental area. The species diversity of plots on the northern side was relatively low and grass species with a low grazing value, such as *A. bipartita*, *E. chloromelas* and *B. eruciformis,* and to a lesser extent *S. incrassata*, were abundant. In contrast, plots on the southern side generally had a higher species diversity and grass species with higher grazing values, such as *T. triandra*, *D. eriantha* and *P. stapfianum*, and to a lesser extent *E. obtusa* and *E. plana*, which were also more abundant.

(ii) The increase in the Increaser II ecological classes between 2003/04 and 2004/05 and decrease in the VCS indicated that the veld is over-utilised.

(iii) There was a relatively close relationship between the species composition based on occurrence and the species composition based on above-ground DM production. The experimental plots with a high occurrence of grass species with a low grazing value generally had higher above-ground DM productions than plots with a high occurrence of grass species with a higher grazing value. This is because the latter plots are grazed preferentially.

(iv) The highly significant ($P < 0.0001$) negative correlation found between above-ground DM production and hectares needed per GU indicates that more hectares are needed to support herbivore populations if the DM production decreases. Thus, stocking rate should decrease with a decrease in DM production. The significant ($P < 0.01$) positive correlation found between Increaser IIa grass species and the hectares needed per GU also indicates that hectares per GU increase with an increase in Increaser IIa grass species (lower grazing capacity).

(v) It is clear that the veld of the experimental area is in a state of ongoing degradation, mainly due to over stocking, ultimately resulting in poor veld with bad soil stabilising characteristics, low quality of feed and a low grazing capacity. Consequently, this is expected to lead to an unstable environment and could result in poor income generation from the area.

(vi) The changes in species composition will subsequently influence the production of the herbivore game species by affecting the quantity, quality, seasonality of plant production and grazing capacity.

(vii) From an ecological perspective the veld is generally in a poor condition. Conversely, these shortly grazed areas, conventionally seen as a result of over grazing, are the preferred habitat of short grass grazers. From a game ranching perspective, where the objective is to maintain short grass grazers, the formation of grazing lawns dominated by Increaser species must not be regarded as being totally undesirable or preventable. Therefore, a compromise between short grazing (habitat suitability) and the maintenance of the veld in a good ecological condition seems to be the proper approach. However, an important question that needs to be resolved is whether the heavily grazed lawns can be maintained in a relatively productive state under sustained continuous grazing, or whether they will eventually be reduced to an unproductive state, either through soil loss or invasion by unpalatable species, where they no longer provide adequate grazing. It is therefore important to monitor the expansion of shortly grazed lawns (which is acceptable unless they invade more fertile - higher potential-areas) and their development (if it is towards bare patches it is unacceptable).

(viii) These results emphasise the need for conservative stocking rates and proper veld management that will improve animal and plant production over the short as well as long term.

Interaction between the soil, grass species and grazing by the herbivore game species will be further discussed in Chapter 8.

CHAPTER 6

SMALL SCALE HABITAT PREFERENCES OF HERBIVORE GAME SPECIES IN GRASSLAND

6.1 INTRODUCTION

The habitat of an animal is that area in which it predominantly occurs by choice. Habitats are composed of geomorphological features such as topography, geological formations, soil types and vegetation (Joubert 2000). The world's habitats are thus extremely diverse and vary widely in terms of plant species composition, structure and productivity. Despite this diversity, extreme spatial and temporal variability also occurs within these habitats. Today, due to human action, many of the natural habitats of wild herbivores are changed through habitat loss or modifications that mostly result in habitat fragmentation (Reid *et al*. 2004).

Knowledge of the habitat itself, along with the habitat preferences and other ecological requirements of herbivore game species, is basic to any management programme for long term sustainability (Dekker *et al*. 1996; Bothma 2000), especially in fragmented habitats. The preferred habitat of some of the most common herbivore game species occurring in the Free State Province, which include the springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*) (Skead 1958; Kettlitz 1962; Bothma *et al*. 2000; Cillié 2000; Liversidge & Berry 2000; Stuart & Stuart 2000; Skinner 2005) and black wildebeest (*Connochaetes gnou*) (Pienaar 1974; Von Richter 1974; Bothma *et al*. 2000; Cillié 2000; Stuart & Stuart 2000; Skinner 2005) is open grassland. However, many biotic and abiotic factors influence the way an animal uses space, both in terms of where it goes and how long it stays in one area. The objective of this study was to determine the small scale habitat preferences of the above- mentioned herbivore game species within the twenty experimental plots demarcated in the study area.

6.2 PROCEDURE

6.2.1 Description of the seasons

The seasons were demarcated based on the growing cycle of the grass plants (Smit 2003b), which are described as follows:

(i) Growth initiation season (GIS) – when temperatures increase, and if water is available, the perennial grass plant starts to grow. From a production viewpoint it is very important that the grasses must start growing rapidly during spring. For rapid initial growth, there must be sufficient growth points in the grass tuft so that new leaves can be formed immediately and there must be sufficient carbohydrate reserves in the roots and crown of the plant to serve as energy sources for growth. This normally takes place in spring (September - October). If the plants are defoliated before sufficient green leaves are available, their survival is determined by available reserves. The reserve nutrient level declines rapidly and is only again supplemented in the mature stage of the plant (autumn) when the growth rate begins to decrease. Continual defoliation can lead to the depletion of the nutrient reserves of the plant.

(ii) Active growing season (AGS) – after the growth initiation stage follows a period where the grass plant grows actively. As more leaves are formed, the plant can produce more nutrients through the process of photosynthesis. The growth rate, therefore, is dependent on the leaf surface and favourable environmental conditions. Any grazing practices that result in a small leaf surface lead to a low growth rate, and therefore, a low production of the veld and animals. Depending on the rainfall, active growth takes place during summer (November - February).

(iii) Reserve storage season (RSS) – after seed production the growth rate decreases and fewer nutrients are needed for above ground development. The nutritive material now produced is mainly stored as carbohydrate reserves in the roots and crown, which is important for growth initiation, regrowth and for keeping the perennial grasses alive during winter. Reserve storage takes place during autumn (March - May).

(iv) Dormant season (DS) – when temperatures decrease and frost occurs the above-ground plant parts become dormant or die. Although the plant is seemingly dead, it is known that perennial grasses survive winter through stored reserves, and therefore, possess the ability to start growing again at the beginning of each new growing season. The dormant season is represented by the winter period (June - August).

6.2.2 Observations

The presence of game species in the twenty experimental plots (see Chapter 3) was monitored through scheduled and opportunistic observations from June 2004 to July 2005. Three observations were made during the first week of each month; thereafter, observations took place once a week. Animals were observed with binoculars from a parked vehicle at a distance of ± 50 m from the experimental site (see section 3.7.1). During summer (November 2004 – February 2005) the animals were observed from 07:30 till 09:30 in the morning, and again from 15:00 till 17:00 in the afternoon. Winter observations took place from 10:30 till 12:30 in the morning, and 15:00 till 17:00 in the afternoon. Observations were thus restricted to periods of active foraging and excluded periods in the middle of the day when herbivores are known to be less active (Bigalke 1972; Irby 1981; Ben-Shahar & Fairall 1987; Vrahimis & Kok 1993; Owen-Smith 1999). Kalemera (1987) referred to this feeding style as a bimodal feeding pattern. The following was noted: (i) experimental plot number in which the herbivore game species occurred, (ii) total number of each species, (iii) time each species spent in the plot, (iv) activity (grazing, lying down or standing) that was carried out, and (v) date and time of observation.

Observations were not done during the reserve storage season (RSS) as the grass in four of the experimental plots had been mown (see Chapter 9), and this may have affected the activity of each herbivore game species.

6.2.3 Data analysis

In order to determine the experimental plot(s) preferred by the herbivore game species, an activity weighted index of occupation termed "animal hours" were calculated for each plot. The "animal hours" each species spent within an experimental plot was calculated by using the following formula:

$$Y = \Sigma\, (n_g \times t_g)\, (n_l \times t_l)\, (n_s \times t_s)$$

where Y = total number of "animal hours" spent within the relevant plot

n_g = total number of individuals grazing

t_g = total time spent grazing

n_l = total number of individuals lying down

t_l = total time spent lying down

n_s = total number of individuals standing

t_s = total time spent standing

Simple descriptive statistics were used to present the results of this investigation (Microsoft Excel 2003). Integrated statistical analyses, including ordinations with the tested soil properties (Chapter 4), vegetation characteristics (Chapter 5) and animal hours as variables are presented in Chapter 8.

6.3 RESULTS

The amount of time, in terms of animal hours with indication of the contribution of each of the three activities (grazing, lying down and standing) that each of the herbivore game species spent in the experimental plots during the different seasons, is presented in Figures 6.1 to 6.9.

6.3.1 Springbok

It is clear that springbok spent more time within the demarcated area during the dry season (DS & GIS) (Figures 6.1 & 6.2). Most of the time was spent grazing in experimental plots B1, D4 and E3, which were preferred during the DS, and plots B1&2 during the GIS. In the AGS, animal hours were mainly spent lying down in plot D1, and very little or no time was spent in the other plots (Figure 6.3).

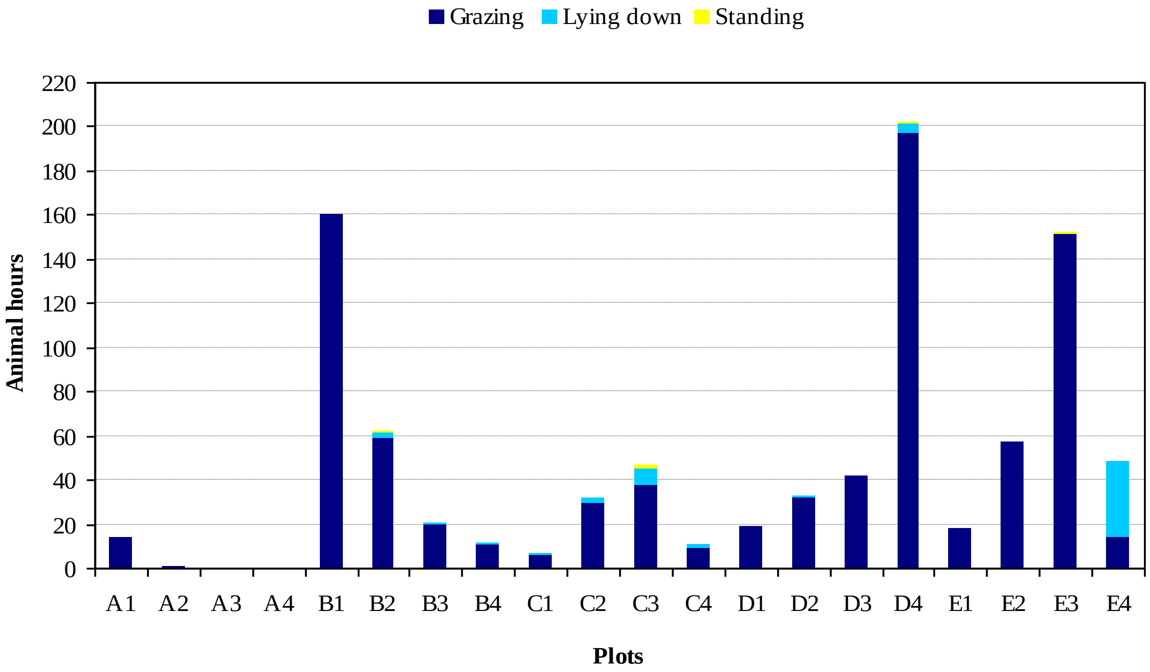

Figure 6.1: Animal hours - consisting of time spent grazing, lying down and standing - springbok spent within the experimental plots during the dormant season (DS) (June 2004 – August 2004).

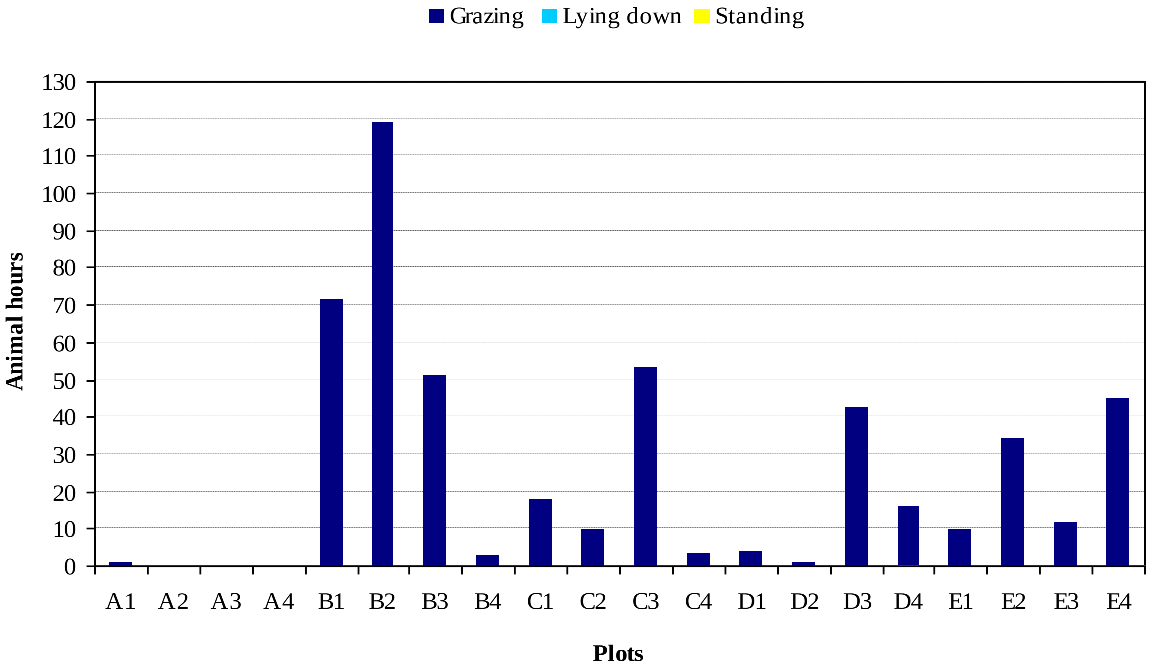

Figure 6.2: Animal hours - consisting of time spent grazing, lying down and standing - springbok spent within the experimental plots during the growing initiation season (GIS) (September 2004 – October 2004).

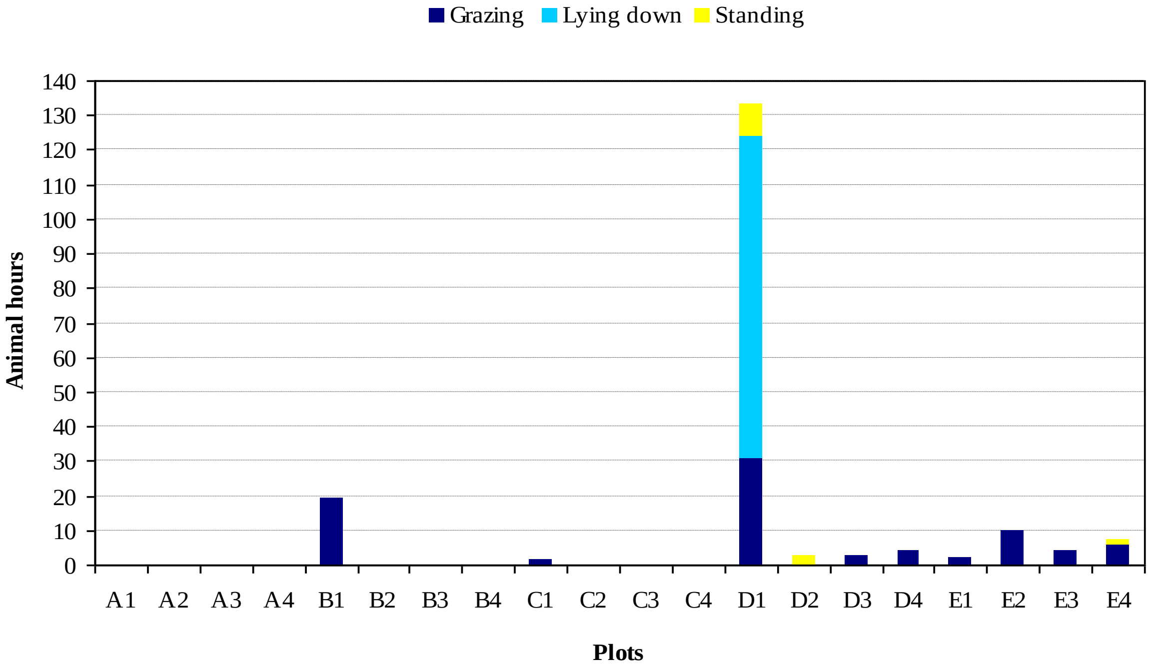

Figure 6.3: Animal hours - consisting of time spent grazing, lying down and standing - springbok spent within the experimental plots during the active growing season (AGS) (November 2004 – February 2005).

6.3.2 Blesbok

During the DS, blesbok spent little time within the demarcated area, which decreased even more during the GIS (Figures 6.4 - 6.5). However, during the AGS the animal hours spent in plot B1 increased drastically (Figure 6.6). Preferred plots included B3 and C1 during the DS and B1 during the GIS and AGS (Figures 6.4 - 6.6). The number of plots utilised decreased during each season (Figures 6.4 - 6.6). In contrast to springbok, blesbok spent less time on grazing and more time lying down, followed by standing.

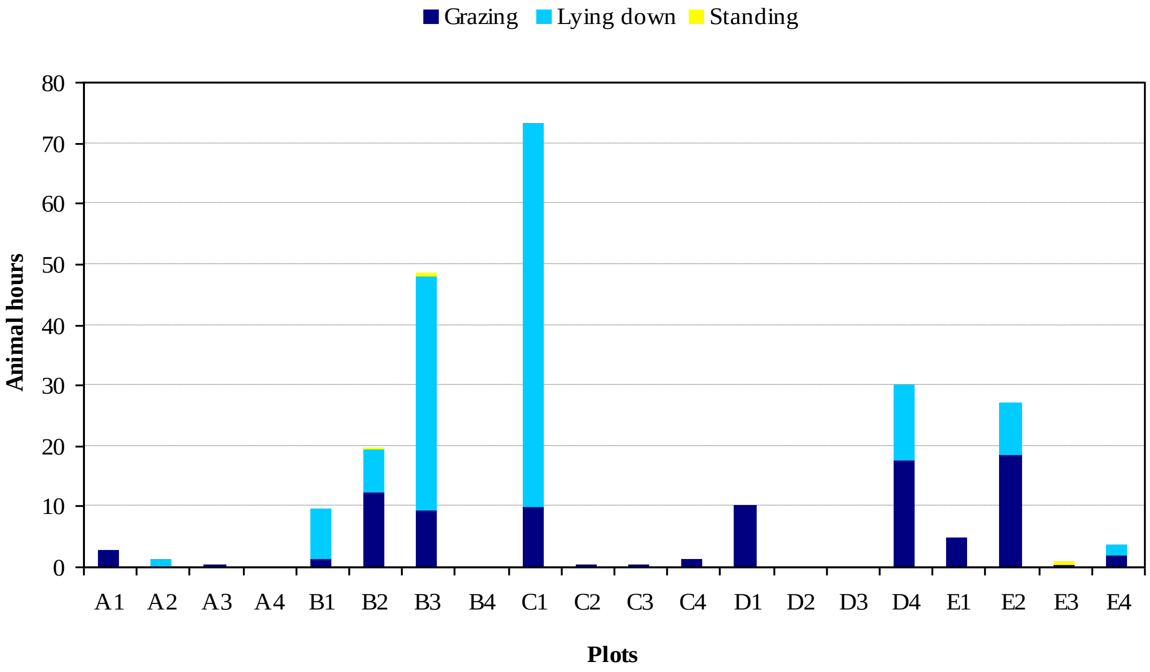

Figure 6.4: Animal hours - consisting of time spent grazing, lying down and standing - blesbok spent within the experimental plots during the dormant season (DS) (June 2004 - August 2004).

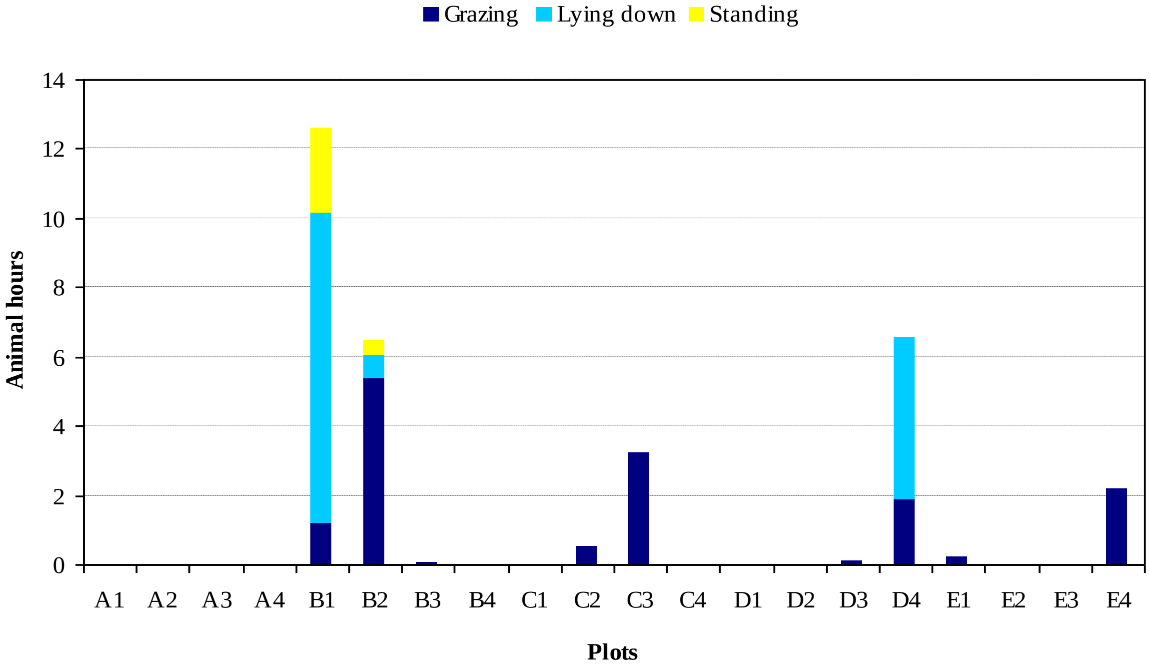

Figure 6.5: Animal hours - consisting of time spent grazing, lying down and standing - blesbok spent within the experimental plots during the growing initiation season (GIS) (September 2004 – October 2004).

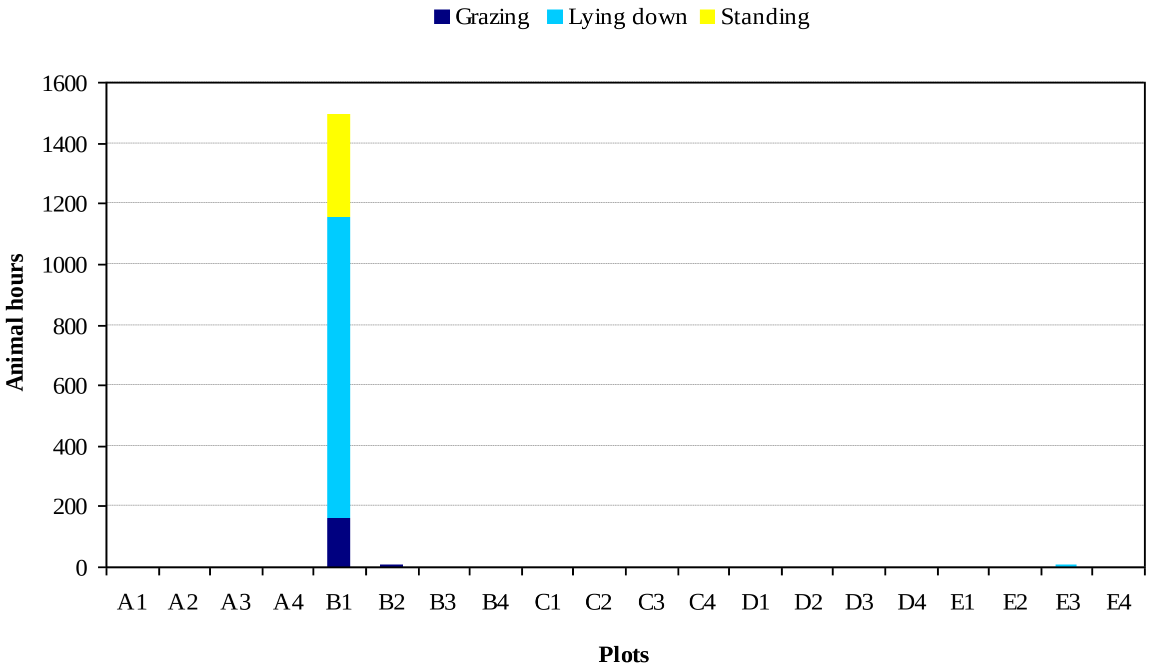

Figure 6.6: Animal hours - consisting of time spent grazing, lying down and standing - blesbok spent within the experimental plots during the active growing season (AGS) (November 2004 – February 2005).

6.3.3 Black wildebeest

The average time spent by black wildebeest within the experimental plots, and the number of plots utilised, decreased during the AGS (Figure 6.9). Preferred plots included B3 during the DS, E3 and to a lesser extent C1 and D1 in the GIS, and C1 during the AGS (Figures 6.7 - 6.9). Black wildebeest also spent less time on grazing during the AGS. However, it was more than the time blesbok spent on grazing during this season (Figures 6.6 & 6.9).

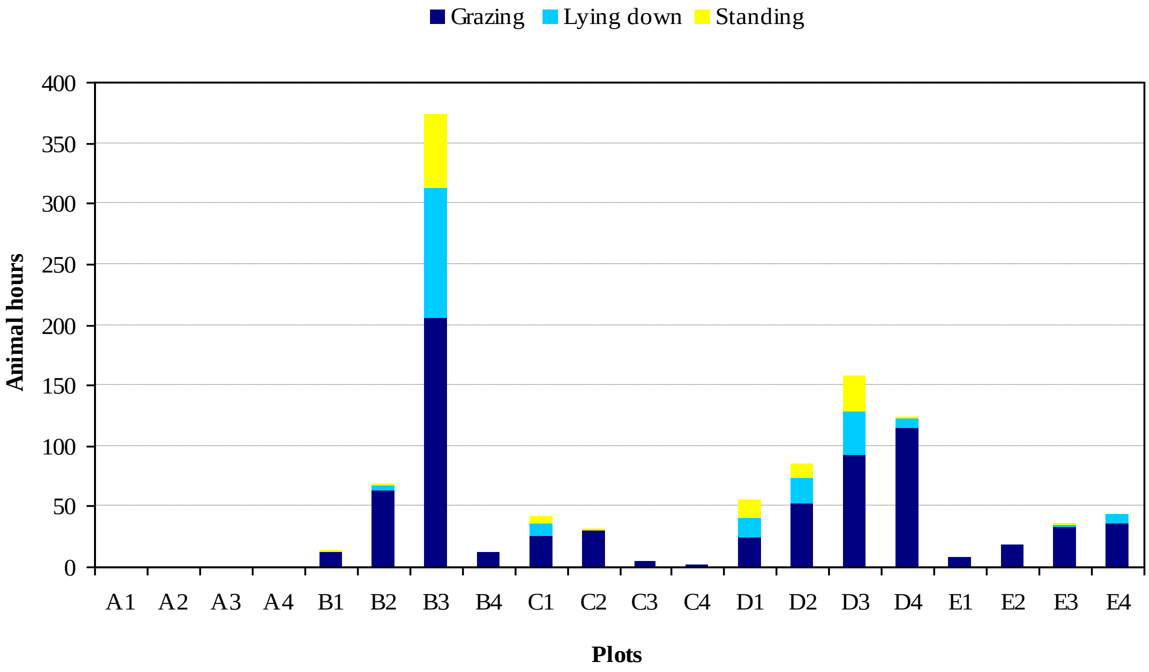

Figure 6.7: Animal hours - consisting of time spent grazing, lying down and standing - black wildebeest spent within the experimental plots during the dormant season (DS) (June 2004 – August 2004).

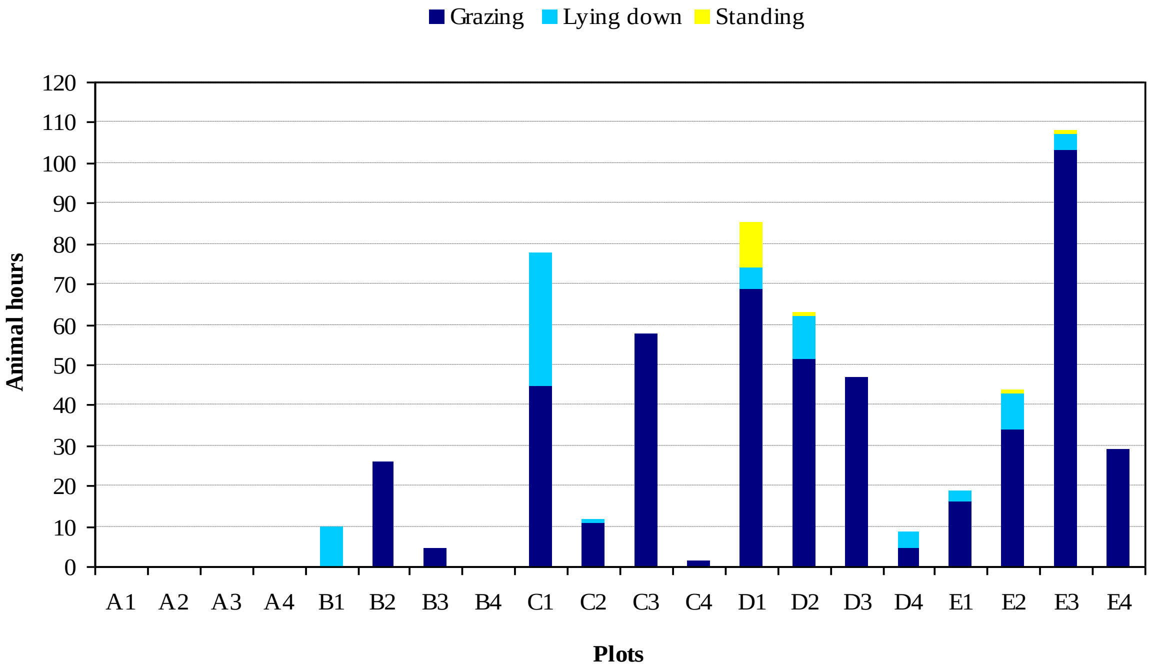

Figure 6.8: Animal hours - consisting of time spent grazing, lying down and standing - black wildebeest spent within the experimental plots during the growing initiation season (GIS) (September 2004 – October 2004).

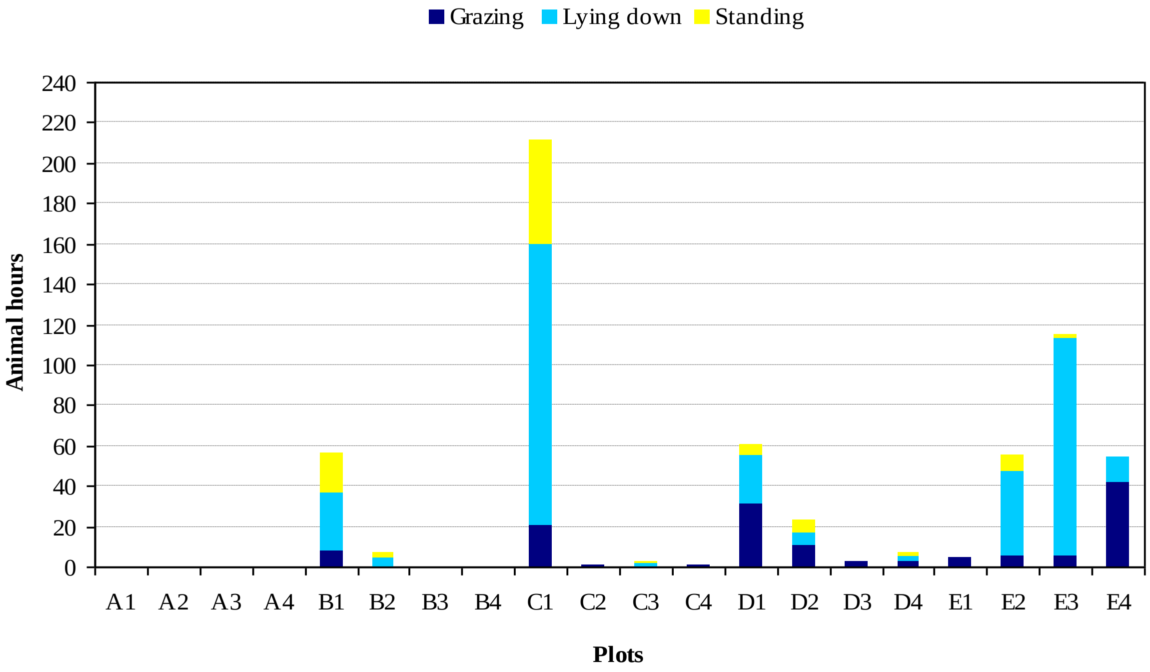

Figure 6.9: Animal hours - consisting of time spent grazing, lying down and standing - black wildebeest spent within the experimental plots during the active growing season (AGS) (November 2004 – February 2005).

6.4 DISCUSSION

Plant species composition and structure are two components of the vegetation that form an important part of the habitat. The plant species of which the vegetation is composed, will determine whether or not the food source is sufficient, and the structure of the vegetation will determine the suitability of the habitat (Joubert 2000). Game species do not roam aimlessly without direction or order through their habitats, but use their habitats in a fixed or orderly manner.

Habitat patches are inherent to natural vegetation and are apparent in all rangelands, especially in fragmented habitats (habitat reduction). Patches may vary in size, sward structure, phenology, nutritive value and plant species composition, but will be identifiable with the landscape unit as a whole. This variability is compounded by various biotic processes, of which the most important are grazing and human modifications. Patchiness arises from the relative distribution and abundance of different plant species in the sward, i.e. even in relatively uniform vegetation animals create patches by only feeding at points where the density of a particular species exceeds some threshold.

Selective defoliation of the sward creates a mosaic of grazed and ungrazed patches of varying size (Bakker *et al*. 1983; Mott 1985; Willms *et al*. 1988). Once initiated, mosaics are maintained by selective grazing, with grazed patches remaining short (Bakker *et al*. 1983) while ungrazed patches become rank and stemmy (Mott 1985). Springbok (Mentis & Duke 1976; Mentis 1980; Novellie 1990), blesbok (Du Plessis 1972; Mentis & Duke 1976; Mentis 1980; Grobler 1983; Novellie 1990) and black wildebeest (Von Richter 1974; Mentis & Duke 1976; Mentis 1980; Novellie 1990) are patch selective grazers, subjecting small areas to intense grazing pressure, so that their habitat typically develops a mosaic of grazed and ungrazed patches. These species graze to a large extent on the same plants, but otherwise no interactions occur (Von Richter 1974). The patch selective grazing habit of short grass grazers has the effect of creating the habitat condition they require, i.e. “grazing lawns” of short grass (Novellie 1990). Large herbivores usually allocate time to different areas of a pasture or habitat, based on the resource levels found there (Bailey *et al*. 1996). Senft *et al*. (1987) applied the term “matching” to this proportional relationship between the time an animal spends in plant communities or patches and the available quantity of nutrients. An energy-intake model by Fryxell (1991) suggests a number of key environmental factors that should determine the impact of forage maturation and spatial variation on herbivore distribution patterns. Urine deposition also creates patches of high quality herbage which may persist for between 2 to 12 months (Ledgard *et al*. 1982). High quality, productive patches may develop around gates, watering points and other sites of localised nutrient deposition or through the actions of other animals such as termites (Ledgard *et al*. 1982).

The extent to which springbok, blesbok and black wildebeest tended to favour certain habitat patches can be seen from the amount of animal hours spent in the experimental plots. On average the preferred plots generally had a relatively high occurrence of Increaser grasses and relatively high species diversity (see Chapter 5). Increaser grass species generally have a lower nutritional value and are less palatable than Decreaser grass species (Van Oudtshoorn 1999). The higher species diversity provided a greater variety of plant species from which the herbivore game species could select. Springbok showed a strong preference for plots with a high occurrence of Increaser IIc such as *Eragrostis obtusa*, *Eragrostis chloromelas, Aristida bipartita* and *Tragus berteronianus*, followed by Decreaser grass species such as *Setaria incrassata* and *T. triandra*. The high level of utilisation, in turn, is a likely cause of the abundance of Increaser grass species in these heavily utilised plots. Decreaser grasses such as *T. triandra* are poorly adapted to a high intensity and frequency of defoliation (Danckwerts & Stuart-Hill 1987). Subsequently it was observed that the occurrence of Increaser II grasses increased in the heavily grazed plots during the 2004/05 growing season (see Chapter 5). Blesbok also preferred plots with a high occurrence of Increaser IIa and IIc species. The preference for plots, where occurrence of Decreaser grass species was higher, increased during the DS. However, blesbok spent most of the time within the preferred plots lying down. The short growth form of Increaser II species may have facilitated blesbok's preference to spent their inactive time in these plots. Black wildebeest tended to favour plots with a high occurrence of Decreaser grass species, although Increaser II species were also relatively abundant in the plots favoured by them. Once more this can be the response of the vegetation to their selective grazing habits.

The herbivore game species tended to favour experimental plots with a low to average veld condition score (VCS) (see Chapter 5). Except for plot E3, none of the preferred plots had a VCS of more than 700. The high occupation rate of plot B1 was strongly influenced by the occurrence of artificial mineral licks at the end of the GIS. In contrast to springbok and blesbok, the licks did not particularly affect the movement of the black wildebeest, since during the whole observation period they were seldom seen in plot B1 (Figures 6.7 - 6.9).

Novellie (1990) found that blesbok and springbok were not strongly associated with tall Decreaser grasses. He found that black wildebeest actively avoid habitats dominated by Decreaser grass species, which differ to some extent with the results of this study. According to him, short grass grazers effectively promote Increaser grasses, and communities dominated by Increaser grasses, in turn, appear to offer a sward structure that suits the foraging requirements of the short grass grazers. According to Stuth (1991), preferred grazing areas have high occupancy:area ratios and high utilisation:herbage mass ratios. The bulk of the game species forage is derived from these areas. Grazing areas avoided (such as plots in row A) contain forage with a low value or are inaccessible to the animal(s) (Stuth 1991).

The experimental plots preferred by the herbivore game species did not have a high above-ground DM production (see Chapter 5). This was to be expected since they prefer shorter grazed areas and keep them short, which will result in a lower production. Fryxell (1991) states that herbivores might tend to prefer less productive vegetative patches, because vegetation in these areas is more readily maintained at a nutritious growth stage. Population density should, however, be positively correlated with primary productivity. It is expected that herbivore densities will increase in primary productivity up to a certain level, but then drop considerably in highly productive patches of vegetation (Fryxell 1991). A more detailed analysis of the influence of vegetation on small scale habitat preferences of these herbivore game species is provided in Chapter 8.

An animal's feeding station is established when it stops walking, moves the orientation of its head (upwards or downwards) and bites a plant. Certain sensory cues cause the animal to stop searching and to select a plant species or combination of species it considers profitable. The pattern of feeding stations is strongly related to the distribution and profitability of patches in a community, the size of the community, and the geographical relationship of the community to the animals' grazing path (Novellie 1978; Ruyle & Dwyer 1985). The consistent response of herbivore game species to patchiness is to select high quality productive patches, but reject those of low quality. Both wild and domestic herbivore species persistently select the higher quality herbage on grazed patches in preference to that on ungrazed patches (Mott 1985; Bakker *et al*. 1983; Ring *et al*. 1985; Willms *et al*. 1988; Hobbs *et al*. 1991). When grazed patches are depleted or collapse, new patches may be initiated in previously ungrazed areas, or grazed areas may expand until patches combine (Ring *et al*. 1985).

The marginal value theorem predicts that animals should graze a patch until the rate of nutrient gain drops to the average for the environment as a whole (Charnov 1976). Occupation time should therefore increase with plot richness and increasing distance to the next plot. This is corroborated by the available evidence, which indicates that both domestic (Laca *et al*. 1994) and wild ungulates (Baharav & Rosenzweig 1985) occupy rich patches longer than poor patches. This is also to some extent apparent in the present study, since less or no time was spent in some plots dominated by Increaser II species that also have a low species diversity (notably row A). Due to the relatively high species diversity of the preferred plots (see Chapter 5) more potentially palatable species occurred which were utilised by selective feeding habits.

Grazing (Chacon & Stobbs 1976) and seasonality (Van Soest 1982; Schwartz & Hobbs 1985; Owen-Smith 1988; Ben-Shahar 1991; Van Wieren 1992; Owen-Smith 1994; Dekker *et al*. 1996; Esler & Rundel 1999) deplete overall herbage availability, depressing bite size and quality. In this study seasonal movement is indicated by changes in the experimental plot preference indices. Animals have evolved a variety of foraging, metabolic and digestive strategies in response to such variability. Animals usually respond to such variability by moving to other patches or areas where forage is better and more readily available (Low *et al*. 1981; Squires 1982). However, under fenced conditions or where other landscape units are unavailable, animals respond by adjusting foraging behaviour. Typically, animals increase biting rates and/or daily foraging time in an attempt to compensate for reduced bite sizes (intake rate) (Allden & Whittaker 1970; Jarman & Jarman 1973; Chacon & Stobbs 1976; Owen-Smith 1988; Hudson & Nietfeld 1985; Spalinger *et al*. 1988), or to allow increased selectivity (Novellie 1978). Encounter rates with forage species may also be increased by seeking out areas where such species are most common (Owen-Smith 1994) or by increasing travel velocity (Collins *et al*. 1978; Novellie 1978; Pettifer & Stumpf 1981; Baharav & Rosenzweig 1985; Spalinger *et al*. 1988; Owen-Smith & Cooper 1988; Ben-Shahar 1991; Dekker *et al*. 1996). This may be the reasons why blesbok and especially springbok and black wildebeest utilised more experimental plots during the DS and GIS than during the AGS when more suitable forage was available elsewhere (Figures 6.1 - 6.9). Dekker *et al*. (1996) found that the highest spatial separation in Mopani veld occurred in the dry season. According to Hodgson (1981) the above mentioned strategies may be successful within fairly narrow limits, but generally fail to maintain intake rates when bite sizes are severely restricted, as bite size is the major determinant of intake (Hodgson 1981).

Metabolically, herbivore game species may respond to seasonal fluctuations in forage quality and quantity by adjusting net energy requirements, or energy may be conserved by reducing activity levels at critical times in the season. This may explain why blesbok spent so little time on grazing during the DS and GIS in comparison to springbok and black wildebeest (Figures 6.1, 6.2, 6.4, 6.5, 6.7 & 6.8). According to Du Plessis (1968) and Novellie (1978), blesbok in the winter season markedly reduce activity levels at critical levels by walking slowly, decreasing grazing time and basking in the sun. Klein & Fairall (1986) also found, in a study done on a reserve near Pretoria that blesbok adjust their energy expenditure to compensate for seasonal variations in quality of their diets. The decrease in grazing time during the AGS by all three species (Figures 6.3, 6.6 & 6.9) can also be partially explained in terms of the daily temperatures. The average maximum temperatures during the cold season varied between 17.5°C and 27.2°C, and during the warm season between 28.5°C and 30.4°C (see Chapter 3). On a game farm situated near

Kimberley, Maloney *et al*. (2005) found that black wildebeest increased their proportion of night feeding when ambient conditions were hotter. Therefore, they spent less time feeding during the day in the warm season. Many laboratory (Hamilton 1971; Johnson & Strack 1989; Torres-Contreras & Bozinovic 1997) and field studies (Leuthold 1977; Lewis 1977; Leuthold & Leuthold 1978; Belovsky & Slade 1986; Klein & Fairall 1986; Owen-Smith 1998) have reported an inhibitory effect of high ambient temperature on feeding.

Maloney *et al*. (2005) further found that black wildebeest spent the majority of their inactive time lying down in cooler conditions and standing in warmer conditions. In this study the average animal hours spent standing also increased slightly during the warm season (AGS) (Figure 6.9). Nagy & Knight (1994) have suggested that springbok may feed preferentially at night during dry conditions because plant moisture content is highest at night. Since the study area is situated in a region with a summer rainfall (see Chapter 3) this behaviour can be expected during the DS and GIS. Ellis (1995) states that in more arid parts of southern Africa, plant growth is erratic and consequently affects animal behaviour, especially feeding behaviour. Studies of the foraging behaviour of blesbok and springbok revealed that in both species seasonal changes in foraging behaviour were correlated with chemical and structural changes in the sward (Novellie 1978).

Reproduction might also have had an influence on the animals' activity and the amount of animal hours spent within the experimental plots. Springbok are not seasonal breeders (Skinner 2005) and started lambing from September. In contrast, blesbok and black wildebeest are seasonal breeders (Skinner 2005) and gave birth in November and December respectively. Consequently, springbok females were lactating during the GIS and AGS, whereas blesbok and black wildebeest females lactated during the AGS. Lactation is energetically the most expensive period in a mammal's life (Poppitt *et al*. 1994) and would have necessitated an increase in forage intake regardless the existing environmental conditions. According to Maloney *et al*. (2005), it is possible that lactating females act as focal animals, directing the herd.

Another influencing factor is the social behaviour of the herbivore game species. Social dominance hierarchies exist among species, herd subgroups and individual free ranging antelope. According to Mosley (1999), dominance hierarchies influence habitat selection. Joubert (2000) states that social behavioural patterns play a key role in determining the means by which different game species utilise their habitats, and therefore also play an important role in the determination of the densities in which different animal species are found in a specific area. According to Joubert (2000), three kinds of behavioural patterns can be distinguished among game species, namely: behavioural patterns that are poorly defined and apparently play a subordinate or irrelevant role in the determination of area utilisation; game in which there are strongly developed behavioural patterns, although the patterns play a minor role in area utilisation; and those game in which strongly developed social behavioural patterns play a decisive role in area utilisation.

High-ranking individuals and sub-groups occupy the preferred habitats or, where home ranges overlap, dominant individuals or subgroups preferentially use habitat resources (Mosley 1999). Social dominance hierarchies help partition resources among species of free-ranging ungulates (Morse 1974). Interspecific dominance hierarchies among wild ungulates are often veiled since other factors also help partition habitat use, such as differences in predator avoidance strategies and differences in diet selection (Mosley 1999). Predators were largely absent in the study area and could therefore not have had an influence on the habitat preferences. Mosley (1999) states that dominance hierarchies are often subtle, especially between species that forage closely together. Animals often feed together, mutually unconcerned, but the subordinate species readily gives way if the dominant animal happens to move too close (Mosley 1999). Low-ranking animals are forced to relocate into areas of lower habitat quality or they must wait their turn until the more dominant animals are satisfied and leave the area. Springbok, blesbok and black wildebeest are territorial (Owen-Smith 1977; Skinner 2005), but no clear pattern of dominance hierarchies emerged. In most ungulates, territoriality is exclusively a male mating strategy that has evolved through processes of intrasexual selection (Owen-Smith 1977).

Different variants of territorial separation occur (Owen-Smith 1977). According to Estes (1969), the territories of wildebeest are centripetally focussed. Territorial black wildebeest bulls are spaced out throughout available habitat, forming a mosaic of territories. The centre of the territory is a patch of bare ground covered with dung, where the bull performs most of his advertising displays (Von Richter 1974). Such areas are referred to as stamping grounds, and the borders between neighbouring territories are diffused (Owen-Smith 1977). This situation seems associated with species occupying open grassland habitats where neighbours are constantly visually apparent to one another (Owen-Smith 1977). This could explain the high occurrence of faeces in plot B1, and the increase in occurrence of black wildebeest in this plot during the AGS (Figure 6.9). Blesbok separate their territories by an unoccupied “no-man’s land” (Owen-Smith 1977). Novellie (1975) found that blesbok territories were aligned along a roadside burn, and therefore, anthropogenic disturbances (e.g. roads) may also affect the establishment of territories in this area. Where territories are held seasonally, occupation occurs during the summer or wet-season months of food abundance (Owen-Smith 1977). The breeding season of blesbok and black wildebeest is usually during the RSS (Skinner 2005). In the case where territories are held year-round, males commonly abandon their territories to feed elsewhere during critical periods of food shortage (Owen-Smith 1977).

The ecological consequences of habitat change are complex (Villard 2002). When habitats are modified or fragmented, animal population processes are often less affected than when habitat is lost, but it reduces the persistence of the animal populations (Fahrig 2002). According to Haila (2002), habitat loss or fragmentation causes the following ecological changes: (i) reduction in the abundance and richness of plant and animal species, (ii) decreased dispersal among fragments, (iii) changes in fitness of animal species and populations, (iv) loss in genetic variation, (v) breeding failure, (vi) changes in competition exclusion relationships, and (vii) changes in the biophysical environment (microclimate, soils, etc.).

Behavioural mechanisms that make populations vulnerable to habitat fragmentation have not been well studied. Species with long distance migrations, cooperative behaviour, or species that modify their environment are likely candidates (Burkey & Reed unpubl.). Fragmented populations are also likely to have evolved behaviour that is beneficial in adjacent habitats, but detrimental in fragmented habitats. Examples would include long-distance dispersal through a now hostile environment and choosy females that risk not finding a suitable mate among the limited number of potential mates in that patch (Burkey & Reed unpubl.). In south-western Kenya, key birthing grounds for wildebeest and zebra were leased to wheat farmers in the 1980's. Their cultivation caused a strong loss and fragmentation of this critical wildlife habitat, and was probably responsible for an approximately 75% decline in the resident wildebeest populations in the last two decades (Ottichilo *et al*. 2000; Serneels & Lambin 2001). Natural habitats in tourism areas are typically manipulated to enhance the tourism experience, in ways that may disrupt the integrity of ecological communities and favour some species over others (Kiss 2004). Kiss (2004) states that some management tools such as controlled burning, clearing of vegetation, artificial water points and artificial feeding have led to ecological changes and decreased resiliency in tourism-oriented protected areas and game ranches.

Fencing has obvious impacts on wide-ranging large and medium-sized mammals, but a lesser or a positive effect on other organisms (Reid *et al*. 2004). For many larger mammals, fences either cause temporary or permanent loss of habitat. The fence will often modify habitat access by slowing or restricting movement of individuals. Increasing grazing pressure will affect vegetation negatively and can have a strong impact on a range of ecosystem functions, particularly productivity and nutrient cycling (Frank *et al*. 1998). Little is known about how long it takes a fragmentation event to cause a response in an animal species population, and whether or not the changes we see in an area interact with the shape of habitat fragments or patches (McGarigal & Cushman 2002). Compared to other studies, no clear deviation in the daily and seasonal activities of the herbivore game species as a result of habitat modification could be detected. Territorial behaviour of the game species appeared to be affected by the small fenced-in area, since no clear boundaries of each species' territorial area could be detected. The vegetation and biophysical environment will definitely be affected by the high grazing pressure, but this will be discussed in more detail in Chapter 8.

6.5 CONCLUSION

The following conclusions can be drawn from the results of this study:

(i) Vegetation and seasonality influenced the small scale habitat preferences of the herbivore game species within this modified (fragmented) habitat to some extent.

(ii) Habitat patches with abundant Increaser herbaceous species, such as *E. obtusa*, *A. bipartita*, *E. chloromelas* and *T. berteronianus*, relatively high species diversity and moderate to low VCS, were mostly preferred by springbok and blesbok. Black wildebeest tended to favour patches with a higher occurrence of Decreaser herbaceous species such as *T. triandra* and *S. incrassata*, although Increaser species were also relatively abundant.

(iii) Experimental plots preferred by the herbivore game species, had low above-ground DM productions. This is because they favour shorter grass areas, which will result in a lower production.

(iv) Seasonal movement was indicated by changes in the experimental plot indices. The number of habitat patches utilised was highest during the dry season when food resources were scarce.

(v) There was an overall decline in active diurnal behaviour of the herbivore game species during the warm season due to the increase in maximum daily temperatures, which decreased the necessity to spend a lot of time feeding.

(vi) The small scale habitat preferences of these game species cannot entirely be explained in terms of vegetation and seasonality, since other factors such as reproduction, social behaviour and size of the fenced-in area also influenced patch preferences.

CHAPTER 7

SMALL SCALE FEEDING PREFERENCES OF HERBIVORE GAME SPECIES IN GRASSLAND

7.1 INTRODUCTION

Management of any habitat for wildlife basically revolves around managing the food resources in the habitat (Scotcher 1979). Ignorance of herbivore game species' dietary preferences and inappropriate rangeland management prevent ranchers from recognising degradational changes in time. By the time that degradation becomes obvious, rangelands have changed their structure and lost a large part of their productivity. The objective of this study is to provide information on the feeding preferences of some of the Free State's most common herbivore game species, which include springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*) and black wildebeest (*Connochaetes gnou*), within the experimental area.

7.2 PROCEDURE

7.2.1 Creating a field reference guide

A representative mature plant of each relevant grass species was collected from the study area and taken to the laboratory where a field reference guide was prepared for the estimation of percentage utilisation. The individual plants were clipped at the following height intervals, each height representing a different degree of utilisation: grass species with a total height of 50 - 300 mm were cut at 10% intervals, species between 400 - 700 mm at 15% intervals, and species between 800 - 1 700 mm at 25% intervals. After each clipping the plant material was placed in a paper bag, marked, and a photograph of the grass plant was taken. The clipped plant material was dried in a drying oven at 70ºC and then weighed. The cumulative mass of the plant material at the different heights was expressed as a percentage of the total mass. These percentages were used as a guideline to associate the different photographs with the different utilisation classes. The developed field reference guide is presented in Appendix C_1.

7.2.2 Data collection

Depending on the percentage occurrence of a given species (see Chapter 5) a maximum of ten individual plants per grass species, were randomly selected in each of the twenty experimental plots (see Chapter 3). The individual plants of each species were numbered and marked with a yellow plastic tag (Figure 7.1). A GPS reading was taken, should the tag get lost or pulled out by the animals. The marked plants were inspected on a weekly basis from June 2004 to May 2005. During each inspection subjective estimates, aided by the developed field reference guide, were made on the degree of utilisation of each individual plant. Marked plants were placed into the relevant utilisation class as presented in Table 7.1.

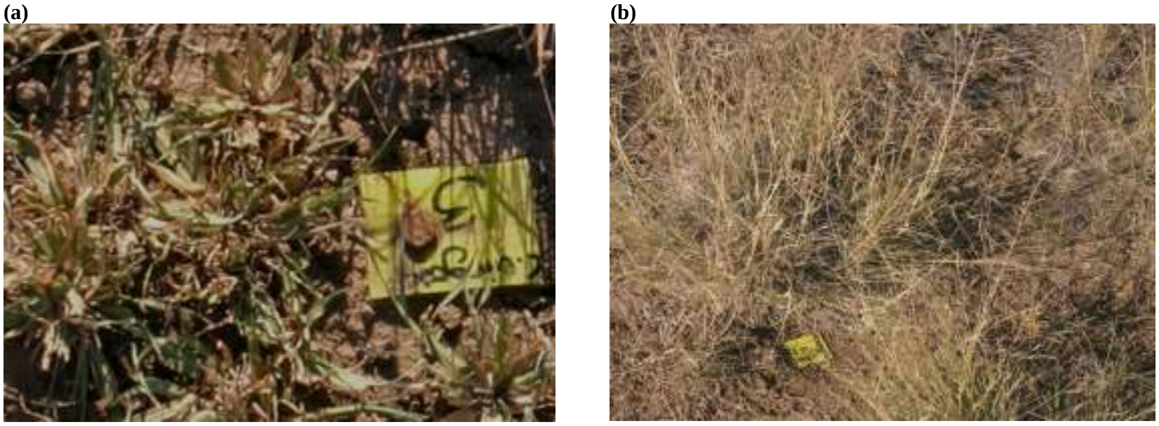

Figure 7.1: An example of how each individual grass plant was marked.

Table 7.1: Different utilisation classes used for classifying the grass plants marked in each experimental plot.

Descriptive names of grazed classes	Range of utilisation by grazed class (%)	Average utilisation by grazed class (%)
Unutilised	0	0
Very light utilisation	0 – 10	5
Light utilisation	10 – 40	25
Moderate utilisation	40 – 70	55
Heavy utilisation	70 – 100	85

7.2.3 Data analysis

A modification of the grazed-class method (Schmutz *et al*. 1963) was used to determine the grass species preferences and percentage utilisation during the different seasons. A number of variations of the grazed-class method have been used to estimate utilisation and diet preferences (Du Plessis 1972; Roos *et al*. 1973; Stoddart *et al*. 1975). The percentage utilisation of each grass species was determined by using the following formula:

$$Y = (0 \times n) + (5 \times n) + (25 \times n) + (55 \times n) + (85 \times n)$$

where Y = percentage utilisation

$0, 5, 25, 55, 85$ = average use factor for each utilisation class (Table 7.1)

n = percentage of grazed plants occurring in the relevant class

This was done weekly in order to determine the average weekly utilisation during the different seasons. The percentage tufts grazed, as well as the frequency of defoliation (amount of times each marked plant was defoliated), was also calculated. Simple descriptive statistics (Microsoft Excel 2004) was used to present the results of this investigation.

The definite percentage occurrence of the grass species in the diet of the herbivore game species (determinable by among others faecal analysis) is not known, and thus, one cannot be certain that these are the preferred species. Therefore, they are only regarded as "favoured species". Favoured grass species refer to grass species with the highest percentage utilisation (calculated as described in section 7.2.3 below) and intensity of utilisation (based on the percentage of marked plants of a species in each grazing class). Less-favoured species include species with a low percentage and intensity of utilisation, and non-favoured species include species with very light to no utilisation.

7.3 RESULTS

7.3.1 Utilisation of grass species in terms of the grazed-class method

The average utilisation of grass species during the different seasons is presented in Table 7.2. During the DS *Eragrostis obtusa*, *Eragrostis plana*, *Digitaria eriantha*, *Themeda triandra* and *Panicum stapfianum* had the highest utilisation (Table 7.2). *Brachiaria eruciformis* and *Chloris virgata* had an average utilisation of less than 31% and *Eragrostis chloromelas* less than 12% (Table 7.2). The remaining species were utilised less than 10% or unutilised. During the GIS, *E. obtusa*, *T. triandra*, *E. plana*, *P. stapfianum* and *D. eriantha* was still heavily utilised (Table 7.2). The high utilisation of *H. contortus* and *C. virgata* is attributed to their palatability and low occurrence (Table 7.2). The utilisation of other grass species was less than 14%. *Eragrostis obtusa*, *T. triandra*, *D. eriantha*, *P. stapfianum* and *E. plana* were utilised the most during the AGS, regardless of the overall decline in utilisation (Table 7.2). Utilisation of the remaining species was less than 10% to none. During the RSS, utilisation was the lowest, with only *T. triandra* utilised more than 10% (Table 7.2).

Ratios between percentage utilisation and percentage occurrence of marked grass species indicated that grass species with the highest average percentage utilisation generally had a lower average percentage occurrence (Table 7.3). Species with low occurrence and high degree of utilisation can be considered as favoured fodder species, but not necessarily the main fodder species.

Table 7.2: Average percentage utilisation of grass species during the dormant season (DS), growth initiation season (GIS), active growing season (AGS) and the reserve-storing season (RSS), respectively. (Standard deviation is given in parenthesis).

	Average utilisation (%)			
	Seasons			
Species	**DS**	**GIS**	**AGS**	**RSS**
Aristida adscensionis	4.6 (± 5.5)	2.6 (± 2.9)	0.0 (± 0.0)	0.5 (± 0.9)
Aristida bipartita	1.6 (± 2.9)	0.4 (± 1.0)	0.0 (± 0.0)	0.1 (± 0.2)
Brachiaria eruciformis	30.2 (± 20.5)	3.4 (± 8.4)	0.2 (± 0.5)	1.0 (± 1.4)
Chloris virgata	25.5 (± 36.1)	22.3 (± 31.5)	8.5 (± 4.4)	2.1 (± 3.0)
Cymbopogon pospischilii	1.8 (± 4.9)	1.6 (± 4.5)	0.1 (± 0.2)	0.0 (± 0.1)
Cynodon dactylon	3.4 (± 5.3)	3.8 (± 4.1)	4.1 (± 4.8)	1.6 (± 2.3)
Digitaria eriantha	39.1 (± 19.8)	40.1 (± 18.2)	12.9 (± 7.1)	6.6 (± 2.6)
Eragrostis chloromelas	11.5 (± 14.2)	13.9 (± 14.0)	2.3 (± 3.2)	0.5 (± 0.6)
Eragrostis obtusa	73.5 (± 24.3)	73.1 (± 24.2)	22.0 (± 7.3)	9.7 (± 4.5)
Eragrostis plana	47.5 (± 27.4)	41.3 (± 28.1)	11.4 (± 5.8)	5.3 (± 3.4)
Heteropogon contortus	29.8 (*)	29.8 (*)	7.4 (*)	0.0 (*)
Panicum stapfianum	37.5 (± 26.5)	37.3 (± 21.7)	11.1 (± 8.1)	5.9 (± 4.0)
Setaria incrassata	7.6 (± 8.3)	9.6 (± 9.2)	4.8 (± 3.9)	3.2 (± 2.0)
Themeda triandra	39.0 (± 23.5)	43.5 (± 24.3)	14.2 (± 6.9)	10.5 (± 4.6)
Tragus berteronianus	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)

* STDEV could not be calculated due to low occurrence and sporadic distribution.

Table 7.3: Percentage utilisation relative to percentage occurrence of marked grass species grazed averaged over four seasons.

Species	**Average occurrence (%)**	**Average utilisation (%)**	**Average utilisation relative to average occurrence**
Aristida adscensionis	0.6	1.9	3.2
Aristida bipartita	16.7	0.5	0.0
Brachiaria eruciformis	1.1	8.7	7.9
Chloris virgata	0.2	14.6	73.0
Cymbopogon pospischilii	0.6	0.9	1.4
Cynodon dactylon	1.1	3.2	2.9
Digitaria eriantha	1.2	24.7	20.5
Eragrostis chloromelas	24.1	7.0	0.3
Eragrostis obtusa	3.1	44.6	14.4
Eragrostis plana	1.8	26.4	14.7
Heteropogon contortus	0.2	16.7	83.7

…Table continues

Table 7.3 continued…

Species	Average occurrence (%)	Average utilisation (%)	Average utilisation relative to average occurrence
Panicum stapfianum	3.5	22.9	6.6
Setaria incrassata	17.2	6.3	0.4
Themeda triandra	12.1	26.8	2.2
Tragus berteronianus	0.5	0.0	0.0

The average percentage utilisation of grass species within each experimental plot is presented in Figures 7.2 to 7.5. The species utilised differed considerably and are influenced by the relative abundance of some grass species in particular plots. Utilisation of grass species in plots A1-4 was extremely low during all four seasons (Figures 7.2 - 7.5). The high percentage utilisation of *Brachiaria eruciformis, C. virgata, T. triandra, P. stapfianum* and *C. dactylon* was due to their palatability and low abundance in these plots (see Chapter 5).

The average utilisation of grass species in plots B1-3 was the highest during the dry season (Figure 7.2 & 7.3). Species such as *E. plana*, *P. stapfianum*, *T. triandra* and *E. obtusa* were the most utilised species in plots B1&2, and *E. obtusa* and *P. stapfianum* in plot B3 (Figure 7.2 & 7.3). Species in plot B4 were poorly utilised during all four seasons (Figures 7.2 - 7.5). The high utilisation of *T. triandra* in plot B4 is again due to its palatability and low occurrence (see Chapter 5). Although the number of grass species utilised increased as the seasons progressed, the average percentage utilisation of all species in general declined drastically in all four plots during the rainy reason (Figures 7.2 - 7.5). The specific species that were utilised the most remained relatively constant during all four seasons.

A similar pattern to row B was found in plots C1&2, where the average utilisation was highest during the dry season, and the number of species grazed increased as the seasons progressed (Figures 7.2 - 7.5). The most intensively utilised species in plots C1-4 during the dry season included *P. stapfianum*, *E. obtusa*, and *E. plana* (Figures 7.2 & 7.3), with a decrease in utilisation of *P. stapfianum* during the GIS (Figure 7.3). During the rainy season the most utilised species included *P. stapfianum*, *E. obtusa*, *T. triandra*, and to a lesser extent *E. plana* (Figure 7.4 & 7.5). The utilisation of *B. eruciformis* and *E. chloromelas* decreased during this season (Figures 7.4 & 7.5). In contrast, the number of grass species utilised increased during the AGS and RSS.

The number of grass species grazed in plots D1&2 increased during the rainy season (Figures 7.4 & 7.5). The most intensively utilised species in plot D1 included *E. obtusa*, *E. plana* and *T. triandra* during the DS, GIS and AGS, and during the RSS *E. obtusa* and *T. triandra*. However, these two species were utilised to a lesser extent during the rainy season (Figures 7.2 & 7.5). In plot D2, *E. obtusa, B. eruciformis, T. triandra*, *D. eriantha* and *E. plana* were mainly utilised during the DS and GIS (Figures 7.2 & 7.3). The most utilised species during the AGS and RSS included *D. eriantha*, *E. obtusa* and *T. triandra* (Figures 7.4 & 7.5). The species with the highest percentage utilisation in plot D3 during the DS and GIS were *P. stapfianum*, *T. triandra*, *E. obtusa* and *D. eriantha*. During the DS, AGS and RSS species with the highest percentage utilisation in plot D4 included *E. obtusa*, *T. triandra* and *P. stapfianum*. There was an overall decline in utilisation from the dry season to the rainy season in all the plots.

In plot E1 *E. obtusa*, *E. plana*, *D. eriantha* and *T. triandra* were the most utilised species during the dry season. The most utilised species during the wet season included *D. eriantha*, *E. obtusa* and *T. triandra*. In plot E2 the average percentage utilisation of grass species and the number of grass species utilised was the highest during the DS, and decreased as the seasons progressed. *Eragrostis obtusa*, *T. triandra*, and to a lesser extent *E. plana* and *P. stapfianum*, were the most utilised species during this season (Figure 7.2). Except for the RRS, these species remained the most utilised species during all four seasons. In plot E3, *E. obtusa*, and to a lesser extent *T. triandra* were species with the highest utilisation during all four seasons (Figures 7.2 - 7.5). The most utilised species in plot E4 included species such as *E. obtusa* and to a lesser extent *T. triandra* during the DS, GIS and AGS, and *T. triandra* and *P. stapfianum* during the RSS (Figures 7.2 - 7.5).

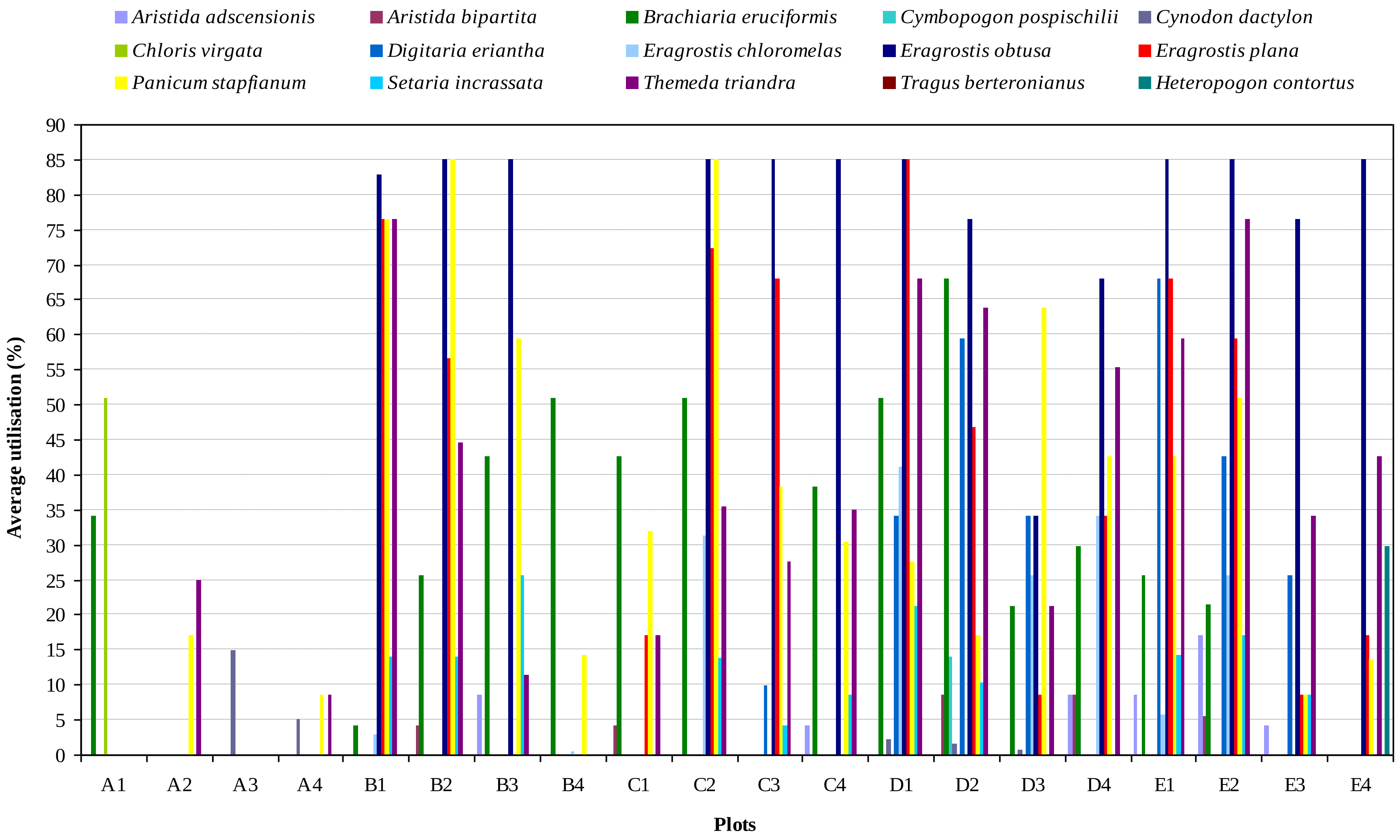

Figure 7.2: Average percentage utilisation of grass species in the experimental plots during the dormant season (DS) (June - August).

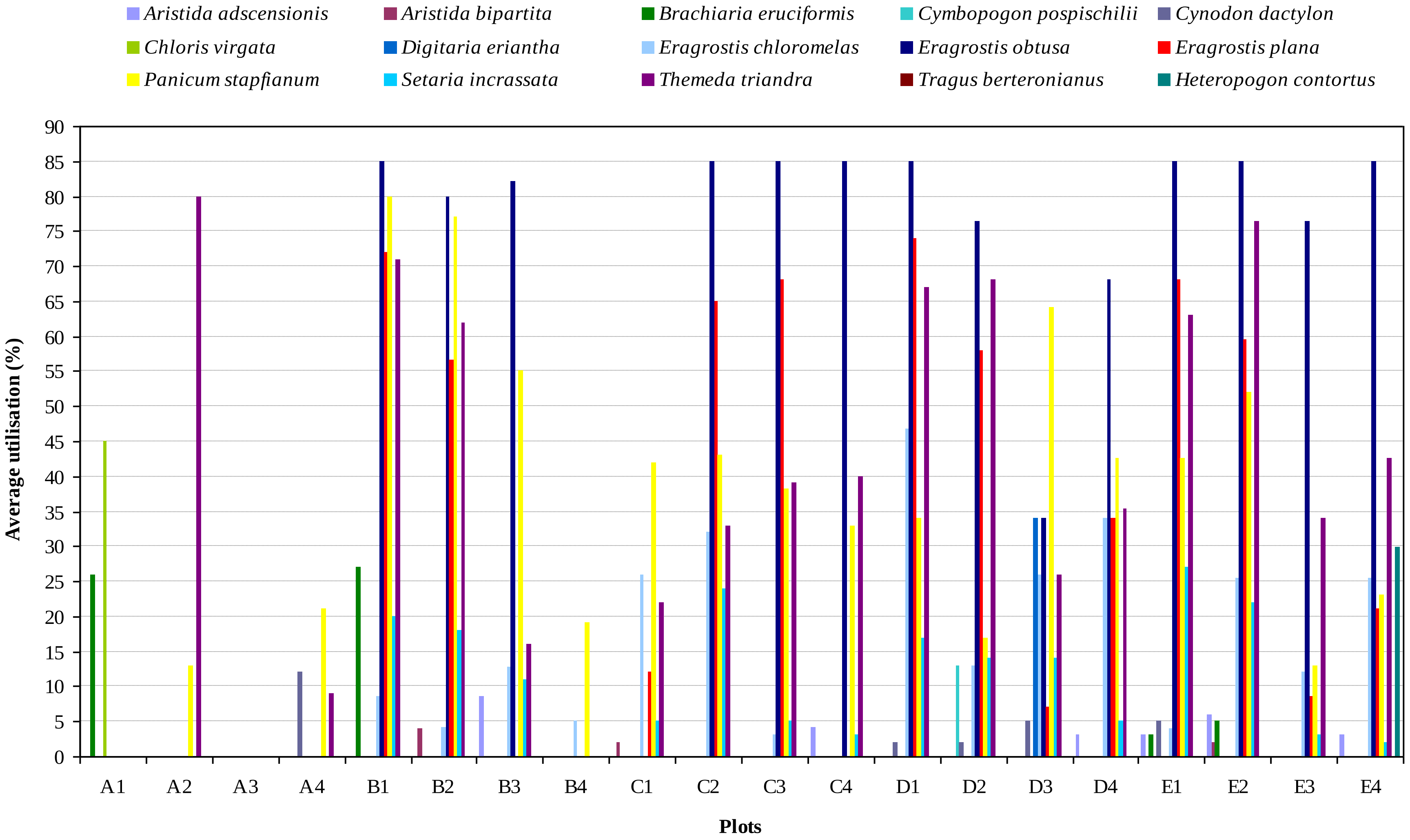

Figure 7.3: Average percentage utilisation of grass species in the experimental plots during the growth initiation season (GIS) (September - October).

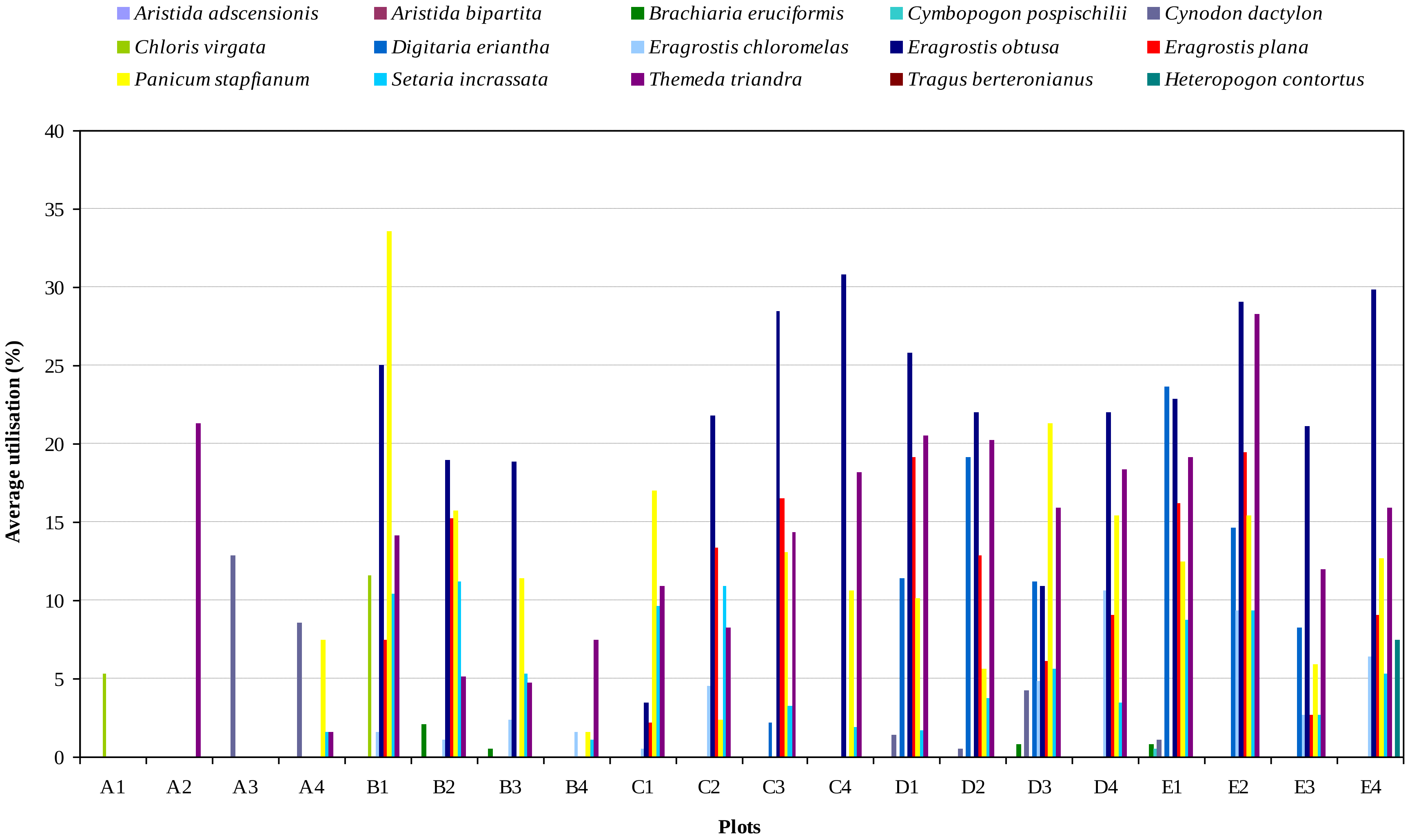

Figure 7.4: Average percentage utilisation of grass species in the experimental plots during the active growing season (AGS) (November – February).

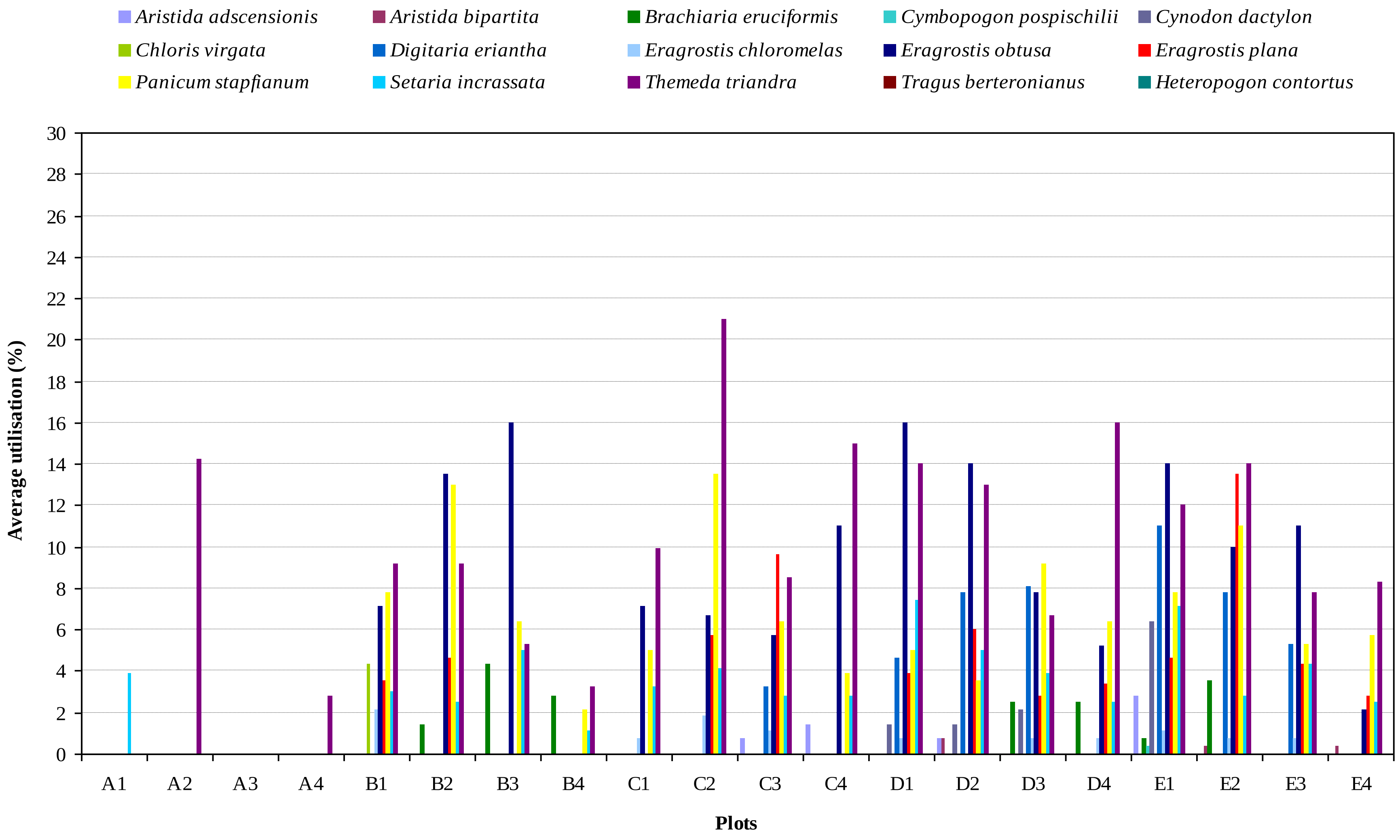

Figure 7.5: Average percentage utilisation of grass species in the experimental plots during the reserve storage season (RSS) (March – May).

7.3.2 Percentage of marked plants grazed

The average percentage marked plants (of each species) grazed during the different seasons is presented in Table 7.4. It was clear that *E. obtusa* and *T. triandra* had the highest percentage tufts grazed during all four seasons. More than 40% of *E. plana*, *P. stapfianum* and *D. eriantha* tufts were defoliated during the DS and GIS. The high percentage utilisation of *Heteropogon contortus* is due to their low occurrence. The percentage marked plants grazed decreased markedly in all grass species as the season progresses. The ranking of the species according to the most tufts grazed, remained relatively the same through all four the seasons. The marked plants of *A. bipartita*, *B. eruciformis, Chloris virgata*, *Cymbopogon pospischilii*, *E. chloromelas, H. contortus* and *S. incrassata* were mostly grazed during the dry season (Table 7.4). None of the marked plants of *T. berteronianus* were grazed (Table 7.4).

Table 7.4: Average percentage of marked plants grazed during the dormant season (DS), growth initiation season (GIS), active growing season (AGS) and the reserve storing season (RSS). (Standard deviation is given in parenthesis).

Species	**Average plants grazed (%)**			
	Season			
	DS	**GIS**	**AGS**	**RSS**
Aristida adscensionis	7.0 (± 6.3)	3.4 (± 3.5)	0.0 (± 0.0)	0.2 (± 0.5)
Aristida bipartita	2.0 (± 3.8)	0.7 (± 1.5)	0.0 (± 0.0)	0.1 (± 0.2)
Brachiaria eruciformis	35.6 (± 24.1)	3.9 (± 9.8)	1.9 (± 7.0)	1.2 (± 1.7)
Chloris virgata	12.0 (± 26.8)	10.5 (± 23.5)	3.1 (± 4.4)	1.0 (± 2.2)
Cymbopogon pospischilii	0.0 (± 0.0)	0.0 (± 0.0)	0.1 (± 0.3)	0.1 (± 0.2)
Cynodon dactylon	3.5 (± 6.0)	4.1 (± 4.9)	4.2 (± 5.5)	1.5 (± 2.5)
Digitaria eriantha	40.2 (± 27.0)	41.3 (± 25.9)	13.3 (± 9.4)	6.8 (± 3.9)
Eragrostis chloromelas	16.2 (± 16.2)	16.3 (± 16.5)	2.6 (± 3.5)	1.0 (± 1.7)
Eragrostis obtusa	86.3 (± 28.5)	86.0 (± 28.4)	26.0 (± 8.6)	11.7 (± 5.0)
Eragrostis plana	55.9 (± 32.2)	54.7 (± 30.6)	13.5 (± 6.9)	6.3 (± 4.0)
Heteropogon contortus	35.0 (*)	35.0 (*)	8.8 (*)	0.0 (*)
Panicum stapfianum	44.1 (± 31.2)	43.8 (± 25.6)	13.1 (± 9.6)	6.9 (± 4.6)
Setaria incrassata	9.3 (± 10.1)	11.8 (± 11.3)	5.7 (± 4.6)	3.9 (± 2.3)
Themeda triandra	45.7 (± 27.6)	52.0 (± 28.3)	16.7 (± 8.1)	11.6 (± 5.8)
Tragus berteronianus	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)

* STDEV could not be calculated due to low occurrence and sporadic distribution.

7.3.3 Intensity of utilisation

Intensity of utilisation based on the percentage marked plants of the various grass species occurring in the different grazed classes during the different seasons is presented in Figures 7.6 to 7.9. It is notable that most species fell either into the unutilised or heavy utilised classes. The intensity of utilisation was the highest during the dry season (Figures 7.6 & 7.7) and the lowest during the AGS (Figure 7.8). Annual species such as *Tragus berteronianus*, *C. virgata* and *B. eruciformis* were mostly dead during the dry season (DS & GIS and the beginning of the AGS). *Eragrostis obtusa*, *E. plana*, and to a lesser extent *D. eriantha*, *P. stapfianum* and *T. triandra*, had the highest intensity of utilisation during the dry season (Figures 7.6 & 7.7).

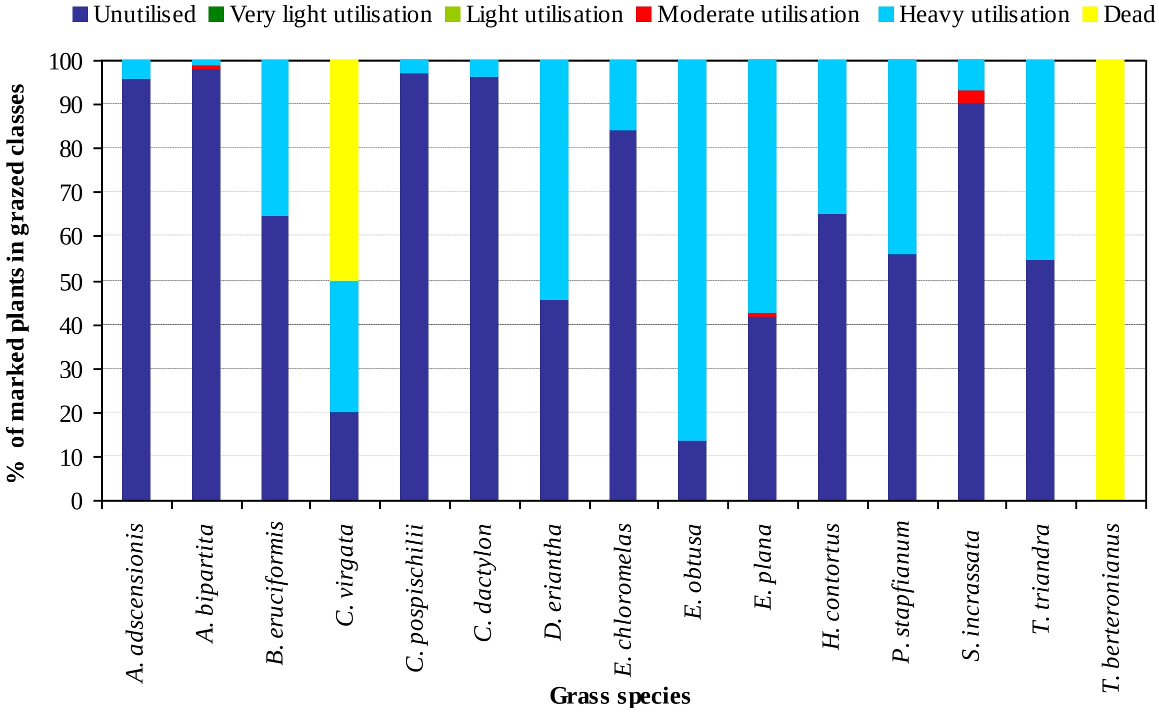

Figure 7.6: Percentage of the marked plants of the various grass species in the different grazed classes during the dormant seasons (DS).

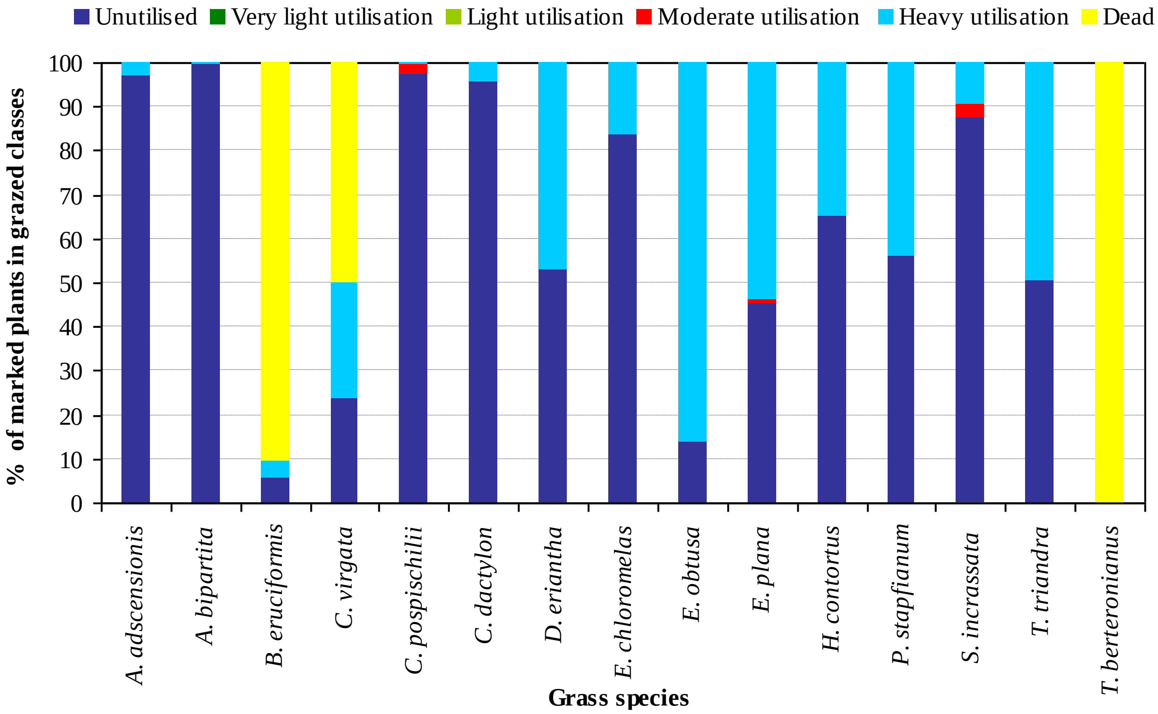

Figure 7.7: Percentage of the marked plants of the various grass species in the different grazed classes during the growth initiation season (GIS).

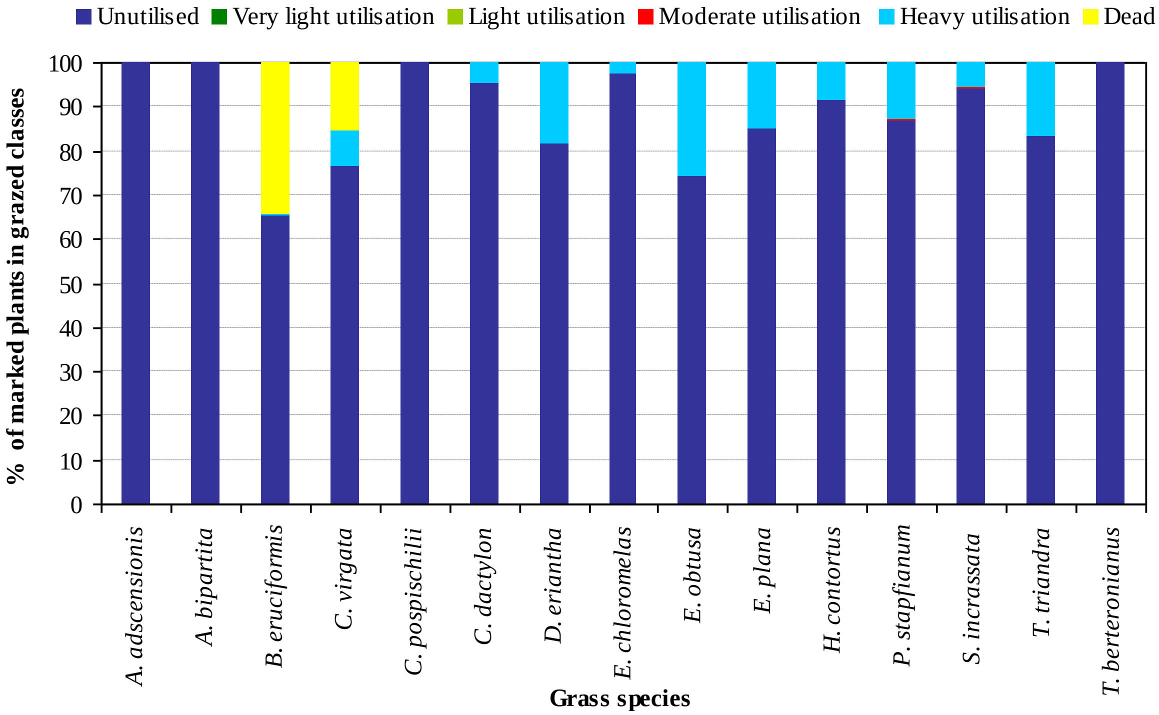

Figure 7.8: Percentage of the marked plants of the various grass species in the different grazed classes during the active growth season (AGS).

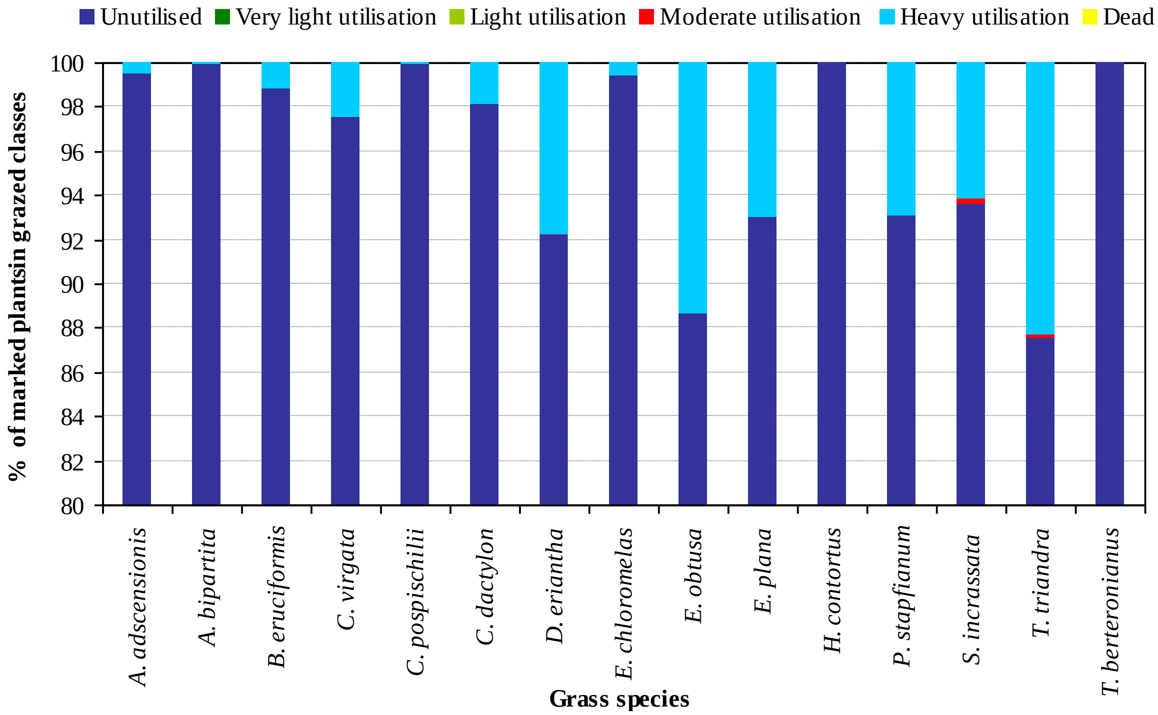

Figure 7.9: Percentage of the marked plants of the various grass species in the different grazed classes during the reserve storage season (RSS).

7.3.3.1 Frequency of utilisation

The average frequency of defoliation of the grass species is presented in Table 7.5. *Eragrostis obtusa*, *T. triandra*, *E. plana*, *D. eriantha* and *P. stapfianum* had the highest frequency of defoliation during all four seasons (Table 7.5). The ranking of the species according to the frequency of utilisation remained relatively the same during the seasons. *Aristida bipartita*, *B. eruciformis*, *Chloris virgata*, *Cymbopogon pospischilii*, *E. chloromelas*, *H. contortus* and *S. incrassata* were mostly defoliated during the dry season (Table 7.5). *Tragus berteronianus* was not defoliated at all (Table 7.5).

Table 7.5: Average frequency of defoliation of marked grass species during the dormant season (DS), growing initiation season (GIS), active growing season (AGS) and the reserve storing season (RSS). (Standard deviation is given in parenthesis).

Species	**Average number of times weekly defoliated**			
	Season			
	DS	**GIS**	**AGS**	**RSS**
Aristida adscensionis	0.6 (± 0.6)	0.3 (± 0.3)	0.0 (± 0.0)	0.1 (± 0.1)
Aristida bipartita	0.2 (± 0.4)	0.1 (± 0.2)	0.0 (± 0.0)	0.0 (± 0.0)
Brachiaria eruciformis	3.5 (± 2.4)	0.4 (± 1.0)	0.0 (± 0.1)	0.1 (± 0.2)
Chloris virgata	1.5 (± 2.1)	1.3 (± 1.9)	0.8 (± 0.2)	0.3 (± 0.4)
Cymbopogon pospischilii	0.3 (± 0.7)	0.2 (± 0.6)	0.0 (± 0.0)	0.0 (± 0.0)
Cynodon dactylon	0.4 (± 0.6)	0.4 (± 0.5)	0.5 (± 0.6)	0.2 (± 0.3)
Digitaria eriantha	4.6 (± 2.3)	4.7 (± 2.1)	1.5 (± 0.8)	0.8 (± 0.3)
Eragrostis chloromelas	1.6 (± 1.6)	1.6 (± 1.6)	0.3 (± 0.4)	0.1 (± 0.1)
Eragrostis obtusa	8.7 (± 2.9)	8.6 (± 2.8)	2.6 (± 0.9)	1.1 (± 0.5)
Eragrostis plana	5.2 (± 3.4)	5.1 (± 3.2)	1.3 (± 0.7)	0.6 (± 0.4)
Heteropogon contortus	3.5 (*)	3.5 (*)	0.9 (*)	0.0 (*)
Panicum stapfianum	4.3 (± 3.1)	4.5 (± 2.6)	1.2 (± 0.9)	0.7 (± 0.4)
Setaria incrassata	0.9 (± 1.0)	1.1 (± 1.1)	0.6 (± 0.5)	0.6 (± 0.7)
Themeda triandra	4.4 (± 2.9)	5.2 (± 2.9)	1.7 (± 0.8)	1.2 (± 0.5)
Tragus berteronianus	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)	0.0 (± 0.0)

* STDEV could not be calculated due to low occurrence and sporadic distribution.

7.4 DISCUSSION

According to Crawley (1983), the most important aspect of understanding plant-animal interactions is to develop an appreciation for the foraging process. When an animal grazes a plant, a hierarchy of instinctive responses and behavioural actions has been undertaken that leads to the point of consumption (McNaughton 1987; Senft *et al*. 1987; Senft 1989). Once an animal has oriented itself in a habitat it must establish a feeding station. Within the feeding station, the animal must select from among the individual plant species on offer those that it will consume. The animal’s experience with available forage is utilised in a plant species-to-species appraisal and selection process, which is specific to the relevant herbivore game species (Stuth 1991). The more experience the animal has with the variety of habitats and plant species available to it, the greater its ability to optimize grazing tactics to survive in an environment (Senft *et al*. 1987; Senft 1989). Herbivores exhibit an evolutionary adaptation to feed on plant species from one or more of their primary food groups (Provenza & Balph 1987). Therefore, the grazing value of a plant depends on the animal species in question (Hanley 1982; Hanley & Hanley 1982; Owen-Smith & Cooper 1987). According to Stuth (1991), the grazing process used to gather food can therefore be best described as a hierarchical system of diet selection interacting with the herbivore species' physiological needs, resulting in a unique pattern of use across a given landscape.

Blesbok and black wildebeest are generally regarded as selective grazers, where their annual diets include more than 70% grasses and sedges (Grunow 1980; Cillié 2000; Van Hoven 2000; Furstenburg 2002a, Skinner 2005). Springbok is considered as a selective mixed feeder with an annual diet that includes 40% to 70% grasses and sedges (Owen-Smith 1979; Grunow 1980; Cillié 2000; Van Hoven 2000; Furstenburg 2002b; Skinner 2005). Based on average percentage utilisation and intensity of utilisation *T. triandra*, *E. obtusa*, *P. stapfianum*, *E. plana* and *D. eriantha* were the favoured grass species (Tables 7.2 & 7.5; Figures 7.6 - 7.9). The high utilisation of *H. contortus* and *C. virgata* is due to their palatability, sporadic distribution and low occurrence, and they are also regarded as favoured species. The average percentage utilisation of the favoured fodder species such as *E. obtusa*, *P. stapfianum*, *E. plana*, *D. eriantha*, *H. contortus* and *C. virgata* was more than the average percentage occurrence in the veld (Table 7.3). The intensity of defoliation and average percentage tufts grazed was generally the highest for the favoured species. During the wet season the utilisation of palatable grass species such as *D. eriantha* and *P. stapfianum* increased, while that of the less palatable species (*E. plana* and *E. chloromelas*) decreased.

The results from this study concur to some extent with the results from other studies. According to Furstenburg (2002b), the favoured grass species of the springbok include *T. triandra*, *C. dactylon*, *Panicum*, *Eragrostis*, *Brachiaria*, *Pennisetum*, *Sporobulus*, *Digitaria*, *Enneapogon* and *Stipagrostis*. The most important grass species in the blesbok's diet on unburned veld in the Highveld of Mpumalanga are *T. triandra*, *E. pseudosclerantha*, *E. curvula* and *Chloromelas* spp. (Du Plessis 1968). According to Bothma *et al*. (2000), blesbok do not graze on herbaceous plants other than grasses, with

T. triandra and *E. curvula* being the main types utilised all year round. In a study done by Vetter (2006) in the Eastern Cape it was found that *C. dactylon* was the dominant grass species in the diet of blesbok. Other species included *D. eriantha*, *Aristida congesta*, *T. triandra* and *Tragus berteronianus*. Vegetation utilisation by black wildebeest has been studied by Roberts (1963) and Van Zyl (1965). In the Willem Pretorius Game Reserve 86.8% of the diet consisted *E. lehmanniana*, *T. triandra*, *P. coloratum* and *C. dactylon* (Roberts 1963). Furstenburg (2002a) wrote that black wildebeest favoured species such as *T. triandra*, *C. dactylon* and *Sporobulus* spp.. Most of the marked plants fell into the unutilised or moderate to heavy utilisation classes, which indicated that the short grazed plants are repeatedly selected (Figures 7.6 - 7.9). However, the fact that re-growth was not taken into consideration could have affected these results.

The favoured grass species contributed on average 21.7% to the species composition (see Chapter 5). It is important to note that the Decreaser grass species (see Chapter 5) feature predominantly as favoured species. This implies that for optimal management of these herbivore game species, the veld should have a high percentage of Decreaser species. However, some Increaser species were also favoured species, which might be because springbok, blesbok and black wildebeest are short grass grazers and keep selecting the shorter grass, irrespective of its palatability. According to Gammon & Roberts (1978) animals tend, in terms of intra-specific variability, to select previously defoliated plants, largely because of their high quality and accessible re-growth (Bakker *et al*. 1983). The patch selective grazing habit of these herbivore game species (Novellie 1990) creates grazing lawns. Decreaser grass species are poorly adapted to frequent heavy defoliation (Danckwerts & Stuart-Hill 1987) and do not persist in grazing lawns. This may have caused an increase in the occurrence of the Increaser species within the preferred grazing patches. These species also generally occurred together in experimental plots with a high species diversity (see Chapter 5). Most of the grazing time was spent within these plots (see Chapter 6).

Shackleton & Mentis (1992) found that the occurrence of unpalatable species in the diet of herbivores can be indicative of the low abundance of palatable species and the generally poor quality of available grazing. Communities of grass species that are produced and maintained by grazing are by no means peculiar to artificially small areas, and also have an effect on large conservation areas (Novellie 1990). Forage from grazing lawns can have higher nutritive values and digestibility, and provide more available biomass to herbivore species (Olubajo *et al*. 1974; McNaughton 1979, 1984; Rodes & Sharrow 1990). Karki *et al*. (2000) found that new flush of vegetation growing on the grazing lawn had a higher nutritive quality compared to new flush of the surrounding grassland. They also found that grazing lawns have a higher species diversity, and differ considerably from neighboring grassland in their physiognomic structure. McNaughton (1983) pointed out that patch-selective grazing is an important agent of plant community diversity.

Non-favoured species included *Tragus berteronianus*, *A. bipartita* and *Cymbopogon pospischilii*. They were unutilised or only very lightly grazed when grazing pressure was high, such as during the DS and GIS. In times of scarcity animals may widen dietary breadth by including other, less palatable species in the diet (Owen-Smith 1994). According to Theron & Booysen (1966), Field (1976), O'Reagain & Mentis (1989) and O'Reagain (1993), animals respond to inter-specific variability by selecting species which are non-stemmy and have accessible leaves of high nutrient content and low tensile strength. Conversely, low quality, stemmy species with inaccessible leaves of high tensile strength are avoided. Grasses such as *C. pospischilii*, which contain secondary compounds like terpenes, are also generally avoided. Species selection appears to be based upon the interplay between plant structure, which determines intake rate and leaf quality, which determines nutrient content (O'Reagain 1993). *Brachiaria eruciformis*, *Cynodon dactylon*, *E. chloromelas* and *S. incrassata*, which are generally regarded as grass species with an average to high grazing value (Van Oudtshoorn 1999), were found to be less-favoured species in this study. Plots where these species had a high occurrence (see Chapter 6) generally had the lowest average percentage utilisation of grass species within them (Figures 7.2 - 7.5). The distribution of the marked plants within the plots could have had an influence on the results. As the game species are patch selective grazers, marked plants could have fallen outside the preferred patches. Nine of the grass species, namely *T. triandra*, *E. obtusa*, *S. incrassata*, *D. eriantha*, *P. stapfianum*, *Chloris virgata*, *B. eruciformis*, *Cynodon dactylon*, *H. contortus* are reported to be valuable for grazing in the arid and semi-arid regions (Roberts 1973; Renvoize *et al*. 1992; Moffett 1997; Van Oudtshoorn 1999). However, only four namely *T. triandra*, *E. obtusa*, D. *eriantha*, *P. stapfianum* were the favoured grass species. It is interesting to note that the main contributors of the above-ground DM production and species composition, *A. bipartita*, *E. chloromelas* and *S. incrassata*, were not regarded as favoured species. The association of springbok, blesbok and black wildebeest with the various grass species will be clarified in Chapter 8. Stuth (1991) states that the broad generalizations about species' selection and preferences should be tempered by the understanding that animal selectivity is a dynamic, situation-specific process. Specialized or focused grazing on some plant species may relate largely to its relative preference ranking at the time of active growth (AGS).

The seasonal variation in favoured species and the intensity of utilisation were probably due to the quantity and quality of the forage. The combined effects of time spent grazing and season of the year affected the intensity of utilisation. During the dry season more time was spent on grazing (see Chapter 6), which resulted in an increase in plants grazed and a higher frequency of defoliation. The intensity of defoliation decreased in accordance with the seasons with a corresponding decline in time spent grazing. It appears as if increased seasonal rainfall led to higher intensities of defoliation in plots where the preferred species had a higher occurrence. Since grasses do not re-grow after defoliation during winter (Wolfson 1999) and maintain their reserves despite intense defoliation, most of the marked plants remained in the same utilisation classes during the DS. The effect of the increasing aridity during the GIS reduced the botanical diversity, forage production and the availability of new growth, and therefore restricted the choice of diet by the herbivore game species. For these reasons, the favoured grass species of herbivore game species during the unproductive rainy season (GIS) closely resemble that of the preceding cold dry season (DS). Late rains also had an influence on the results found during the AGS, because of the high values found early in the AGS.

The dry season was also the time of year during which most of the females were pregnant. Poor nutritional circumstances at this stage will decrease their own performance as well as the growth ability of their offspring. According to Mduma *et al*. (1999), winter and under-nutrition most severely affect animal productivity. Sponheimer *et al*. (2003) suggests that further research on the influences of social structure and breeding behaviour on diet selection is necessary since this can also influence the process of diet selection. For example it is known that if a male leaves a bachelor herd and establish a harem its social status may affect its diet.

Various authors reported that seasonality affects the quality and quantity of forages available so that diets consumed by grazing herbivores vary throughout the year (Underwood 1982; McNaughton 1985; Senft *et al*. 1985; Tolsma 1987; Barnes *et al*. 1991; Ben-Shahar 1991; Everett *et al*. 1991; Shackleton 1992; Kirkman & Carvalho 2003). The term ‘quality’ refers to the nutritional value of the forage and includes the chemical composition of dietary components and their adequacy for supporting the physiological functions of the consuming animal (Huston & Pinchak 1991). Generally, animals select first from the highest quality components of the available forage pool. Some plant species are highly nutritious but available only in limited quantities, while more readily available species are less nutritious. As the pool of the highest quality plants is depleted, increasing quantities of the lower quality components are consumed. This was seen in the increasing utilisation of *E. plana*, *B. eruciformis* and *E. chloromelas* when the plant material of the favoured species became less available.

In accordance with Stuth (1991), the preference status of a particular plant species is largely dependent upon its inherent abundance, its morpho/phonological characteristics, the array of species on offer and the species of animal in question. The inherent morphological, anatomical, physiological and chemical characteristic of each plant species determines its potential nutritive value (Huston & Pinchak 1991). The preference for a grass species constantly changes as abiotic and temporal factors (i.e. season and weather conditions) alter the nature and potential nutritive value of the plant community (Stuth 1991; Augustine 2003). In a study done by Tolsma *et al*. (1987) it was found that there were differences in the phenology between *Eragrostis rigidior* (which had only one growth period just at the start of the wet season) and *Panicum maximum* (which produced new leaves after showers even at the end of the rainy season). The nutrient concentration of *P. maximum* was also generally higher than that of *E. rigidior*. Various factors could thus have influenced the nutritive value of the grass species and the degree of grazing.

The aggregation of herbivores - which locally affects the vegetation by consumption, excretion and trampling - may also cause a variation in the quantity and quality of vegetation (Jeltsch *et al*. 1997; Nash *et al*. 1999). Some species are only selected under specific conditions. Nutrient quality declines as the rate of development or recruitment of new leaf tissue decreases and the rate of senescence increases (Briske 1991). Because the forage quality of grass decreases with age (Mowat *et al*. 1965), the inter-related processes of growth and ageing cause a negative relationship between forage quantity and quality in natural grasslands. Tolsma *et al*. (1987) found that the N, P and K concentration was higher in new leaves than in old leaves. Wilson (1981) and Shipley (1999) found that the amount of cell wall and lignin (and thus the nutritional value) of grasses changes more drastically among seasons and with age. According to Huston & Pinchak (1991), semi-arid and arid rangelands are usually dominated by a particular forage type that is relatively high in quality during the early vegetative growth stage but rapidly declines in quality as the forage accumulates and matures. *Eragrostis obtusa* is palatable during the rainy season and becomes less palatable as the seasons become drier (Van Oudtshoorn 1999), which may explain the increase in utilisation of *E. obtusa* during the AGS (Table 7.2). According to Arnold (1960) new greener leaves during the rainy season are of higher quality than either stems or dead material.

The cohort of favoured grass species declined in botanical abundance from the 2003/04 to 2004/05 growing season (see Chapter 5). This is probably due to the frequent utilisation of these grass species. Favoured grass species differed in their tolerance to defoliation, but nearly all eventually became less abundant and their individual tufts became less vigorous. *Themeda triandra*, *E. obtusa*, *D. eriantha* and *P. stapfianum* decreased on average by 11.98% in abundance from 2003/04 to 2004/05. *Eragrostis plana* increased by 21.74% (see Appendix $B_{2\text{-}6}$). Although minor, if this pattern of utilisation continues over a few years, it may lead to the replacement of favoured grass species by less-favoured grass species. The herbivore game species will then be forced to increasingly utilise less-favoured grass species, which they have not utilised extensively before.

According to Westoby (1974), diet selection is dominated by the need to meet nutritional criteria. The response of the diet to availability of particular foods should not be continuous, but take the form of a cutoff at very low availability. This implies that as food becomes rarer in a plant community, grazing pressure on it will increase, at least until the cutoff is reached. Regardless of the high increase in annual pioneer species, the herbaceous layer of the study area was still dominated by perennial climax grass species (see Chapter 5). However, the species transformation that occurs in the herbaceous layer due to over-utilisation may result in a reduction in the nutrient content of the forage on offer, indicating that overgrazed rangeland is less nutritious (Rothauge 2000). Veld quality should be maintained by keeping the grass in a vegetative state (Tainton 1981). This can be achieved by using conservative stocking rates, combined with regular defoliation, using rotational grazing with livestock and mowing or burning of moribund grass (Everett *et al*. 1991).

7.5 CONCLUSION

The following conclusions can be drawn from the results of this study:

(i) *Themeda triandra*, *E. obtusa*, *P. stapfianum*, *E. plana* and *D. eriantha* were the favoured grass species of springbok, blesbok and black wildebeest.

(ii) Less-favoured species included *B. eruciformis*, *Cynodon dactylon*, *E. chloromelas* and *S. incrassata*, and non-favoured species included *Tragus berteronianus*, *A. bipartita* and *Cymbopogon pospischilii*.

(iii) The intensity of defoliation and percentage marked plants grazed were higher for favoured grass species than for less- or non-favoured species.

(iv) Because it was not possible to determine which herbivore game species selected which grass species, the utilisation values only give an indication of the grass species favoured by short grass grazers as a group.

(v) It appears as if the herbivore game species repeatedly selected the short grazed grasses irrespective of quality. This habit could, therefore, have been reflected in the results of grass species where short grazed plants contributed more to the total number of selected marked plants than non-grazed plants.

(vi) Seasonal changes occurred in the feeding preferences, where the general utilisation of less palatable species such as *E. plana*, *B. eruciformis* and *E. chloromelas* was higher during the dry season due to the lack of suitable forage.

(vii) The diversity of grass species grazed increased as the seasons became wetter, due to larger availability of new growth, which is more nutritional and palatable.

The association of springbok, blesbok and black wildebeest with the different grass species is discussed in more detail in Chapter 8.

CHAPTER 8

THE ASSOCIATION BETWEEN SOIL, VEGETATION AND GRAZING BY HERBIVORE GAME SPECIES

8.1 INTRODUCTION

Patch grazing has been described as the frequent and intense re-grazing of localised areas within an apparently uniform sward (Hatch & Tainton 1990). The resulting mosaic of heavily grazed patches and moderately grazed or ungrazed areas may be desirable in that it promotes sward heterogeneity (Arnold 1981; Kotliar & Wiens 1990), and also allows the animals to select a higher-quality herbage than the sward average (Olubajo *et al*. 1974; McNaughton 1979; McNaughton 1984; Ring *et al*. 1985; Mott 1985, 1987; Rhodes & Sharrow 1990), potentially resulting in increased animal performance. Although patch grazing may have short-term advantages, in the long-term patch grazing is considered to be detrimental to the sward (Mott 1985; Hatch & Tainton 1990) and could reduce the animal production potential of an area of the rangeland. Regardless the physical damage to plants due to grazing, herbivores also cause soil disturbances (Seagle *et al*. 1992; Milchunas & Lauenroth 1993; Owen-Smith 1999; Alfaro *et al*. 2004). Soil plays a vital role in the determination of the botanical composition, and may thus indirectly influence the occurrence of grazing lawns in an area. There is reason to believe that soil texture and defoliation interact because the effects of herbivores on plant production depend on water and nutrient availability (Georgiadis *et al*. 1989; Wise & Abrahamson 2005).

The objectives of this study were to determine:

(i) the association between soil properties and the vegetation, and

(ii) the association between grazing by springbok (*Antidorcas marsupialis*), blesbok

(*Damaliscus pygargus phillipsi*) and black wildebeest (*Connochaetes gnou*) and the vegetation.

8.2 PROCEDURE

8.2.1 Data collection

Procedures for the collection of the data used in this investigation were described in detail in Chapter 4, 5 and 6. Soil variables included texture (% silt, clay and sand), total nitrogen (N) (mg kg^{-1}), organic carbon (C) (mg kg^{-1}), phosphorus (P) (Bray I) (mg kg^{-1}), exchangeable cations, *viz*. sodium (Na) (mg kg^{-1}), potassium (K) (mg kg^{-1}), magnesium (Mg) (mg kg^{-1}) and calcium (Ca) (mg kg^{-1}), zinc (Zn) (mg kg^{-1}) content and the electrical resistance (Ω) (see Chapter 4). The vegetation variable included the species composition based on the percentage occurrence of the different grass species in each experimental plot (see Chapter 5). The grazing variable was represented by the time springbok, blesbok and black wildebeest spent grazing in each plot. An activity weighted index of occupation termed “animal hours” were calculated for each plot (see Chapter 6).

8.2.2 Data analysis

Principal Component Analysis (PCA) and Canonical Correspondence Analysis (CCA) were performed with the statistical programme CANOCO (version 2.1) (Ter Braak 1988) on: (i) the chemical and physical properties of the soil in each experimental plot, which included the soil variables listed above, (ii) species composition and (iii) the animal hours (index value) spent grazing by springbok, blesbok and black wildebeest during the dormant season (DS), growing initiation season (GIS) and the active growing season (AGS) in each experimental plot.

The PCA and CCA gave a visual representation of the relationships between the tested variables. Through ordination analysis the most influential factor on the botanical composition of the herbaceous layer in the experimental area was determined, as well as the association between the tested soil properties and the different grass species. By using CCA an indication of the associations between grazing by springbok, blesbok and black wildebeest and the different grass species and soil properties was obtained.

Observations were not done during the reserve storage season (RSS) as the grass in four of the experimental plots had been mowed (see Chapter 9), and this would have affected the results.

8.3 RESULTS

8.3.1 Principal Component Analysis (PCA) of the soil properties

The PCA ordination diagrams of the experimental plots based on the soil variables, and the soil variables are presented in Figures 8.1 & 8.2 respectively. Except for D4 and E2, experimental plots with a high clay content were largely situated in quadrants 1-3 (numbered clockwise) (Figure 8.1). The plots in quadrant 4, including D4 and E2, had a higher sand content (Figure 8.1). Experimental plots were thus ordinated across a soil texture gradient, where axis 1 clearly represents soil texture and axis 2 the Ca content in the soil. The plots in quadrant 1 and 2 had a higher calcium (Ca) content than the plots in quadrant 3 and 4 (Figure 8.1). The Eigen value for the first axis = 0.9031 and the second axis = 0.0494. The first axis explains 90.7% of the variance and the second axis only 4.96%. This indicates that soil texture is the most important determinant which explains most of the variation. The Ca content had a close association with axis 1 (Figure 8.2). Potassium (K) and magnesium (Mg), nitrogen (N) and zinc (Zn), and silt and phosphorus (P) had close associations with each other (Figure 8.2).

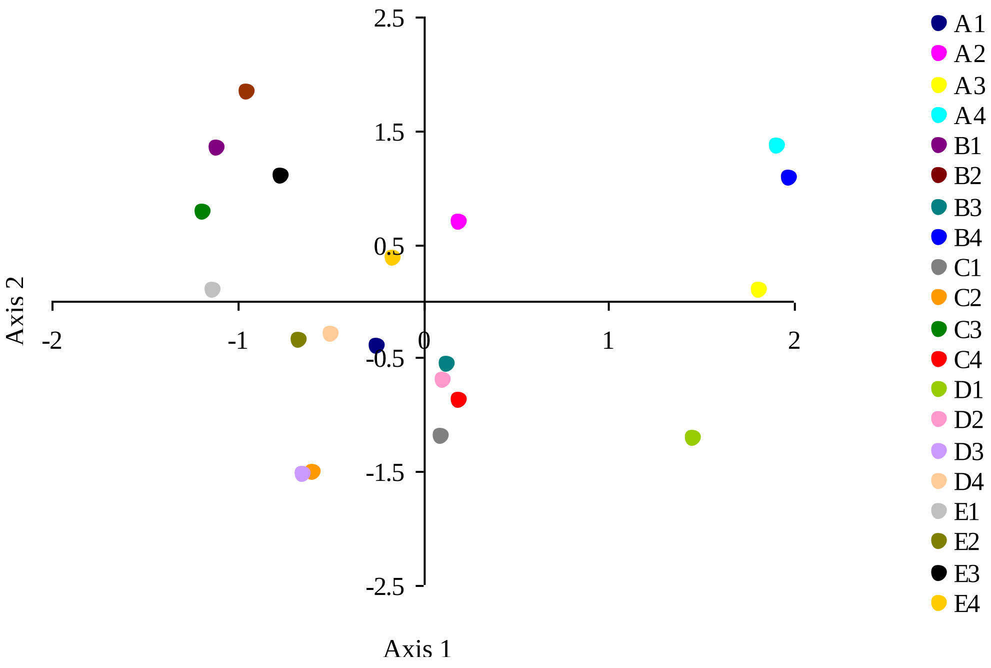

Figure 8.1: PCA quadrant ordination diagram of the twenty experimental plots on axis 1 (soil texture % sand, silt and clay) and axis 2 (Ca mg kg^{-1}) based on the tested soil variables. Eigen values: axis 1 = 0.9031; axis 2 = 0.0494.

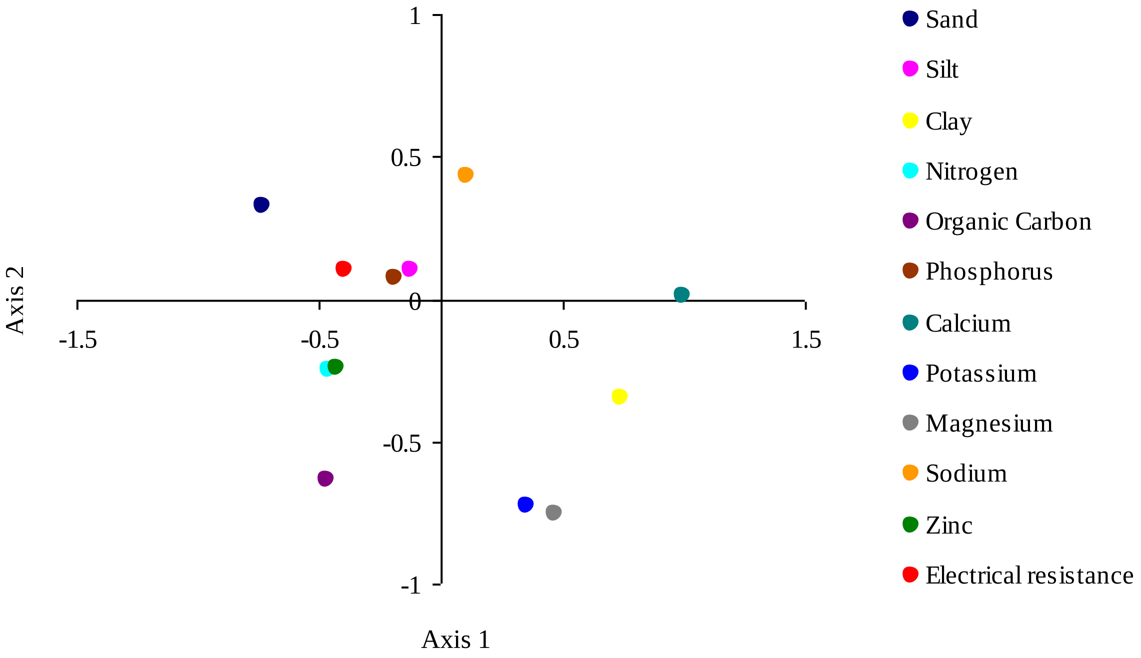

Figure 8.2: PCA quadrant ordination diagram of the soil variables on axis 1 (soil texture % sand, silt and clay) and axis 2 (Ca mg kg^{-1}). Eigen values: axis 1 = 0.9031 and axis 2 = 0.0494.

8.3.2 Principal Component Analysis (PCA) of the grass species composition based on occurrence

The PCA ordination diagrams of the experimental plots (based on grass species composition) and grass species composition based on occurrence for 2003/04 and 2004/05 are presented in Figures 8.3 & 8.4 and 8.5 & 8.6, respectively. It is clear that plots were ordinated along a soil texture gradient on axis 1, and a degradation (disturbance) gradient on axis 2. During 2003/04 the Eigen value for the first axis = 0.6826 and the second axis = 0.2200, and during 2004/05 axis 1 = 0.6078 and axis 2 = 0.2168. Experimental plots in quadrants 1 and 2 were dominated by grass species occurring on disturbed or overgrazed areas (Increaser species), and plots in quadrants 3 & 4 had a higher occurrence of Decreaser grass species (Figures 8.3 & 8.5). It is clear from Figures 8.4 & 8.6 that *Setaria incrassata*, *Brachiaria eruciformis*, *Eragrostis chloromelas* and *Aristida bipartita* were associated with soil with a high clay content. *Themeda triandra*, *E. plana*, *E. obutsa*, *Digitaria eriantha*, *Panicum stapfianum*, *Cymbopogon pospischilli*, *Heteropogon contortus*, *Cynodon dactylon* and *A. adscensionis* were mostly associated with soil with a higher sand content. The position of *T. berteronianus* is mostly explained by Axis 4, which may represent trampling (Figures 8.4 & 8.6). The low occurrence of *Chloris virgata* may have influenced its position along the various axes (Figures 8.4 & 8.6). *Brachiaria eruciformis* had a closer association with *E. chloromelas* and *A. bipartita* during 2004/05 (Figure 8.6). It is clear from Figure 8.7 that no major changes occurred in the ordination of the experimental plots based on species composition from 2003/04 to 2004/05.

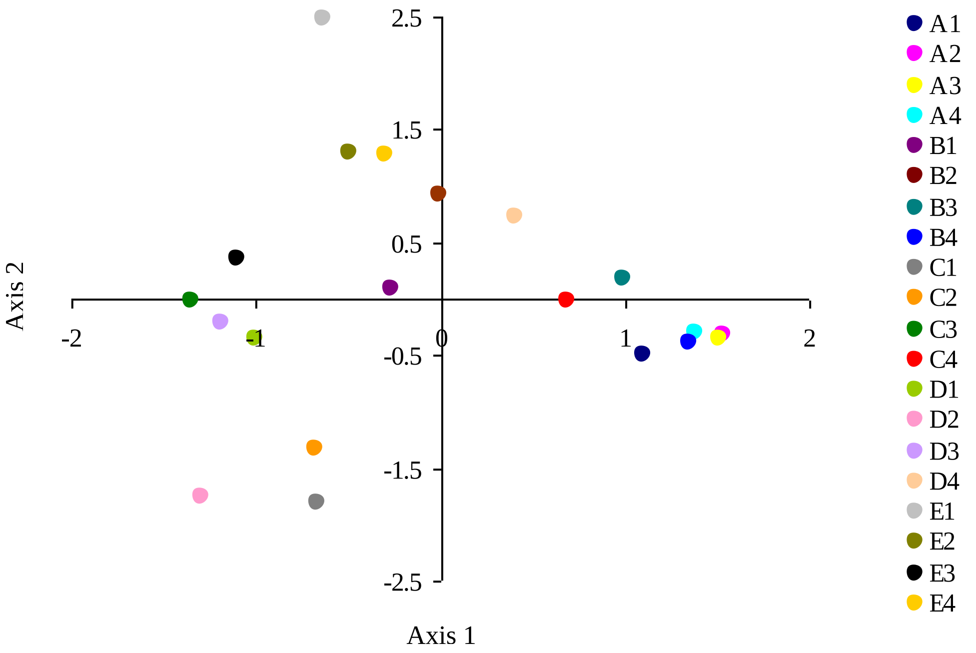

Figure 8.3: PCA quadrant ordination diagram of the twenty experimental plots according to the species composition on axis 1 (soil texture) and axis 2 (degradation) during 2003/04. Eigen values: axis 1 = 0.6826; axis 2 = 0.2200.

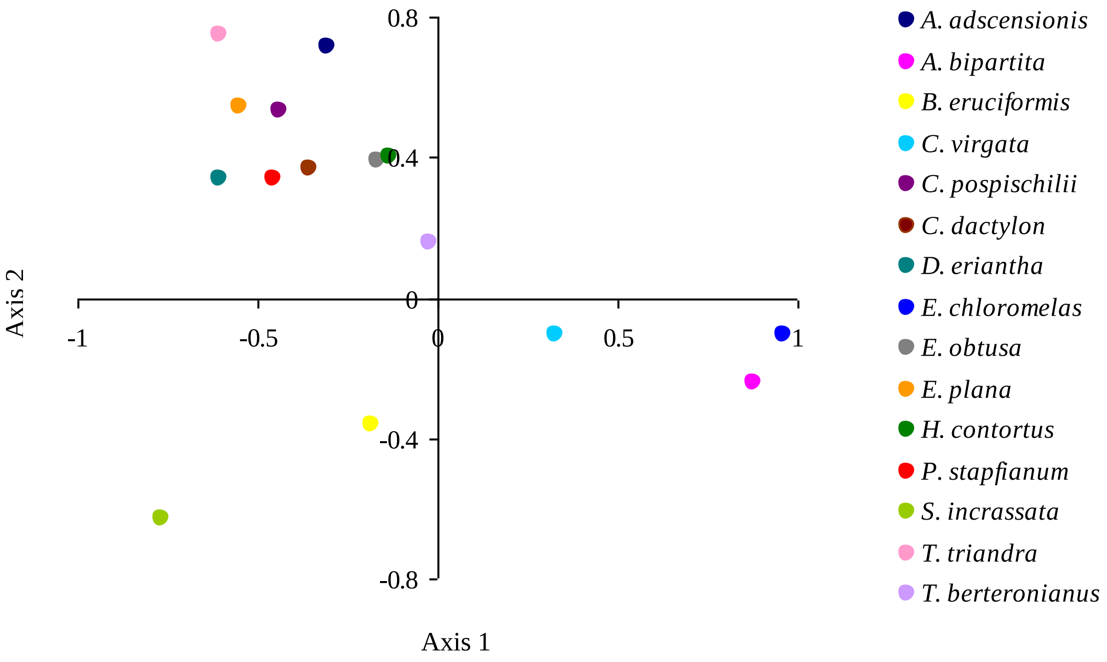

Figure 8.4: PCA quadrant ordination diagram of the grass species based on occurrence on axis 1 (soil texture) and axis 2 (degradation) during 2003/04. Eigen values: axis 1 = 0.6826; axis 2 = 0.2200.

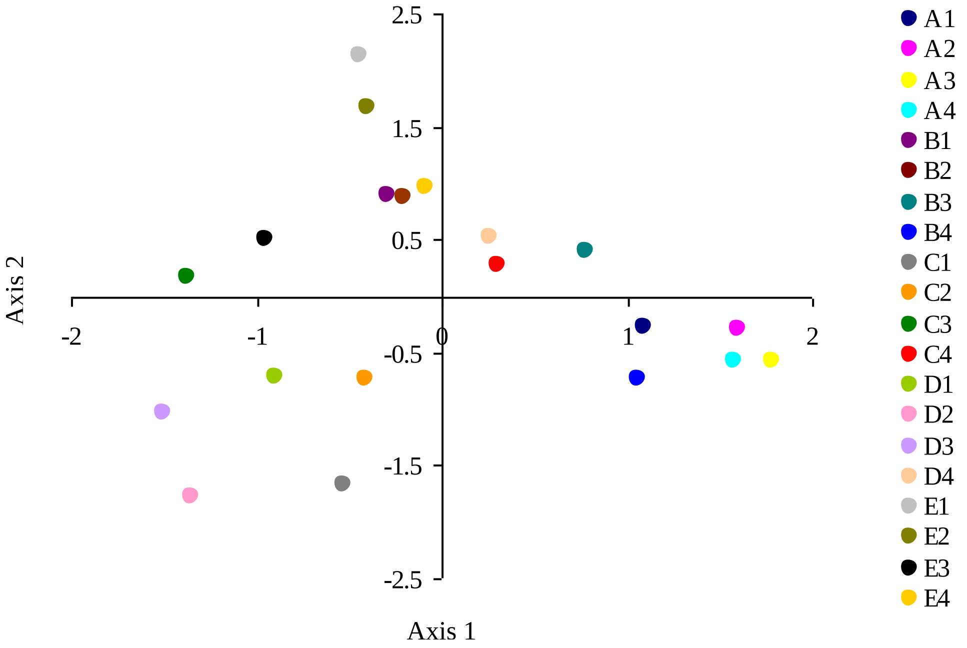

Figure 8.5: PCA quadrant ordination diagram of the twenty experimental plots according to the species composition on axis 1 (soil texture) and axis 2 (degradation) during 2004/05. Eigen values: axis 1 = 0.6078; axis 2 = 0.2168.

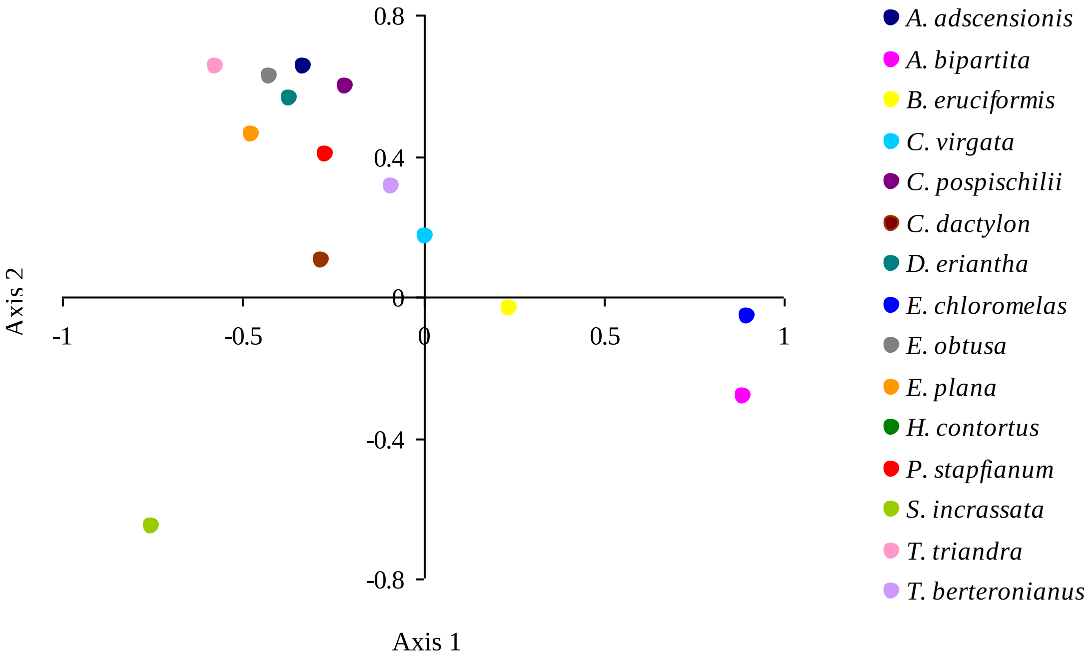

Figure 8.6: PCA quadrant ordination diagram of the grass species based on occurrence on axis 1 (soil texture) and axis 2 (degradation) during 2004/05. Eigen values: axis 1 = 0.6078; axis 2 = 0.2168.

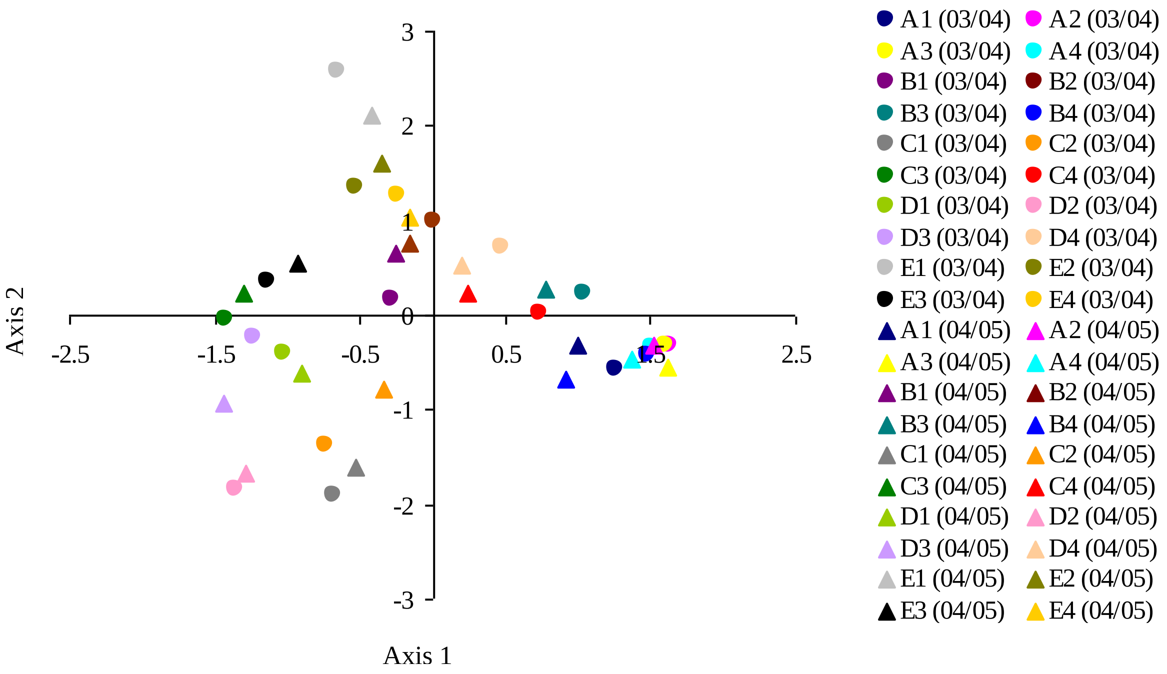

Figure 8.7: PCA quadrant ordination diagram on axis 1 (soil texture) and axis 2 (degradation) showing the changes in terms of species composition from 2003/04 to 2004/05 in the twenty sample plots. Eigen values: axis 1 = 0.6288; axis 2 = 0.2125.

8.3.3 Canonical Correspondence Analysis (CCA) of the vegetation and soil properties

The CCA ordination diagram of the association between the grass species and the soil variables is presented in Figure 8.8. The Eigen values for the first and second axis were 0.3941 and 0.1739, respectively. The first two canonical axes explained 52.56% and 23.19% of the total variance, respectively. Thus, the total variance explained by the first two axes of the joint species/soil biplot was 75.75%. From the inter-set correlations of the soil variables with axes of the CCA, shown in Table 8.1, it can be seen that the first axis was correlated with N, Zn, C and percentage clay, while the second axis was defined by K and Mg. Sand, Na and Ca also had a relatively high correlation with axis 1 (Table 8.1). These trends were also evident in the ordination diagram (Figure 8.8).

Figure 8.8 depicts the species scores and canonical coefficient scores of the environmental variables from the CCA ordination. The variables are represented by arrows pointing in the direction of maximum variation, with their length proportional to the rate of change. Each arrow determines an axis on which the species points can be projected. Generally, these projected points estimate the optima of species distribution for each environmental variable. Three species groupings are evident in Figure 8.9. The first group (mostly quadrants 1-3) is highly associated with clay, Na, Ca, Mg, K, and to a lesser extent P, and includes species such as *B. eruciformis*, *E. chloromelas*, *A. bipartita* and *S. incrassata*. A second group of species was evident in the upper left quadrant (4) of the biplot , and is associated with sand, silt, Zn, N, C, and to a lesser extent electrical resistance (ER), and includes *T. triandra*, *E. plana*, *D. eriantha*, *P. stapfianum*, *E. obtusa*, *A. adscensionis*, *Cymbobogon pospischilii* and *H. contortus* (Figure 8.9). A third general group of species was evident in the upper area of quadrant 3 and 4, and included *Tragus berteronianus* and *Chloris virgata*, which had no association with any of the soil variables (Figure 8.9). This might be because of their sporadic distribution and low occurrence.

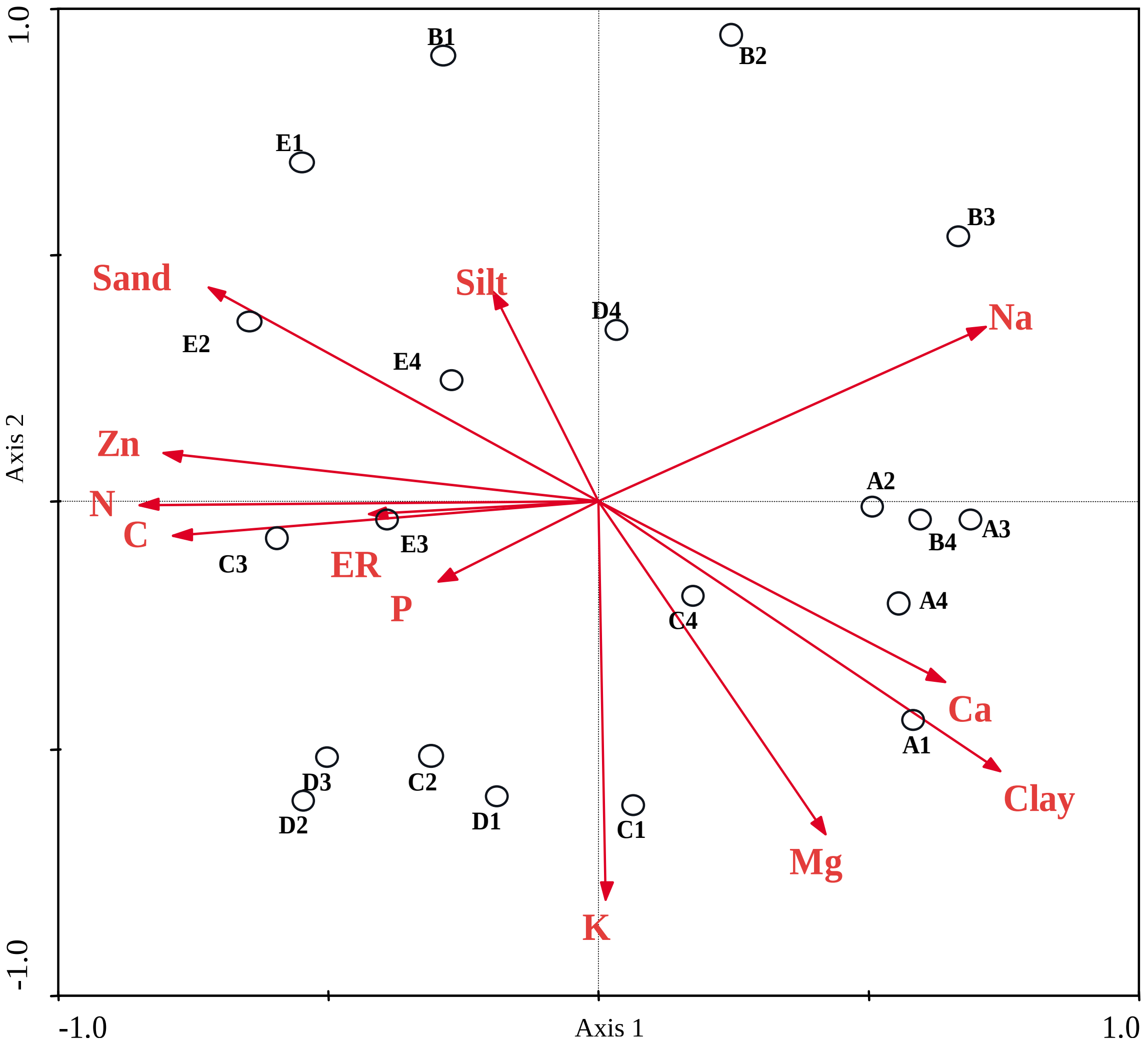

Figure 8.8: CCA ordination diagram of axes 1 (soil texture) and axis 2 (degradation) showing the distribution of the experimental plots in relation to the soil variables. Eigen values: axis 1 = 0.3941 and axis 2 = 0.1739.

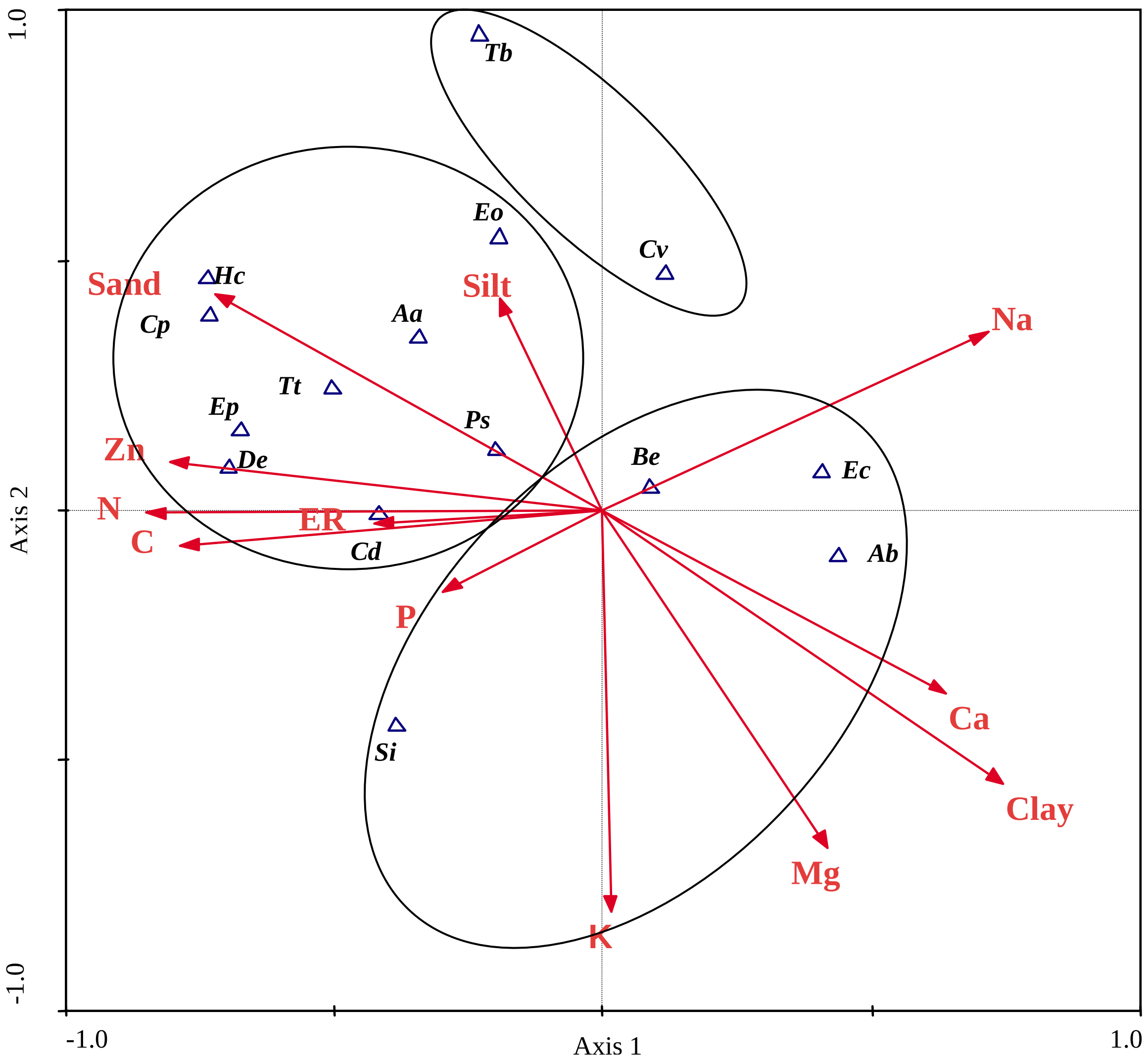

Figure 8.9: CCA ordination diagram of axes 1 (soil texture) and axis 2 (degradation) showing the distribution of the grass species and the soil variables. Eigen values: axis 1 = 0.3941 and axis 2 = 0.1739.

Table 8.1: Canonical coefficients and the inter-set correlations of soil variables with the four axes of CCA.

Soil variables	Canonical coefficients				Inter-set correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Sand	-6.18	-11.23	14.22	-6.91	-0.69	0.40	-0.02	0.30
Silt	-1.86	-3.12	4.26	-2.75	-0.18	0.39	-0.26	-0.48
Clay	-6.08	-11.65	15.89	-8.22	0.71	-0.50	0.11	-0.14
N	-0.27	-0.60	-0.20	-0.59	-0.81	0.00	-0.29	-0.19
C	-0.34	0.17	0.35	-0.12	-0.75	-0.07	-0.11	-0.19
P	-0.26	-0.07	0.64	-0.02	-0.28	-0.15	0.54	0.10
Ca	0.17	-0.12	-0.76	-0.40	0.61	-0.34	-0.14	-0.22
K	-0.20	-0.85	0.08	-0.14	0.02	-0.74	-0.19	-0.27
Mg	0.27	-0.02	-1.01	0.31	0.40	-0.62	0.04	-0.04
Na	0.37	0.07	-0.12	-0.90	0.68	0.33	0.39	-0.03
Zn	0.28	0.48	-0.20	-0.79	-0.77	0.09	-0.13	-0.24
ER	0.28	-0.03	-0.88	-0.30	-0.40	-0.02	-0.12	0.26

ER = Electrical Resistance

8.3.4 Canonical Correspondence Analysis (CCA) of the animal hours spent grazing and vegetation

The CCA ordination diagram of the association between springbok, blesbok and black wildebeest and the experimental plots in terms of animal hours spent grazing (see Chapter 6), and between the grass species composition based on occurrence and animal hours spent grazing during the DS, GIS and AGS is presented in Figures 8.10 - 8.15. The Eigen values for the first and second axes during the DS were 0.1105 and 0.0418 respectively. The first two canonical axes explained 19.61% and 7.42% of the total variance respectively. Thus, the total variance explained by the first two axes of the joint species/animal hour's biplot was 27.03% during the DS. The third axis explained 69.30% of the variation, which indicates that other important environmental factor(s) may have played a role. From the inter-set correlations of the animal hour variables with axes of the CCA shown in Table 8.2, it can be seen that the first axis was correlated to springbok, while the second axis was defined by blesbok. These trends were also evident in the ordination diagrams (Figures 8.10 & 8.11). Springbok had the closest association with plots B1, D4 and E3, and blesbok with plots B2, D4 and E2 (Figure 8.10). Black wildebeest did not show a close association with any plots during this season. Four plant species groupings were evident from Figure 8.11. The first group, situated in the centre of quadrant one, is associated with springbok and blesbok and includes *D. eriantha*, *E. plana*, *T. triandra*, *B. eruciformis*, *P. stapfianum*, *A. adscensionis* and *E. obtusa*. The second and third grouping are in the bottom right and top left corner respectively with no association to any herbivore game species and include species such as *Cympobogon pospischilii*, *Chloris virgata* and *Tragus berteronianus*. The fourth group of species includes *Cynodon dactylon*, *E. chloromelas*, *A. bipartita* and *S. incrassata* and again did not show any association with the game species (Figure 8.11). Black wildebeest had no association with any of the groups (Figure 8.11).

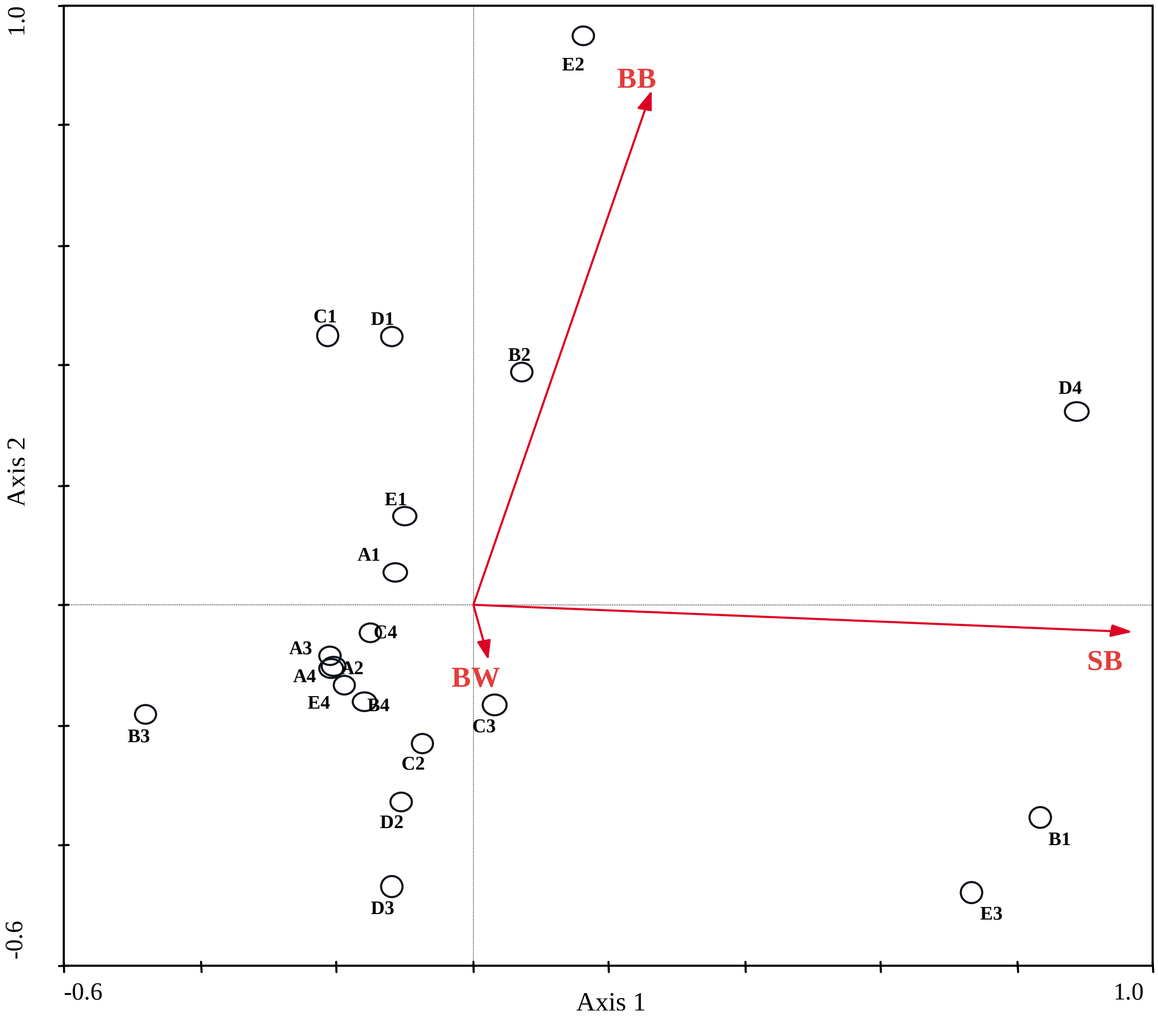

Figure 8.10: CCA ordination diagram of the first two axes showing the distribution of the experimental plots in terms of animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the dormant season (DS). Eigen values: axis 1 = 0.1105 and axis 2 = 0.0418.

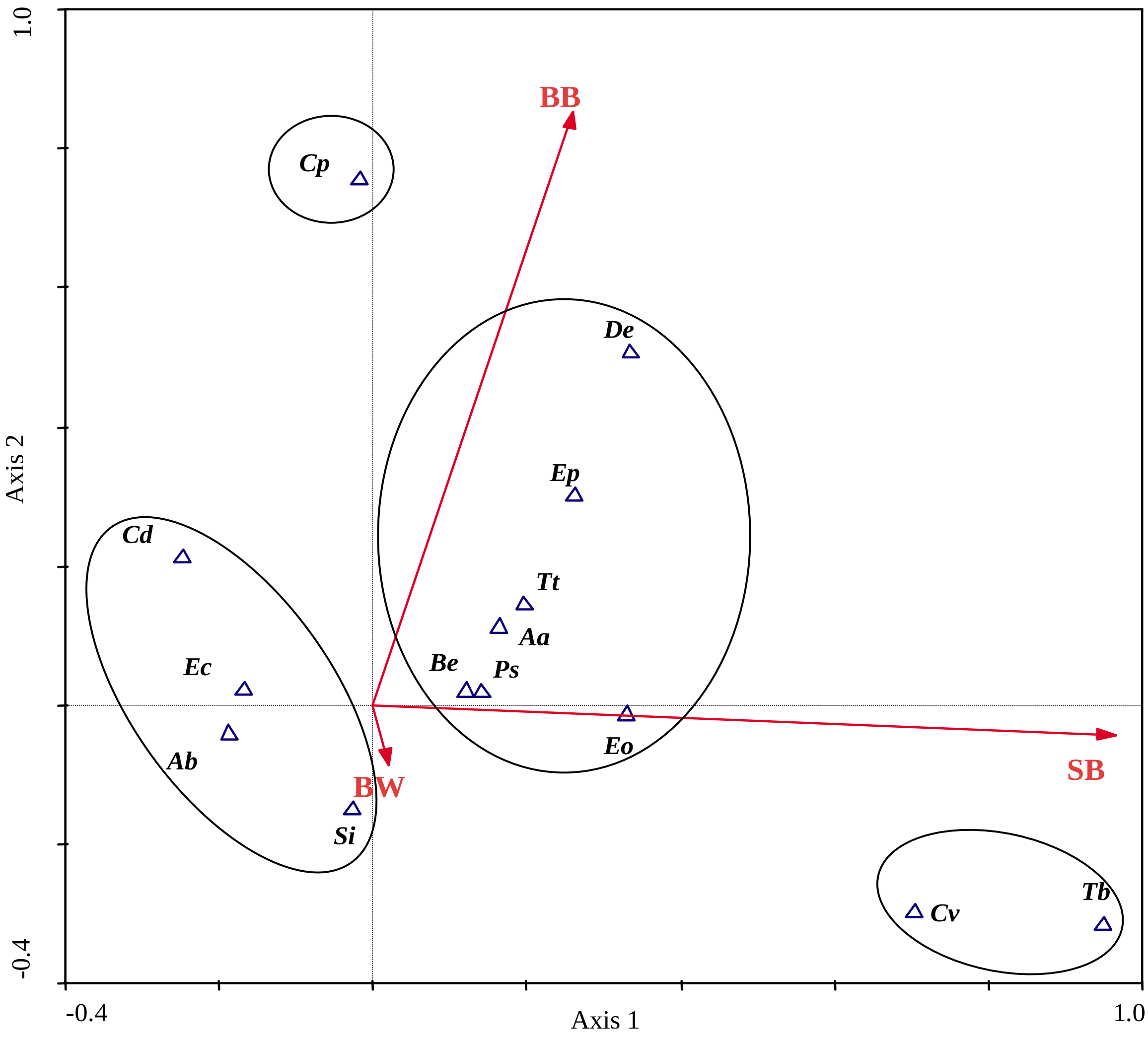

Figure 8.11: CCA ordination diagram of the first two axes showing the distribution of grass species based on occurrence and animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the dormant season (DS). Eigen values: axis 1 = 0.1105 and axis 2 = 0.0418.

Table 8.2: Canonical coefficients and the inter-set correlations of the animal hours spent grazing by springbok, blesbok and black wildebeest with the four axes of CCA during the dormant season (DS).

Species	**Canonical coefficients**				**Inter-set correlations**			
	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Springbok (SB)	1.04	-0.29	-0.05	0.00	0.59	-0.02	0.13	0.00
Blesbok (BB)	0.02	1.12	0.09	0.00	0.16	0.38	0.22	0.00
Black wildebeest (BW)	-0.28	-0.43	0.97	0.00	0.01	-0.04	0.48	0.00

The Eigen values for the first and second axes during the GIS were 0.2805 and 0.1339 respectively. The first two canonical axes explained 40.81% and 19.48% of the total variance respectively. Thus, the total variance explained by the first two axes of the joint species/animal hour's biplot was 60.29% during the GIS. The third axis explained an unpredicted 34.02%. From the inter-set correlations of the animal hour variables with axes of the CCA shown in Table 8.3, it can be seen that the first axis was correlated to black wildebeest, while the second axis was defined by springbok. These trends were also evident in the ordination diagrams (Figures 8.12 & 8.13). Springbok and blesbok were closely associated with plots C3, D3, E2 and E4 (Figure 8.12). Springbok were also closely associated with plot B2. Black wildebeest showed a close association with plot C1, and a lesser association with plots D1&2 and E3 during this season (Figure 8.12). Three plant species groupings were evident from Figure 8.13. The first is associated with springbok, blesbok and black wildebeest and include *D. eriantha*, *E. plana, T. triandra, P. stapfianum*, *A. adscensionis*, *E. obtusa*, *Cymbopogon pospischilii*, *Cynodon dactylon* and *S. incrassata*. The third group is in the top left corner of quadrant 4 with no association to any herbivore game species, and includes *Chloris virgata* and *Tragus berteronianus*. The fourth group of species includes *E. chloromelas, A. bipartita* and *B. eruciformis,* and again did not show any association with the game species (Figure 8.13).

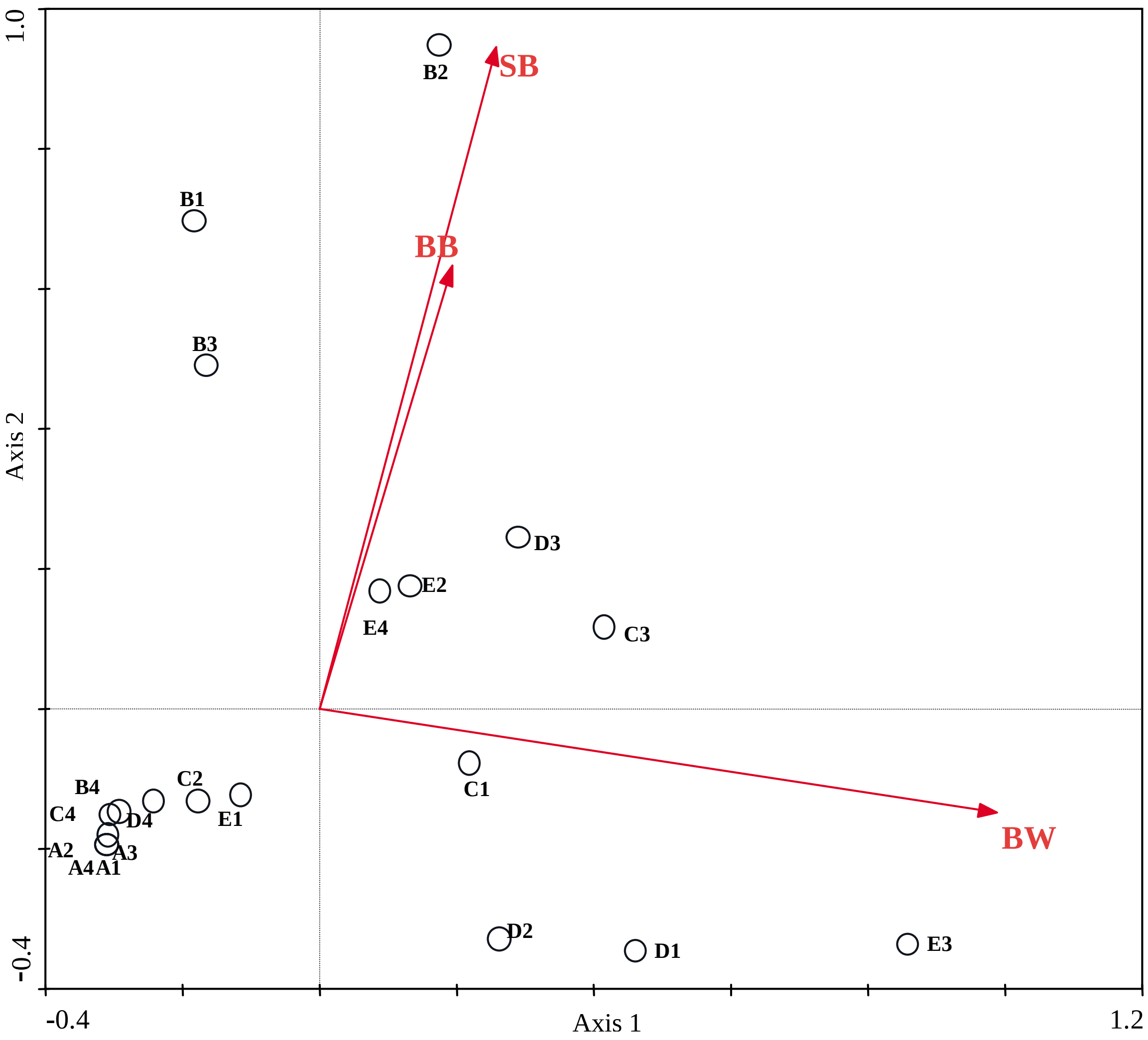

Figure 8.12: CCA ordination diagram of the first two axes showing the distribution of the experimental plots in terms animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the growth initiation season (GIS). Eigen values: axis 1 = 0.2805 and axis 2 = 0.1339.

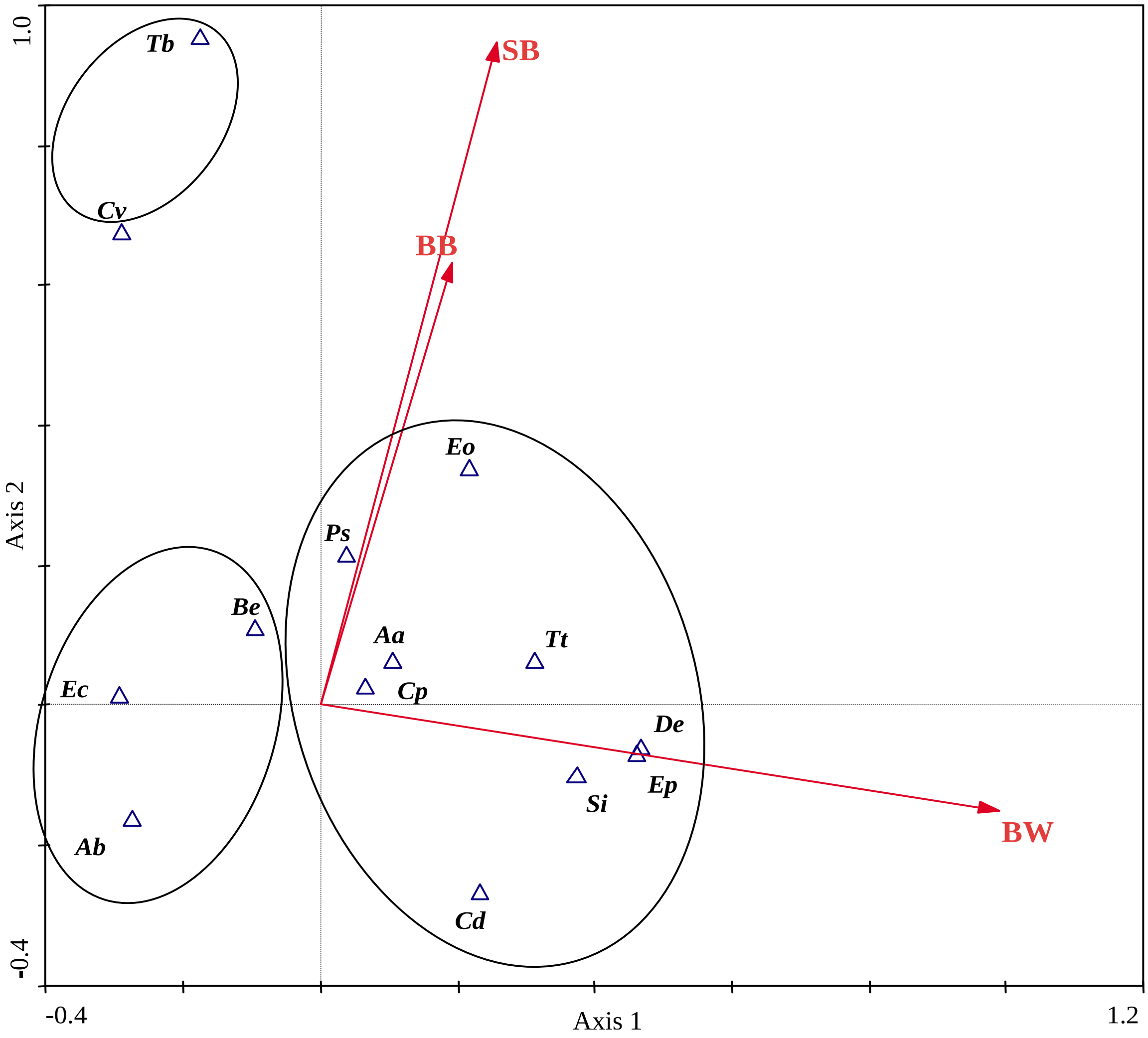

Figure 8.13: CCA ordination diagram of the first two axes showing the distribution of the grass species based on occurrence and animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the growth initiation season (GIS). Eigen values: axis 1 = 0.2805 and axis 2 = 0.1339.

Table 8.3: Canonical coefficients and the inter-set correlations of the animal hours spent grazing by springbok, blesbok and black wildebeest with the four axes of CCA during the growth initiation season (GIS).

Species	**Canonical coefficients**				**Inter-set correlations**			
	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Springbok (SB)	0.17	1.23	-1.08	0.00	0.22	0.68	0.15	0.00
Blesbok (BB)	-0.02	-0.32	1.61	0.00	0.16	0.45	0.58	0.00
Black wildebeest (BW)	0.97	-0.26	-0.03	0.00	0.82	-0.11	-0.01	0.00

The Eigen values for the first and second axes during the AGS were 0.2429 and 0.0728 respectively. The first two canonical axes explained 35.16% and 10.54% of the total variance respectively. Thus, the total variance explained by the first two axes of the joint species/animal hour's biplot was 45.7% during the GIS. The third axis explained 51.43%, which indicates that other environmental factor(s) had an influence on the distribution pattern. From the inter-set correlations of the animal hour variables with axes of the CCA shown in Table 8.4, it can be seen that the first axis was correlated to blesbok while the second axis was defined by springbok and black wildebeest. These trends were also evident in the ordination diagrams (Figures 8.14 & 8.15). Blesbok were closely associated with plot B1 (Figure 8.14). Black wildebeest showed a close association with plots C1, D1, E2&4 during this season (Figure 8.14). Springbok had no association with any of the plots. Four plant species groupings were evident from Figure 8.15. The first is associated with blesbok and includes *Tragus berteronianus* and *Chloris virgata*. The second group is on the positive side near the centre of the diagram and consists of *E. obtusa*, *P. stapfianum* and *B. eruciformis* (Figure 8.15). The third grouping is near the centre of the quadrant and contains species such as *D. eriantha*, *E. plana*, *T. triandra*, *A. adscensionis*, *Cymbopogon pospischilii*, *Cynodon dactylon* and *S. incrassata*. The fourth grouping is situated near the centre of the third quadrant and had no association with any of the herbivore game species. This group included *E. chloromelas* and *A. bipartita* (Figure 8.15).

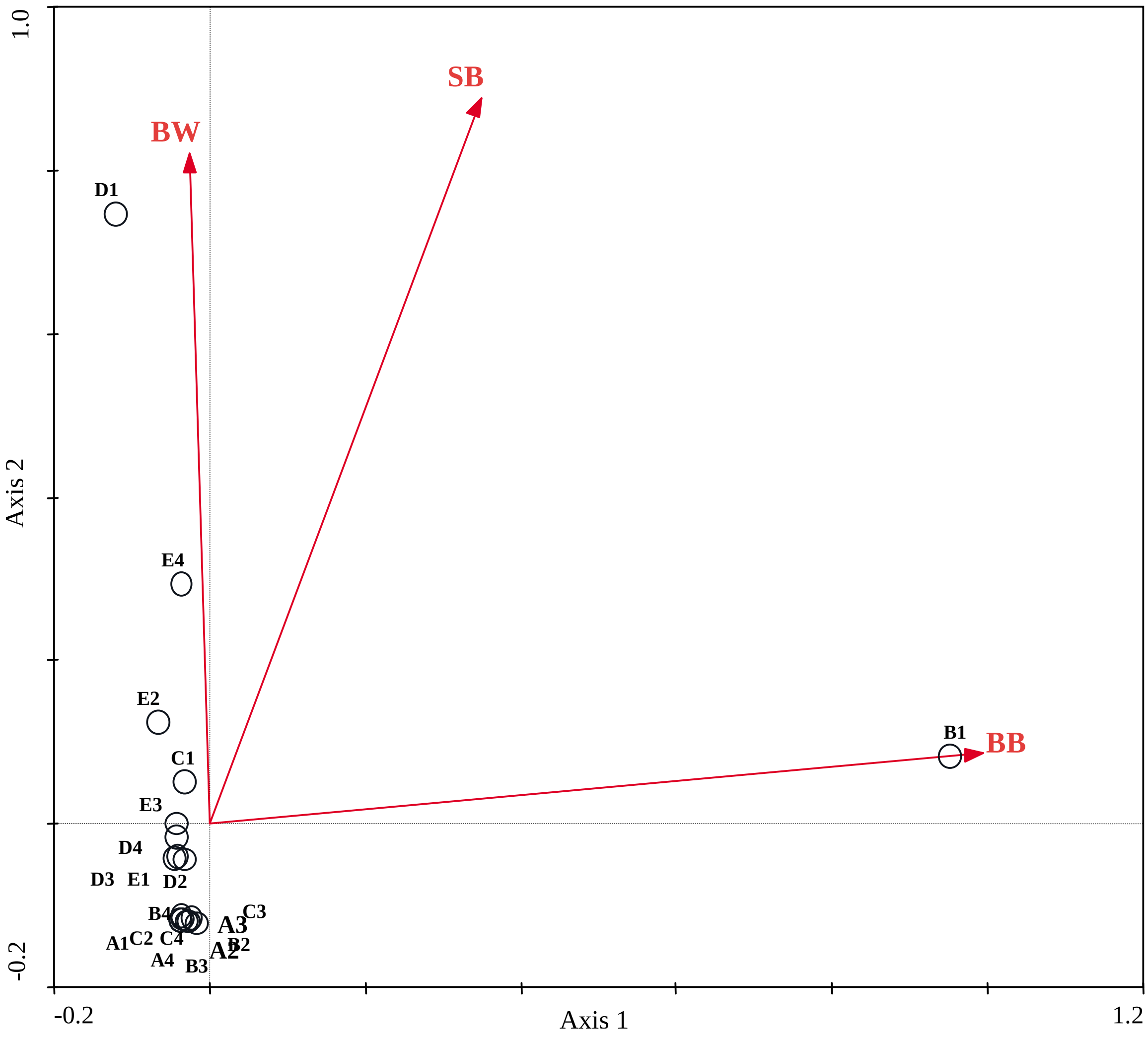

Figure 8.14: CCA ordination diagram of the first two axes showing the distribution of the experimental plots in terms of animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the active growing season (AGS). Eigen values: axis 1 = 0.2429 and axis 2 = 0.0728.

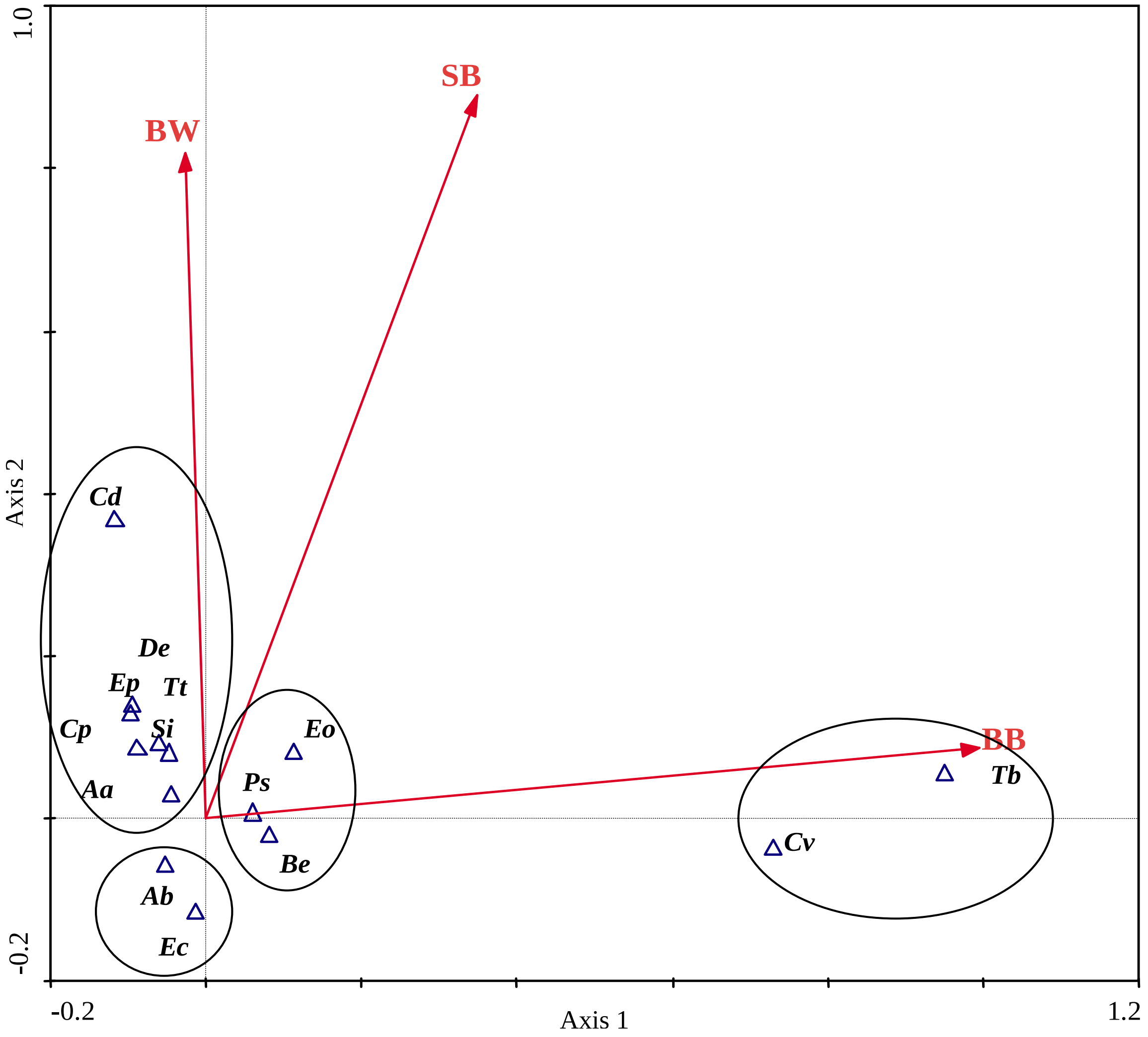

Figure 8.15: CCA ordination diagram of the first two axes showing the distribution of the grass species based on occurrence and animal hours spent grazing by springbok (SB), blesbok (BB) and black wildebeest (BW) during the active growing season (AGS). Eigen values: axis 1 = 0.2429 and axis 2 = 0.0728.

Table 8.4: Canonical coefficients and the inter-set correlations of the animal hours spent grazing by springbok, blesbok and black wildebeest with the four axes of CCA during the active growing season (AGS).

Species	**Canonical coefficients**				**Inter-set correlations**			
	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Springbok (SB)	-0.13	0.79	-1.14	0.00	0.33	0.40	-0.14	0.00
Blesbok (BB)	1.05	-0.27	0.43	0.00	0.95	0.04	-0.02	0.00
Black wildebeest (BW)	0.03	0.39	1.19	0.00	-0.03	0.37	0.28	0.00

8.4 DISCUSSION

Multiple environmental factors including fire (McNaughton 1983), nutrients (Anderson *et al*. 2004), rainfall (McNaughton 1985), soil factors such as texture and type (Anderson & Talbot 1965; Belsky 1986; Peel & Smith 1994; Burke *et al*. 1999), and grazing herbivores (McNaughton 1983, 1985; Burke *et al*. 1999) influence plant community patterns and coexistence. In the present study it appears as if soil texture and degradation, due to the grazing history and human activity at the study site, are the most important measured environmental variables causing floristic differences. These results concur to some extent with the findings by Bosch & Janse van Rensburg (1987), Bosch *et al*. (1987), and Janse van Rensburg & Bosch (1990) in the semi-arid climatic grasslands of the Free State, where soil depth and clay content of the A-horizon were identified as having an important influence on the distribution of sites in ordination space. McNaughton (1983) found that in the Serengeti annual grazing and soil texture showed the greatest correlation with the distribution of the plant community types.

The grouping of experimental plots (based on species composition) and grass species (based on occurrence) on the PCA axes during 2003/04 and 2004/05 (Figures 8.3 - 8.6) corresponded to the soil texture, which was confirmed by the correlation produced by the CCA (Figures 8.8 & 8.9). Seventy percent of the variation was explained by soil texture (Eigen value 0.6826). Little change occurred from 2003/04 to 2004/05 (Figure 8.7). The existing soil texture gradient which varied from heavy clay soils in the northern side to sandier clay soils in the southern side resulted in a gradient of available soil water, since soil water content increased as the soil becomes finer in texture (Salter & Williams 1965). The soil water content, therefore, was probably one of the most important determinants that resulted in vegetation variations from north to south in the demarcated area. The nutrient content consisting of Ca, Na, Mg and K, was also higher in finer textured soils. Soil texture is an important environmental variable (Austin 1980; Austin & Smith 1989) that influences plants through modifying other factors such as its effects on microbial dynamics (Burke *et al*. 1995) and soil water (water holding capacity, moisture availability etc.) and nutrient availability (Fernandes-Illescas *et al*. 2001; Anderson *et al*. 2006). For many herbaceous plants, soil heterogeneity provides a physical template on which plant species have different germination success, growth capabilities, reproductive capacity and competitive abilities (Miller & Donahue 1995). The ability of a soil to provide the conditions required for plant growth (soil fertility), is a result of the physical, chemical and biological processes that act together to provide nutrients, water, aeration and stability to the plant, as well as freedom from any substances that may inhibit growth (Stockdale *et al*. 2002).

Herbivore game species are not evenly distributed while foraging, but rather favour certain habitat types or patches within a specific habitat over others (Jarman 1974; Pienaar 1974; Hirst 1975). The type of habitat patches preferred by springbok, blesbok and black wildebeest appear to be based primarily on contrasts in physiognomy. They generally showed no association with experimental plots with heavy clay soils (Figures 8.10, 8.12, 8.14), and the preferred grazing plots were commonly associated with sand and silt (Figure 8.8). This suggests that soil type indirectly affects the selection of habitat patches. It is assumed that the soil water content and exchangeable cation contents (Ca, Na, Mg and K) of the experimental plots that were utilised more (B1&2, C3, D4, E1-4, and to a lesser extent C2 and D2&3) was lower than the less utilised plots due to a higher sand and silt content (see Chapter 4) (Du Preez personal communication[5]). However, the stronger adhesion in clay soils and higher runoff may have had an influence on the soil water availability. The differences in soil water content were reflected by the grass species present in the plots at the two extremes of soil texture gradient. *Setaria incrassata*, *B. eruciformis, E. chloromelas* and *A. bipartita* are typical species occurring in heavy clay soils with a high water content (Van Oudsthoorn 1999; Du Preez personal communication*), and had a high occurrence in plots (A1-4, B3&4, C1&4 and D1) with an elevated clay content (see Chapter 5). In the CCA these species were also closely related to clay, Na, Ca, Mg and K contents (Figure 8.9). The high soil water availability in clay soils promotes carbohydrate photosynthesis, and grasses growing in such regions

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tend to have nutrient concentrations reduced by a high cell wall fraction (Heitkönig & Owen-Smith 1998).

Experimental plots with a higher sand and silt content, hence lower soil water content, were mostly associated with *T. triandra*, *E. plana*, *D. eriantha*, *P. stapfianum*, *C. pospischilii*, *Cynodon dactylon*, *E. obtusa*, *H. contortus* and *A. adscensionis*, and strongly related to sand, silt, Zn, N and C content on the CCA diagram (Figure 8.9). Grasses growing in these plots may therefore contain nutrients that are less diluted by structural carbohydrates. According to Moretto & Distel (2002), N mineralisation is lower under unpalatable grasses than under palatable grasses. The shift in species composition, caused by a high degree of selection of palatable grasses and rejection of unpalatable grasses, may reduce soil N availability and slow down the rate of ecosystem nutrient cycling. This may explain the association of N with the group of grasses that contain more palatable species (Figure 8.9).

The occupation of springbok, blesbok and black wildebeest showed close associations, in terms of animal hours spent grazing, with most of the grass species that have a high occurrence on soils with a higher sand and silt content. Seasonal variations occurred in the association between animal hours spent grazing and species composition (based on occurrence grass species). The animal hours spent grazing by springbok and blesbok were closely correlated to *D. eriantha*, *E. plana*, *T. triandra*, *B. eruciformis*, *P. stapfianum*, *A. adscensionis* and *E. obtusa* during the DS (Figure 8.11). During the GIS springbok, blesbok and black wildebeest, based on animal hours spent grazing, showed a close association with these grass species as well as *Cymbopogon pospischilii*, *S. incrassata* and *Cynodon dactylon* (Figure 8.13). During the AGS, animal hours spent grazing by blesbok was associated with *Tragus berteronianus*, *Chloris virgata*, *E. obtusa*, *P. stapfianum* and *B. eruciformis* (Figure 8.15). Animal hours spent grazing by springbok was correlated to species such as *E. obtusa*, *P. stapfianum* and *B. eruciformis*, and black wildebeest was correlated to *D. eriantha*, *E. plana*, *T. triandra*, *A. adscensionis*, *Cymbopogon pospischilii*, *Cynodon dactylon* and *S. incrassata* (Figure

8.15). Therefore, it appears that the diversity of grass species utilised by the herbivore game species increased during the dry season. The association with the less- and non-favoured grass species may be accidental because the favoured grass species occurred together within the same grazing patch.

Heavy grazing can detrimentally affect soil and water functions in grassland (McIntyre & Tongway 2005). McIntyre & Tongway (2005) found that infiltration and nutrient cycling index declined progressively across patch structures, consistent with increasing grazing pressure. In the Serengeti defoliation has been linked to the improved water status of the grasses (Toft *et al*. 1987). Grazing could therefore also have influenced the water content. Seagle *et al*. (1992) found that N cycling processes are affected differentially by grazing in the short grass and tall grass areas. Net N mineralised by the microbial biomass in the short grass simulations declined from the ungrazed condition at low grazing intensities and proceeded to increase from moderate to high grazing intensities. This may explain why *T. triandra*, *E. plana*, *D. eriantha*, *P. stapfianum*, *C. pospischilii*, *Cynodon dactylon*, *E. obtusa*, *H. contortus* and *A. adscensionis* had the highest association with N, since five of them are favoured species (see Chapter 7). Defoliation has been demonstrated to stimulate grass nutrient uptake and alter nutrient allocation (McNaughton & Chapin 1985), resulting in high forage quality (Ruess & McNaughton 1984) which may further enhance its attractiveness to grazing animals (Day & Detling 1990). *Tragus berteronianus* - and to a lesser extent *Chloris virgata* - were strongly associated with areas that are apparently subject to a high occurrence of trampling.

Soil quality has been typically associated with soil organic matter or its associated indicator elements, C and N (Gregorich *et al*. 1993). Soil organic matter is a source of plant nutrients in soil and is important in aiding infiltration of air and water, promoting water retention and reducing erosion (Gregorich *et al*. 1993). In studies done by Jones (1973) in the West African savanna, and Foster (1981) in Uganda, it was found that clay content and moisture are important factors that determine the amounts of organic matter and thus soil fertility. According to Snyman (1998), organic matter content plays an important role as a key element in soil fertility, as shown by other semi-arid ecosystems. Jones (1973) found that organic matter content was lower in soils with a sandy nature. Ruess & McNaughton (1988) concluded that Serengeti soils with a higher clay content had a higher fertility and sandier soils had a lower nutrient content. By looking at the indicator elements of organic matter, the opposite was found in this study, since sand and silt were closely associated with N and C (Figure 8.9). Habitat patches on soils with a higher sand and silt content may have facilitated the intake of nutrient-rich plant material by the herbivore game species. The herbivore game species thus selected patches of particular soil types with elevated levels of mostly N, C and Zn within the grassland area. This working theory may help explain seasonal sward selection by springbok, blesbok and black wildebeest. Bell (1984) offered a working hypothesis explaining regional differences in plant nutrient levels linked to soil moisture and nutrient status. These patches generally also had a higher species diversity (see Chapter 5).

The higher N status of the soil in those plots preferred by the herbivore game species may also be due to the amount of time the herbivore game species spent in the plots, since animals generally spent considerably more time in selected areas than elsewhere within fenced areas. Consequently, there is a redistribution of nutrients within enclosures through the uneven distribution of faeces and urine. The overall effect is for animals to collect nutrients from a large area and concentrate them on relatively small areas. Norman & Green (1958) measured 11% higher plant crude protein content and a 57% higher dry matter (DM) production near dung pads than away from them. In the vicinity of urine patches, plants had 24% higher crude protein content and 5% higher DM production than further away from the patches. Total soil N levels measured close to water points in Botswana were three times higher than further away, due to the much greater enrichment of mineral nutrients (Tolsma *et al*. 1987). However, high grazing concentrations of ungulates in the Serengeti Park in Tanzania did not result in substantial N losses. This was apparently due to rapid uptake of N by plants and soil microbes (Ruess & McNaughton 1988). Such a high concentration of soil N normally has a major impact on the species composition of veld communities (Norman & Green 1958).

Grazing by herbivores prior to and during the study also contributed to the differences in the botanical composition, but according to the PCA, had a lesser effect than the soil properties. Heavily grazed plant species are placed at a disadvantage when competing with associated species grazed less severely. The grazing of herbivore game species therefore benefits certain grasses and eliminates others. Species that are able to rapidly replace photosynthetic surfaces gain a competitive advantage over associated species that grow more slowly following defoliation. The reduced photosynthetic capacity of the plant will invariably affect vigour and in particular the growth rates of the roots and lateral daughter tillers, both of which are much more sensitive to a deficiency of energy-rich substrates than is the main stem (Wolfson 1999).

Species composition is altered when a particular intensity, frequency and/or season of grazing shifts the competitive advantage from one group of plant species to another. This may currently be happening in the study area. Plots dominated by *A. bipartita* and *E. chloromelas* could previously have had a high occurrence of more palatable species, such as *T. triandra*, but due to repeated heavy defoliation and no resting periods it was replaced by the former two less palatable species. It appears as if this pattern is continuing, since there was an increase in Increaser grass species (see Chapter 5). Lütge *et al*. (1996) found that *T. triandra* tufts in already established heavily grazed patches in KwaZulu-Natal were shown to have significantly lower re-growth potential at the beginning of the growing season than tufts situated in non-grazed patches.

Grazing-induced modifications in species composition have been documented in numerous grasslands throughout the world (Noy-Meir *et al*. 1989; O’Connor 2005). Several studies in homogeneous grasslands have shown that defoliation by grazing/browsing and fire, which will have an influence on the dynamics of any plant community, are of primary importance in determining the condition of veld in an area (Foran 1976; Bosch & Janse van Rensburg 1987; Hardy & Hurt 1989; Janse van Rensburg & Bosch 1990; Van Rooyen *et al*. 2000). Defoliation by herbivores, a direct biotic process, affects the growth (Ferraro & Oesterheld 2002), reproduction (Anderson

& Frank 2003) and competitive abilities (Berendse 1985; Van der Wal *et al*. 2000) of herbaceous species. According to Bosch & Janse van Rensburg (1987), Janse van Rensburg & Bosch (1990) and Morris *et al*. (1992) these impacts can be controlled.

Some grass species respond differently to the same grazing impact because of differences in the soil (Bosch & Janse van Rensburg 1987; Janse van Rensburg & Bosch 1990) and time of the year. As an example of this, *T. triandra* growing in the semi-arid savanna of the Eastern Cape seems sensitive to intense and frequent defoliation during the growing season, particularly during spring. In contrast, *Sporobolus fimbriatus* seems well adapted to severe defoliation during the growing season, when it is less adversely affected by frequent defoliation than *T. triandra* (Danckwerts 1984). These results indicate that even though the two species grow side by side, they prefer very different defoliation regimes.

The effects of season and stocking rate on the herbaceous layer are additive, and it can be expected that severe grazing during an unproductive rainy season will damage plants more than during a productive rainy season, initiating fundamental transformation of the grass sward (O'Connor 1995). The growth point of grasses located at the base of the plant contains the greatest concentration of nutrients is more exposed during the GIS due to the lack of leaves. Repeated defoliation during the same grazing cycle in the growing season depletes the reserves of grasses (Kirkman & Carvalho 2003), their vigour (Oosthuizen & Snyman 2001), and thus their ability to recover from defoliation (Wolfson & Tainton 1999). Repeatable defoliation during the GIS and AGS, will therefore severely affect plant growth and grass production. In contrast, repeated defoliation of grasses during the DS is less damaging, as their photosynthetic activity has slowed down due to a lack of soil moisture and cool night-time temperatures (Barnes 1989). The impact - based on occupation of the experimental plots - that the herbivore game species had on the vegetation was the highest during the DS and GIS and the lowest during the AGS, whereafter it increased again during the RSS (see Chapter 6). Most damage was caused by black wildebeest and least by springbok due to their differences in body size, metabolic requirements and grazing habit. The abundance of Increaser IIc and bare patches in plot B1 may be the result of trampling by the herbivore game species, since this was the plot where most animal hours were spent during the study period (see Chapter 6). It is clear that the grazing herbivore game species exerted the highest impact on the plots in the southern-side and it is expected that they will cause drastic changes to the vegetation if no management interferences are applied in the near future.

In addition to defoliating plants, animals physically damage plants by cutting, bruising, and breaking them. Whole plants may be dislodged and uprooted, particularly among plants of which the leaves have a high tensile strength, such as *E. plana* (Owen-Smith 1999). Uprooting by those concentrate feeders that feed particularly close to the ground, may be very severe.

8.5 CONCLUSION

The following conclusions can be drawn from the results of this study:

(i) Soil texture and over utilisation were the most important determinants that caused spatial variation in the botanical composition of the grassland area.

(ii) Grass species such as *A. bipartita*, *E. chloromelas*, *S. incrassata* and *B. eruciformis* with a low grazing value, mainly occurred on heavy clay soils and were closely associated with soil Na, Ca, Mg and K.

(iii) Grass species such as *T. triandra*, *E. obtusa*, *P. stapfianum*, *E. plana* and *D. eriantha* with high grazing value mostly occurred on sandier soils and were closely associated with N, C and Zn.

(iv) Grass species generally associated with degraded or disturbed areas, i.e. *A. bipartita*, *E. chloromelas*, *B. eruciformis* and *T. berteronianus*, were more abundant on heavy clay soils.

(v) Time (animal hours) spent grazing by springbok, blesbok and black wildebeest were closely associated with grazing patches that occurred on soil with a higher sand and silt content and a relatively high soil quality in terms of N and C.

(vi) The associations between the time (animal hours) spent grazing by the herbivore game species and the grass species (based on occurrence) indicated that they mostly grazed in areas where *T. triandra*, *E. obtusa*, *E. plana*, *P. stapfianum*, *D. eriantha*, *C. pospischilii*, *Cynodon dactylon*, *H. contortus* and *A. adscensionis* were abundant. The association of springbok, blesbok and black wildebeest with Decreaser as well as Increaser grass species can be attributed to patch heterogeneity.

(vii) Seasonal variation occurred in the associations between time (animal hours) spent grazing and grass species (based on occurrence). During the rainy season the associations were weaker due to the increase in availability of more suitable forage outside the experimental area.

CHAPTER 9

HABITAT USE BY GRAZING HERBIVORE GAME SPECIES IN RELATION TO CHANGES IN THE SWARD STRUCTURE

9.1 INTRODUCTION

Trophic interactions among large herbivores are mediated largely through their impacts on vegetation (Vesey-Fitzgerald 1960; Bell 1970; Owen-Smith 1985; Murray & Illius 2000). Competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species (Illius & Gordon 1987; Murray & Illius 2000; Prins & Olff 1998; Fritz *et al*. 2002). Alternatively, by reducing grass biomass one species may benefit another by facilitating access to forage of a suitable height or quality (Vesey-Fitzgerald 1960; Bell 1970, 1971; McNaughton 1976).

The impact of herbivore game species on plant communities and the habitat can be detrimental (competition) or beneficial (facilitation) to other species. Collinson & Goodman (1982) made a functional classification of herbivores based mainly on the impact of game species on the vegetation and habitat. These authors identified four main categories, namely Type I, II, III and IV species. Type I species are herbivores such as elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*) and zebra (*Equus burchelli*). These animals are relatively unselective feeders which remove large quantities of vegetation and have powerful effects on plant dynamics and the physical environment, hence on the biodiversity of ecosystems. Their large body size leads to large food requirements and tolerance of low quality food (Bell 1971; Jarman 1974; Demment & Van Soest 1985; Illius & Gordon 1987; Illius & Gordon 1992). Owen-Smith (1988) used the classification of megaherbivores, which mainly include species weighing more than 1 000 kg as adults. According to him these species are of particular interest because of the drastic changes they cause to the environment.

The changes caused by the Type I species have a negative impact on the more sensitive species, which are Type II herbivore species. As a result, this negative impact will cause a decrease in abundance of the Type II species. These include such species as roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), tsessebe (*Damaliscus lunatus*), waterbuck (*Kobus ellipsiprymnus*), oribi (*Ourebia ourebi*) and common reedbuck (*Pelea capreolus*). According to Grossman *et al*. (1999), it is not inconceivable that changes in vegetation caused by Type I species (particularly bush encroachment) have contributed to a decline in numbers of these species, all of which require a relatively open woodland/mesic grassland mosaic.

Species such as springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*), black wildebeest (*Connochaetes gnou*), blue wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus melampus*) and red hartebeest (*Alcelaphus buselaphus*) are termed Type III species and increase as a result of the impact of Type I species. When grazing, the Type I species remove large quantities of vegetation, regardless of the quality. There is, however, still some food for the more selective grazers to feed on. Type I species may therefore facilitate suitable habitat to some grazers by creating favourable feeding patches. Type III species further modify the vegetation, and perpetuate this new state by their selective feeding habits. These species consequently have the ability to exploit the new vegetation state created by the impact of Type I species.

A further suite of herbivores, the Type IV group, are influenced by and may increase due to changes brought about by Type I and III species, but have little further impact on the vegetation. These species will increase and exploit an increase in woody density and biomass without markedly influencing this vegetation. Examples are kudu (*Tragelaphus stepsiceros*), bushbuck (*Tragelaphus scriptus*) and duiker (*Cephalophus natalensis* and *Philantomba monticola*). According to Cumming (1982), wild herbivore game species the size of buffalo and smaller do not appear to be responsible for large scale habitat changes, except in situations where predators were eliminated, movements confined to small areas by fencing, or locally in the vicinity of water points.

The objective of this study was to determine whether the simulated influence of Type I herbivores, which are capable of causing drastic changes to the vegetation on the sward structure, will affect the small-scale habitat preferences of other herbivore game species, notably Type III species, in the experimental area. The Type III species in the study area include springbok, blesbok and black wildebeest.

9.2 PROCEDURE

9.2.1 Treatments

For this study four of the twenty experimental plots (see Chapter 3) that were under utilised were selected. Plots A2&4 were selected because they were dominated by the relatively unpalatable *Aristida bipartita* and *Eragrostis chloromelas* and were almost completely avoided by the animals (see Chapter 5 & 6). Plots C3 and E4 were selected because they had a high occurrence of more palatable grass species such as *Themeda triandra* (see Chapter 5), yet they were also under utilised due to the tall and mature nature of the grass sward.

The simulated effect of Type I species on the grass structure was achieved by mowing two of the selected plots (A2 and C3) at a height of 5 cm and the other two plots (A4 and E4) at a height of 15 cm with the aid of a lawnmower (Figure 9.1). The plots were grouped in such a way that there was a plot with palatable and unpalatable grass species for each of the mowing treatments. The mowing height of 5 cm was chosen because blesbok (Du Plessis 1972; Grobler 1983; Novellie 1989), springbok (Grobler 1983; Novellie 1989; Furstenburg 2002b) and black wildebeest (Novellie 1989; Furstenburg 2002a) are short grass grazers and select areas with short grass. The height of 15 cm represents an intermediate height that may not be preferred by the short grass grazers yet, but which may facilitate increased utilisation. The mowed grass was removed from the plots (Figure 9.2). Illustrations of the relevant plots before and after the grass mowing treatments are presented in Figure 9.3.

Figure 9.1: (**a**) The lawnmower used for mowing the grass in the selected plots; (**b**) mowing grass of experimental plots A2 and C3 at a height of 5 cm.

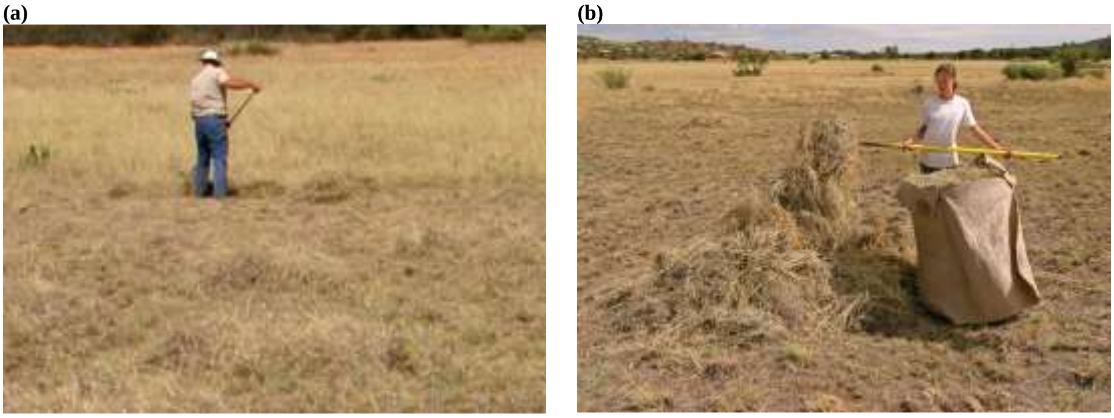

Figure 9.2: (**a**) Raking and (**b**) removal of mowed grass from the plots where mowing was carried out.

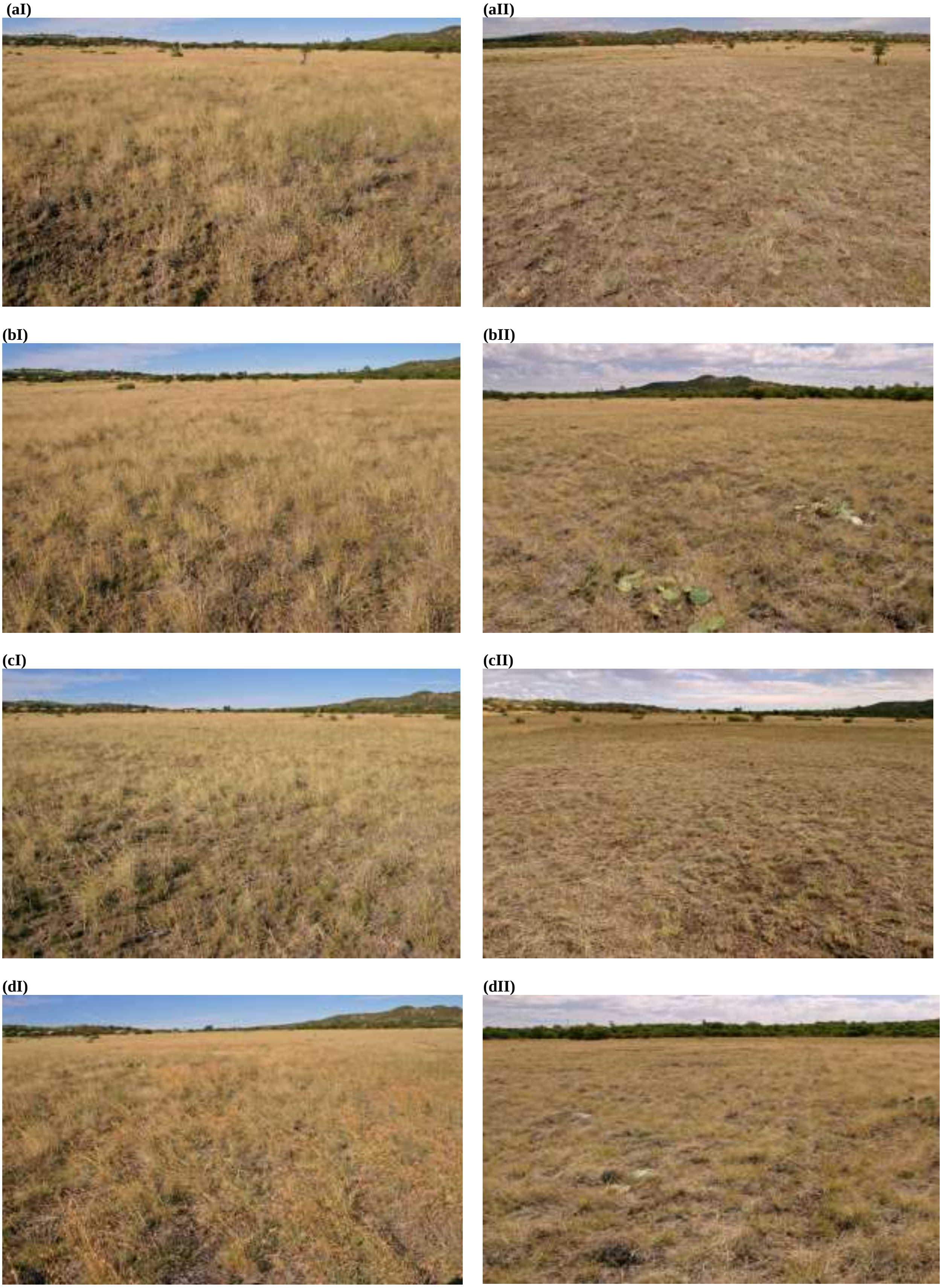

Figure 9.3: An illustration of experimental plots A2 (**a**), A4 (**b**), C3 (**c**) and E4 (**d**) before (**I**) and after (**II**) the mowing treatments.

9.2.2 Animal observations

To determine whether the simulated grazing effects of Type I herbivores influenced Type III herbivores, it was necessary to assess the temporal variation in plot occupation before and after the mowing treatments were executed. This was done by doing observations during three consecutive seasons (June 2004 – February 2005) namely the dormant season (DS), the growing initiation season (GIS) and the active growing season (AGS) prior to the mowing, which was carried out at the beginning of March 2005, followed by similar observations in the reserve storing season (RSS) (March 2005 – May 2005). A detailed description of the four seasons is given in Chapter 6.

Observations as described in Chapter 6 were done from an observation position some distance from the experimental plots. The plot selection, group size, duration spent by each animal in a plot, and activity (grazing, lying down or standing) of each individual were noted in order to assess the spatial and temporal utilisation of the various experimental plots by the herbivore game species.

9.2.3 Data analysis

Animal hours, which is the sum of the time each herbivore game species spent on an activity (grazing, lying down and standing) multiplied by the number of animals executing the same activity, were calculated for each experimental plot before (during the DS, GIS and AGS) and after (during the RSS) the mowing treatments. Plot(s) with a higher number of animal hours were considered as preferred plot(s). The four plots that were mowed are presented separately as A2, A4, C3 and E4, and the remaining unmowed plots are grouped as "other". The animal hours each species spent within a plot was calculated by using the formula described in Chapter 6, section 6.2.3.

9.3 RESULTS

The average amount of time each herbivore game species spent in the four treatment and other plots combined is presented in Figure 9.4. It can be seen from Figure 9.4 that springbok showed a stronger preference for the other unmowed plots after the mowing treatments and avoided the mowed plots. Most of the time was spent grazing within these plots (Figure 9.5). Plots A2&4 were also avoided before mowing treatments were carried out. Prior to the treatments time was mostly spent grazing and lying down in plots C3 and E4 (Figure 9.5).

There was an evident increase in the time blesbok spent in plot C3 after being mowed at a height of 5 cm (Figure 9.4). The animal hours spent within this plot was mostly spent lying down (Figure 9.6). The time spent in plot A2 which was also mowed at a height of 5 cm, was negligible (Figures 9.4 & 9.6). Blesbok spent slightly more time in plot E4 which had a mowed height of 15 cm, in contrast to plot A4 which was mowed at the same height but was completely avoided (Figures 9.4 & 9.6). There was a slight increase in their lying activity in plots E4 after the mowing (Figure 9.6).

The time black wildebeest spent within the experimental area as a whole declined after the mowing treatments (Figures 9.4 & 9.7). Plots A2&4 were avoided prior to and following the mowing treatments (Figures 9.4 & 9.7). More animal hours, mostly spent grazing, was spent in plot E4 before the treatments. After the treatments no time was spent within this plot (Figures 9.4 & 9.7). Time spent in plot C3 also decreased following the mowing treatments (Figures 9.4 & 9.7).

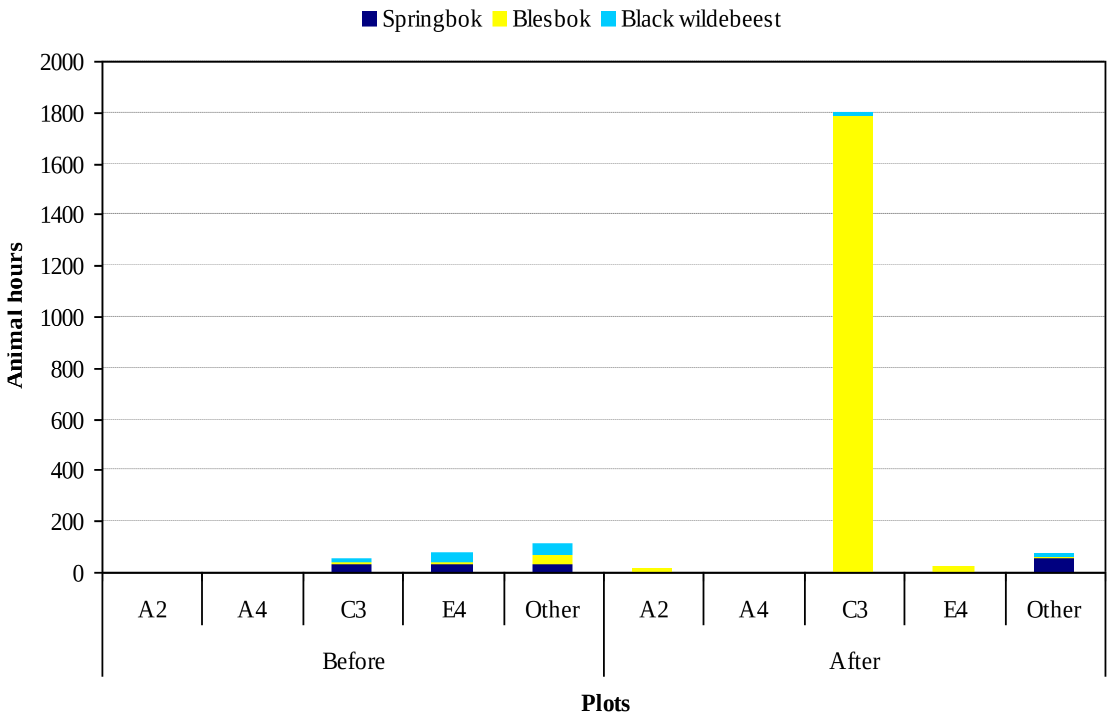

Figure 9.4: Average amount of time (animal hours) springbok, blesbok and black wildebeest spent in the treatment and other experimental plots before and after the mowing treatments.

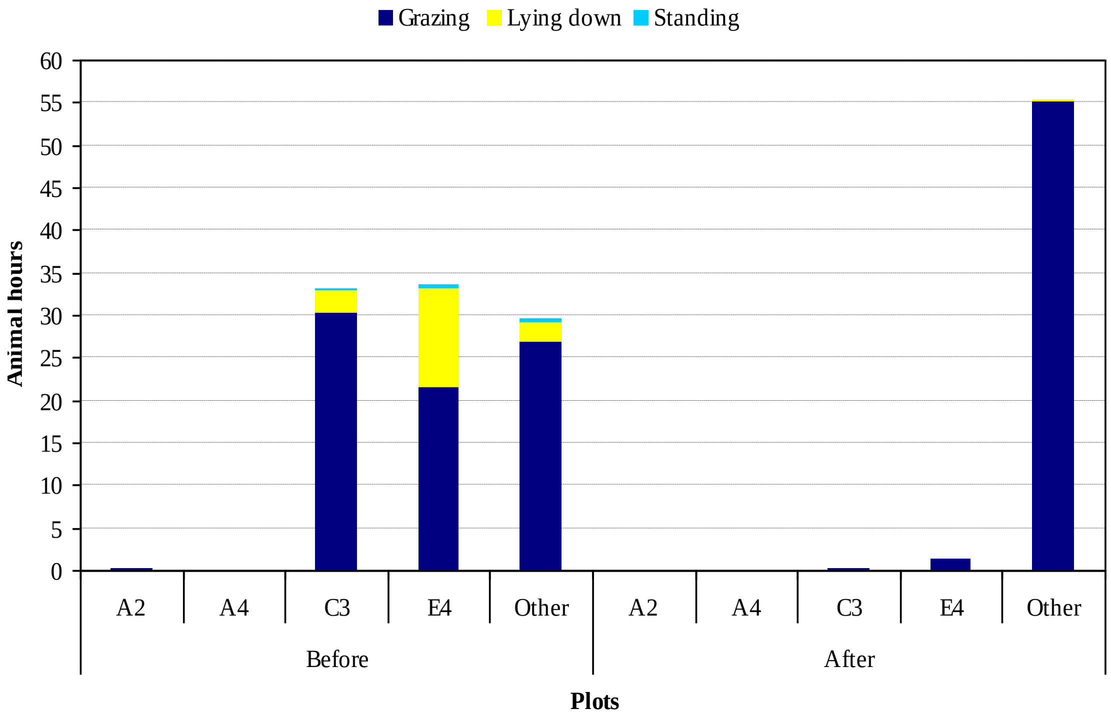

Figure 9.5: Average animal hours, consisting of time spent grazing, lying down and standing, springbok spent in the treatment and other experimental plots before and after the mowing treatments.

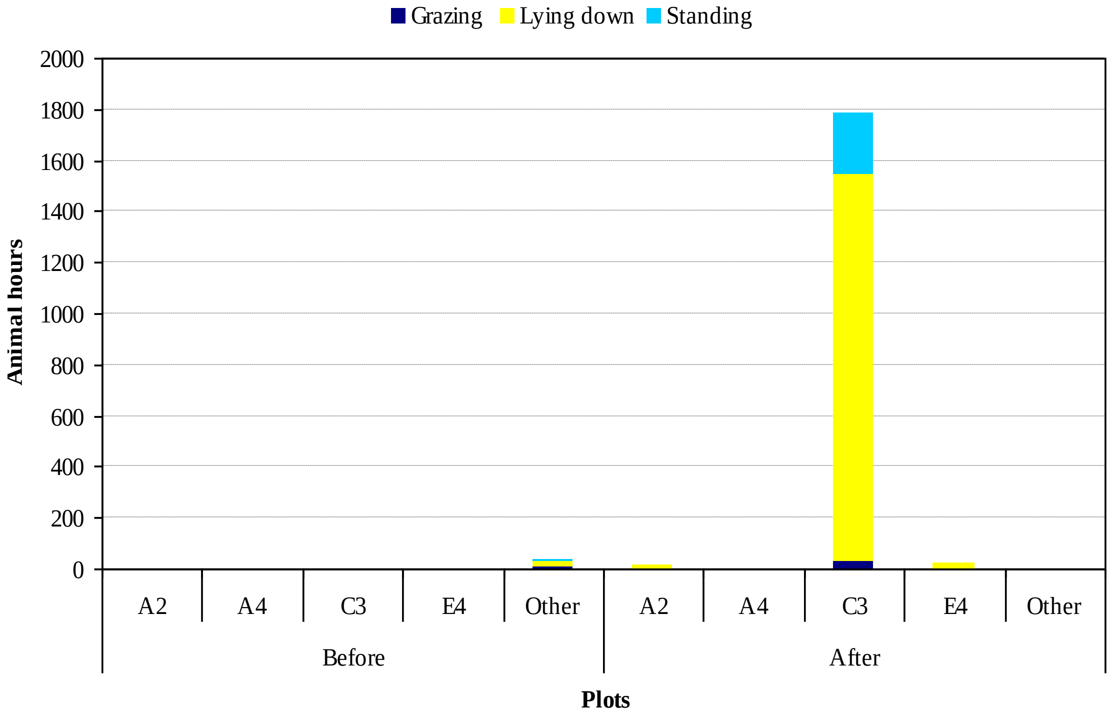

Figure 9.6: Average animal hours, consisting of time spent grazing, lying down and standing, blesbok spent in treatment and other experimental plots before and after the mowing treatments.

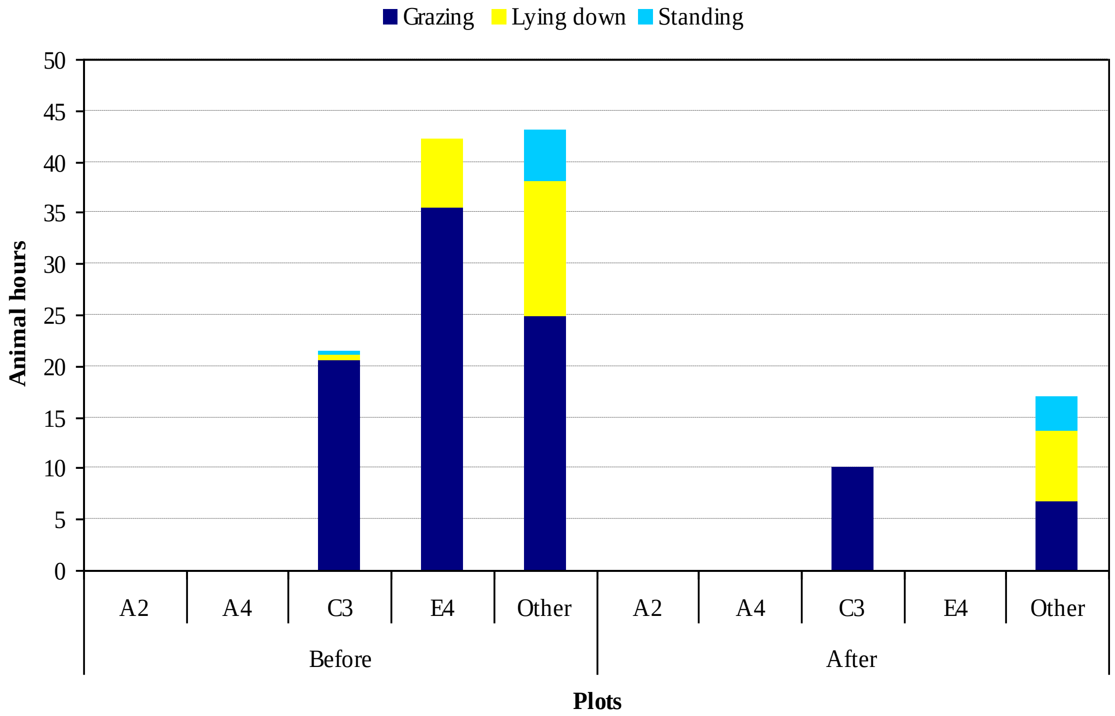

Figure 9.7: Average animal hours, consisting of time spent grazing, lying down and standing, black wildebeest spent in the treatment and other experimental plots before and after the mowing treatments.

9.4 DISCUSSION

According to Arsenault & Owen-Smith (2002), the vegetation changes induced by feeding and destructive impacts of Type I species can have a positive or negative effect on the habitat and/or feeding of other species. The results from this study give the impression that the simulated impact of Type I species mostly facilitated the non-feeding activities (lying down and standing) and not the feeding of blesbok. Blesbok showed a distinctive shift towards the experimental plot (C3) with a grass height of 5 cm (Figures 9.4 & 9.6) and dominant grass species *Setaria incrassata* and *T. triandra* (see Chapter 5). The other treated plots were, however, poorly utilised. It appears that the grass quality in combination with grass height played an important role since the similarly treated plot (A2) dominated by the unpalatable *A. bipartita* (see Chapter 5) was avoided (Figures 9.4 & 9.6). However, the grazing activity did not increase much in the treated plot with a high occupation of blesbok (Figure 9.6). This could be due to the availability of more suitable forage in some of the unmowed plots where grazing patches already existed, and species diversity and occurrence of preferred species is higher. Except for *T. triandra*, the occurrence of preferred species (see Chapter 7) and the species diversity (see Chapter 5) were generally low in plot C3. It appears from Chapter 6 that the herbivore game species tended to favour plots with a higher species diversity owing to their selective grazing behaviour. Springbok and black wildebeest generally did not show any distinctive changes in their activity as a result of the mowing treatments.

The overall lower available herbage tends to lower the bite size and bite quality (Chacon & Stobbs 1976). Animals usually respond to such variability by moving to other areas where forage is more readily available (Low *et al*. 1981; Squires 1982). As the study was done in the reserve storage season (RSS) (see Chapter 6), the quality of plant species was declining, and due to the average decrease in seasonal rainfall (see Chapter 3), less nutritional re-growth was available. Dietary quality frequently declines sharply during periods of water deficit but subsequently recovers when soil moisture levels are replenished (McKay & Frandsen 1969; O'Reagain 1994). Their previous experience with the forage in plots A2&4 may have resulted in the avoidance of this specific area. Cattle and probably most ungulates, appear to have well developed, long-term spatial memories (Baily *et al*. 1989), allowing them to remember both the location and amount of food present in the environment. Information transfer between individual animals about the location and quality of different food resources, may also occur. This is most common from mother to off-spring, but may also occur from adults to unrelated juveniles and between individuals in the same herd (O'Reagain & Schwartz 1995).

Foraging behaviour could also have had an influence on plot selection, since blesbok tend to decrease their active behaviour during the colder seasons in order to conserve energy (Du Plessis 1968; Novellie 1978). Some northern hemisphere cervids show a photoperiod-induced reduction in metabolic rate with the approach of winter (O'Reagain & Swartz 1995). Natural temporal variability arises from diurnal variation in plant chemical composition due to normal, daily fluctuations in photosynthesis, transpiration and other physiological processes. This results in predictable fluctuations in water content and the levels of carbohydrates (Smith 1973) and secondary chemicals, like alkaloids (Fairburn & Suwal 1961). Evidence suggests that animals may match foraging behaviour with diurnal changes in plant composition. Nagy (1994) found that springbok in the arid Kalahari select the inflorescences of desert shrubs before dawn, when the water content is highest.

The fact that mowing does not have the same effect as grazing could have had an influence on plot selection. Feeding facilitation may arise in two different ways: (i) when grazing by one species makes more grass accessible to another species, e.g. by reducing grass height and removing cover and stems (Vesey-Fitzgerald 1960; Bell 1970, 1971; Grobler 1983; McNaughton 1985; Kabigumila 1993), or (ii) when grazing and trampling by one species induces regrowth of higher quality forage, thus facilitating another more selective species (Vesey-Fitzgerald 1974; McNaughton 1976; Owen-Smith 1988). The mowing of grass does not have the same mechanical impact as trampling, which could have influenced the occurrence of new shoots and plants. Trampling promotes decomposition through the trample of litter, promote germination by burrowing seeds and distributed plant material (Owen-Smith 1999).

A model developed by Huisman & Olff (1998) showed that generalist herbivores can facilitate selective herbivores by suppressing competition for light. This favours the small plant species, and thereby the selective herbivores. Furthermore, by selectively grazing on green leaves in taller swards, smaller or more narrow-muzzled species also have the ability to deplete this component to the detriment of forage quality for larger species (Murray & Illius 2000). The results found by Fritz *et al*. (2002) from an analysis done on 31 natural ecosystems from East and southern Africa suggest that very large herbivore species may compete with the smaller herbivore species for food or may alter the vegetation communities unfavourably.

Facilitation through increased access to resources was described qualitatively by Vesey-Fitzgerald (1960) in terms of grazing succession. He found that trampling and feeding by elephants exposed medium-height grasses to buffalo, which in turn generated shorter grass exploited by topi (*Damaliscus lunatus*). Further evidence supporting the grazing succession concept was provided by Bell (1970, 1971), who studied the distribution of resident animal species such as buffalo, zebra, blue wildebeest, topi and Thomson's gazelle (*Gazella thomsonii*) across the catenary sequence of grasslands in the western Serengeti. He came to the conclusion that the presence of one species can be beneficial to the other species and suggested that the benefit is due to the effect of the herbivores on the structure of the herbaceous layer. Subsequent authors have, however, questioned Bell's (1970, 1971) interpretation of the patterns of species association as representing grazing facilitation (Sinclair & Norton-Griffiths 1982; Illius & Gordon 1987; De Boer & Prins 1990; Prins & Olff 1998). McNaughton (1976) provided convincing evidence that Thomson's gazelle were attracted to areas where prior grazing by wildebeest improved the quality of the grass sward on the Serengeti plains. Concentrations of migratory wildebeest removed 85% of the green biomass of *Themeda-Pennisetum* tall grassland over a two to three week period. This stimulated grass leaves' regrowth and increased the green biomass concentration. McNaughton (1984) demonstrated furthermore that grassland productivity, as well as the green leaf concentration within swards, was enhanced by quite high levels of grazing. Arsenault & Owen-Smith (2002) suggest that feeding facilitation occurs through the improved forage quality of grass regrowth during the growing season, rather than simply through increased resource access through the removal of obstructing grass structures.

Generally, no distinctive changes in the activity of springbok and black wildebeest could be found as a result of changing sward structure caused by the simulated impact of Type I species. This could have been influenced by territoriality, seeing that the mowing treatments were carried out during the mating season (autumn), and springbok, blesbok and black wildebeest are territorial animals (Owen-Smith 1977; Skinner 2005). The size of the treated area (number of plots) may also have played a role. If the mowing treatments were applied to a larger area and repeated on a regular basis for a longer period, it would be expected that all three these herbivore game species will move to the treated areas. Blesbok occupied the plot which had palatable species mowed at a height of 5 cm (C3) and could have prevented the movement of the other species to this plot. Animals may track environmental changes by constantly monitoring the quality and availability of different plant species or patches. This may be achieved by sampling at both plant and patch level e.g. Illius *et al*. (1992), to detect changes in forage quality and availability. Since springbok, blesbok and black wildebeest are short grass grazers (Novellie 1990) they would prefer short grass habitat patches (grazing lawns). The facilitation of such suitable habitat may result in higher animal production and population growth.

Springbok, blesbok and black wildebeest are the only species that had a population growth from 2003/04 to 2004/05 (see Chapter 3). None of the other herbivore game species within the fenced in property had a definite increase in their population size. This might be because their preferred habitats were in the minority. Parker (1983) found that the vast increase in elephants in the Tsavo region of Kenya, and consequent opening of dense shrubland, was followed by increases in the abundance of grazers like gemsbok and zebra (*Equus burchelli*), while browsers such as lesser kudu (*Tragelaphus imberbis*) and gerenuk (*Litocranius walleri*) declined. The tendency of elephants to transform savanna woodlands into either open parkland or shrubland, depending on underlying soil type, is well known (Laws 1970; Bell 1981). According to Owen-Smith (1989), declines in some grazing ungulates, plus the increases in browsers, in the Hluhluwe Game Reserve in South Africa were attributed to habitat thickening following the extermination of elephants a century earlier. Grazing hippopotamus and white rhinoceros can likewise transform tall grasslands into extensive grazing lawns (Olivier & Laurie 1974; Owen-Smith 1988). Elimination of hippos from the Mweya Peninsula region of the Queen Elizabeth National Park, was followed by a substantial increase in elephant, buffalo and waterbuck (species favouring tall grass) after the lakeshore grassland had recovered from the short state maintained by hippo grazing (Eltringham 1974). Following the recovery of the hippo population, numbers of these three species reportedly declined in this region. The increase in the white rhino abundance in the Hluhluwe-Umfolozi Park was associated with declines of reedbuck (*Redunca arundinum*) and waterbuck, both dependent on tall grass (Owen-Smith 1988). Species preferring short grass - specifically wildebeest, zebra, impala and warthog - maintained or increased their abundance. A comparison between West Africa and East and southern Africa showed that in the former the medium-sized ungulates appear to have partially compensated in terms of biomass for the absence of the very largest herbivores (Fritz 1997), suggesting that the latter had a competitive effect on the other herbivores. According to Arsenault & Owen-Smith (2002), there seems to be sufficient evidence demonstrating population responses by herbivores in response to facilitative habitat alteration by other species, in some situations. However, they state that habitat facilitation is not restricted to the major vegetation impacts caused by the very largest herbivores.

9.5 CONCLUSION

The following conclusions can be drawn from the results of this study:

(i) The modification of the sward structure of under-utilised grassland may facilitate the occupation of such grassland by short grass grazers, notably blesbok, which previously avoided these areas.

(ii) Blesbok showed a strong preference for the area where the simulated effect of Type I species resulted in a grass height of 5 cm, but only in areas where more palatable grass species occurred.

(iii) The changing grass structure mainly facilitated the non-feeding habitat use and not the feeding of blesbok. However, various factors could have influenced the latter observation.

(iv) Generally, no distinctive changes in the activity of springbok and black wildebeest could be found as a result of changing sward structure. However, it is speculated that if the treated area was larger, springbok and black wildebeest would also have been attracted to the mowed area.

(v) It is concluded that by changing the structure of vegetation, herbivores may effectively permit the utilisation of that resource by other species, as well as the increased occurrence of some species in that area. This has important consequences for the management of small fenced game properties where the inclusion of Type I species (such as buffalo) is considered.

CHAPTER 10

GENERAL CONCLUSIONS AND RECOMMENDATIONS

10.1 INTRODUCTION

The fencing of small areas and stocking them with game species is becoming a common practice in South Africa. Under these conditions, herbivore populations often exceed natural densities, which require more intensive management inputs. The main objectives of this study were to determine (i) the small-scale habitat and feeding preferences of springbok, blesbok and black wildebeest, (ii) the association between soil, grass species and grazing by the herbivore game species, and (iii) the influence of simulated impact of Type I species on the habitat preferences of herbivore game species within the small fenced-in grassland area.

10.2 GENERAL CONCLUSIONS

The following general conclusions can be drawn from the results of this study:

(i) The fencing of this area has resulted in the modification of the natural habitat of the herbivore game species. This may have reduced the suitability of the habitat for some species through alteration of the botanical composition and structure of available grazing, but not to the extent that it is not usable. This is confirmed by the healthy populations of the herbivore game species.

(ii) Habitat patches with a high abundance of Increaser herbaceous species, relatively high species diversity, low above-ground dry matter production and moderate to low veld condition score, were mostly preferred by springbok and blesbok. Black wildebeest tended to favour patches with a higher occurrence of Decreaser herbaceous species, although Increaser species were also relatively abundant.

(iii) The herbaceous layer of the experimental area was generally in a poor ecological condition. However, the short grazed areas that are in a poor condition appear to be the preferred habitat of the short grass grazers.

(iv) Small-scale seasonal movements through changes in the preference for certain habitat patches were observed for all three species. More habitat patches were utilised during the dry season when food resources were scarce.

(v) Grass species favoured by springbok, blesbok and black wildebeest included *Themeda triandra*, *Eragrostis obtusa*, *Panicum stapfianum*, *Eragrostis plana* and *Digitaria eriantha*. Less-favoured species included *Brachiaria eruciformis*, *Cynodon dactylon*, *Eragrostis chloromelas* and *Setaria incrassata*, and non-favoured species were *Tragus berteronianus*, *Aristida bipartita* and *Cymbopogon pospischilii*. Results from the ordination analysis indicated that the herbivore game species mostly grazed in areas where *T. triandra*, *E. obtusa*, *E. plana*, *P. stapfianum*, *D. eriantha*, *Cynodon dactylon*, *H. contortus* and *A. adscensionis* were abundant. The association of springbok, blesbok and black wildebeest with Decreaser as well as Increaser grass species can be attributed to patch heterogeneity. It appears that the herbivore game species preferentially selected the short grazed grasses, irrespective of their quality.

(vi) Seasonal changes occurred in the feeding preferences of the herbivore game species, where the general utilisation of less palatable grass species was higher during the dry season due to the lack of suitable forage. The diversity of grass species being grazed increased during the rainy season, and the association between time spent grazing and the percentage occurrence of the grass species, was also weaker. This was due to the increase in availability of more suitable forage outside the demarcated experimental area.

(vii) Soil texture, and degradation due to over utilisation, were the most important factors that caused spatial variation in the botanical composition of the grassland area.

(viii) Less-favoured and non-favoured grass species mainly occurred on heavy clay soil and were closely associated with soil Na, Ca, Mg and K. In contrast, favoured grass species mostly occurred on soil with higher sand and silt content and were closely associated with soil N, C and Zn. Time (animal hours) spent grazing by springbok, blesbok and black wildebeest was closely associated with grazing patches that had soil with higher sand and silt content, and a relatively high soil quality in terms of N and C.

(ix) The small-scale habitat and feeding preferences of these game species cannot entirely be explained in terms of vegetation and seasonality, since other factors such as reproduction, social behaviour, size of the fenced-in area and interaction with the other herbivore game species not studied may also have influenced the results.

(x) The simulated influence of Type I species on the sward structure of under-utilised grassland may facilitate the occupation of such grassland by short grass grazers, particularly blesbok, which previously avoided these areas.

(xi) Blesbok showed a strong preference for an area where the modification of the sward structure resulted in a grass height of 5 cm, and where more palatable grass species occurred. The changing grass structure mainly facilitated the non-feeding habitat use and not the feeding of blesbok.

(xii) Generally, no distinctive changes in the activity of springbok and black wildebeest could be found as a result of changing sward structure. However, it is speculated that if the area with the modified sward structure was larger, springbok and black wildebeest would also have been attracted to the area.

(xiii) By changing the structure of the vegetation, herbivores may effectively permit the utilisation of that resource by other species, as well as the increased occurrence of some species in that area. This has important consequences for the management of small fenced game areas where the inclusion of Type I species (such as buffalo) is being considered.

10.3 RECOMMENDATIONS

Successful management and utilisation of any game ranch is dependent on the availability of regular and appropriate information on which decisions can be based. Components such as rainfall, soil type, soil nutrients, availability of water, vegetation characteristics such as structure, cover, composition and productivity, as well as herbivore game species and numbers, are key determinants and indicators of the health of the ecosystem. The regular monitoring (at least once a year) of most of these determinants is necessary to evaluate habitat and game population trends and changes over time.

There is a widespread tendency to view short grass grazers, particularly black wildebeest, as being damaging to veld. It is no doubt true that if the animals are kept at high stocking rates in restricted areas, severe exposure of the soil to erosion and poor animal condition are often evident, but the prejudice against the short grass grazers, appears to stem largely from the assumption that veld dominated by Decreaser grass species is generally "superior" to veld dominated by Increaser grass species. However, for a game ranch dedicated to the production of short grass grazers the formation of grazing lawns dominated by Increaser species and a high species diversity must not be regarded as totally undesirable or preventable. Since favoured grass species included both Decreaser and Increaser species, management should aim at areas with a range of veld condition scores rather than a homogeneous area with a single high veld condition value. A compromise between short grazing (habitat suitability) and veld in a good ecological condition seems to be the proper approach for management under these circumstances.

The spatial variation in the vegetation of the experimental area demonstrates the heterogeneity of the veld. It was evident that the most important factors causing these variations were soil texture and degradation due to over utilisation. It is recommended that the stocking rate be reduced in order to keep the grazing lawns in a productive condition under continuous grazing and to prevent soil loss or invasion by unpalatable species that provide low quality grazing. Stocking rates should be adjusted to compensate for the effect of rainfall on resource availability and quality. It would, therefore, be appropriate to base stocking rates on resource availability during the dry season, when resources are limited. The botanical abundance of the favoured grass species as well as their vigour should be used to monitor the degrading impact of grazing on rangeland condition. Veld assessment should thus be done at regular intervals in order to determine whether retrogression is continuing.

A proper understanding of the biotic requirements of plant species and the response of plants to biotic factors such as grazing intensity and frequency, as well as the feeding and habitat preferences of the herbivore game species, must form the basis of proper veld management strategies. This will conserve rangeland resources and maintain production stability and long-term sustainability, especially of small fenced areas.

ABSTRACT

SMALL-SCALE FEEDING AND HABITAT PREFERENCES OF HERBIVORE GAME SPECIES IN THE GRASSLAND OF THE CENTRAL FREE STATE

by

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MAGISTER SCIENTIAE

The fencing of small areas and stocking them with game species is becoming a common tendency in South Africa. The main objective of this study, conducted during the 2003/04 and 2004/05 seasons in a small fenced in game enclosure (78 ha) in the Bloemfontein district, Free State Province, was to determine the small-scale habitat and feeding preferences of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*) and black wildebeest (*Connochaetes gnou*) within the same vegetation type. The associations between soil, vegetation and grazing time by these herbivore game species were also determined, as well as whether the simulated influence of Type I herbivores on the sward structure will affect the small-scale habitat preferences of these herbivore species, which are all regarded as Type III species.

A relatively homogeneous area of 250 x 200 m (5 ha) in the middle of an open grassland area was selected for intensive study. The selected area was subdivided into twenty experimental plots of 50 x 50 m (0.25 ha), which were permanently marked and allocated an identification code.

Analysis of the soil was done to assess the physical properties, ionic content and electrical resistance of the soil in each experimental plot. Plots varied considerably in terms of the

chemical content of the soil, which was largely influenced by soil texture. This may account for the heterogeneity of the vegetation of the demarcated area. Prior land use and small-scale variation could also have influenced the soil quality and vegetation.

The botanical composition of the herbaceous layer was determined using a wheel point apparatus according to the nearest plant method, based on occurrence. Surveys were done at the end of each growing season (2003/04 & 2004/05). Above-ground dry matter production was determined by harvesting all plants in 20 randomly-selected 0.25 m² quadrates within each experimental plot, and weighing them. Plots on the northern side had a lower number of grass species with a lower grazing value (predominantly Increaser species), while plots on the southern side had a higher number of grass species with a higher grazing value (predominantly Decreaser species). Changes in the botanical composition between the two seasons (an increase in Increaser species) and the decrease in veld condition scores suggest that the veld is over-utilised and in a poor condition, and that stocking rates are currently too high. However, veld in this condition is the preferred habitat of short grass grazers. Therefore, a compromise between short grazing (habitat suitability) and veld in a good ecological condition seems to be the proper approach.

The small-scale spatial preferences of the three herbivore game species were studied by making observations, using binoculars, from a parked vehicle during the morning and afternoon. Both springbok and blesbok preferred habitat patches with a high abundance of Increaser species, relatively high species diversity and moderate to low veld condition score. Black wildebeest tended to favour patches with a higher occurrence of Decreaser species, although Increaser species were also relatively abundant in these plots. The preferred experimental plots generally had a low above-ground DM production. The number of habitat patches utilised was highest during the dry season.

A modification of the grazed-class method was used to determine the favoured grass species and percentage utilisation during the different seasons. Marked plants were inspected weekly from June 2004 to May 2005, and subjective estimates were given for utilisation using a developed field reference guide. *Themeda triandra*, *Eragrostis obtusa*, *Panicum stapfianum*, *E. plana* and *Digitaria eriantha* were the favoured grass species of springbok, blesbok and black wildebeest. Less-favoured species included *Brachiaria eruciformis*, *Cynodon dactylon*, *E. chloromelas* and

Setaria incrassata, while non-favoured species included *Tragus berteronianus*, *Aristida bipartita* and *Cymbopogon pospischilii*. Seasonal variation in utilisation was demonstrated, with a larger number of species that were utilised during the rainy season.

Associations between soils, the herbaceous layer and time spent grazing indicated that soil texture, and degradation due to over utilisation, were the most important factors that caused spatial variation in the botanical composition of the grassland area. Less-favoured and non-favoured grass species mainly occurred on heavy clay soil and were closely associated with soil Na, Ca, Mg and K. In contrast, favoured grass species mostly occurred on soil with higher sand and silt content and were closely associated with soil N, C and Zn. Time spent grazing by springbok, blesbok and black wildebeest were closely associated with the favoured grass species (as listed above).

To determine the influence of the simulated effect of Type I species on the small-scale habitat preferences, the grass was mown in two plots with a lawnmower at a height of 5 cm, and in another two plots at a height of 15 cm. Each cutting treatment consisted of a plot containing palatable and unpalatable grass species. Observations were conducted as described previously. The simulated influence of Type I species on the sward structure (grass mown at 5cm) of under-utilised grassland may facilitate the occupation of such grassland by short grass grazers, particularly blesbok, which previously avoided these areas. Generally, no distinctive changes in the activity of springbok and black wildebeest could be found.

It is recommended that stocking rates in the game enclosure be reduced and maintained at sustainable levels to allow the vegetation to recover and reduce further degradation. Continual assessment of the vegetation is essential to monitor further changes in the herbaceous layer and evaluate long-term sustainability of the game enclosure. Similar monitoring is recommended for all small fenced game ranches.

Keywords: Grassland, soil, vegetation, herbivore game species, game enclosure, feeding, habitat preferences, seasons.

OPSOMMING

KLEINSKAALSE VOEDING- EN HABITATVOORKEURE VAN HERBIVOOR WILDSPESIES IN DIE GRASLAND VAN DIE SENTRALE VRYSTAAT

deur

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Die omheining van klein areas en die belading daarvan met wildspesies is ‘n algemene neiging in Suid-Afrika. Die hoof doelstelling van dié studie, uitgevoer gedurende die 2003/04 en 2004/05 seisoen in a klein omheinde wildkamp (78 ha) in die Bloemfontein distrik in die Vrystaat Provinsie, was om die kleinskaalse habitat- en voedingsvoorkeure van springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus phillipsi*) en swart wildebees (*Connochaetes gnou*) binne dieselfde plantegroei tipe te bepaal. Die assosiasie tussen grond, plantegroei en tyd spandeer aan wei deur hierdie wildspesies is ook bepaal, sowel as die invloed van die gesimuleerde impak van Tipe I spesies op die plantegroei struktuur en die kleinskaalse habitat voorkeure van hierdie herbivoor spesies, wat as Tipe III spesies beskou word.

‘n Relatiewe homogene area (in terme van topografie) van 250 x 200 m (5 ha) in die middel van ‘n oop grasveld area is geselekteer vir intensiewe studie. Die geselekteerde area is onderverdeel in twintig eksperimentele persele van 50 x 50 m (0.25 ha), wat permanent gemerk is en waaraan ‘n identifikasie kode toegeken is.

Grondanalises is gedoen om die fisiese eienskappe, ioniese inhoud en elektriese weerstand van die grond in elke eksperimentele perseel te bepaal. Persele het aansienlik verskil in terme van die

chemiese inhoud in die grond, wat grootliks beïnvloed is deur die grondtekstuur. Dit kan moontlik die relatiewe heterogeniteit van die plantegroei van die afgebakende gebied verklaar. Vorige land- gebruik asook kleinskaalse variasie kon ook die grondkwaliteit en plantegroei beïnvloed het.

Die botaniese samestelling van die graslaag is bepaal m.b.v. 'n wielpunt apparaat volgens die naaste plant metode. Opnames is gedoen aan die einde van elke groeiseisoen (2003/04 & 2004/05). Bo-grondse droëmassaproduksie is bepaal deur alle plante in 20 ewekansig geselekteerde 0.25 m² kwadrate binne elke eksperimentele perseel te sny en te weeg. Persele aan die noordekant het minder grasspesies en ook spesies met 'n laer weidingswaarde (hoofsaaklik Toenemer spesies) gehad, terwyl persele aan die suiderkant 'n groter getal spesies en ook spesies met 'n hoër weidingswaarde (hoofsaaklik Afnemer spesies) gehad het. Die afname in die veld-toestandtelling dui aan dat die veld oorbewei en in 'n swak toestand is en dat die veelading huidiglik te hoog is. Veld in hierdie toestand is egter die voorkeur habitat van kortgrasvreters en daar moet dus 'n kompromie getref word tussen kort beweiding (habitat geskiktheid) en veld in 'n goeie ekologiese toestand.

'n Gewysigde wei-klas metode is gebruik om voorkeur grasspesies en persentasie benutting gedurende die verskillende seisoene te bepaal. Gemerkte plante is weekliks van Junie 2004 tot Mei 2005 geïnspekteer en deur gebruik te maak van 'n veldverwysingsgids is subjektiewe skattings gemaak van die graad van benutting. *Themeda triandra*, *Eragrostis obtusa*, *Panicum stapfianum*, *E. plana* en *Digitaria eriantha* was voorkeur grasspesies van die springbokke, blesbokke en swart wildebeeste. Minder-voorkeur spesies sluit in *Brachiaria eruciformis*, *Cynodon dactylon*, *E. chloromelas* en *Setaria incrassata*, terwyl nie-voorkeur spesies *Tragus berteronianus*, *Aristida bipartita* en *Cymbopogon pospischilii* ingesluit het. Seisoenale variasie in die benutting van grasspesies het voorgekom. Die hoeveelheid spesies wat benut is het toegeneem gedurende die reënseisoen.

Assosiasies tussen grond, die graslaag en tyd spandeer aan wei het aangedui dat grondtekstuur en degradasie, as gevolg van 'n hoë wildbelading, die belangrikste faktore was wat ruimtelike variasie in die botaniese samestelling van die grasland area veroorsaak het. Minder-voorkeur en nie-voorkeur grasspesies het hoofsaaklik op swaar kleigronde voorgekom en was nou geassosieer

met grond Na, Ca, Mg en K. Daarteenoor, het voorkeur grasspesies hoofsaaklik voorgekom op grond wat ‘n hoër sand en slik inhoud het en het ‘n noue assosiasie getoon met grond N, C en Zn. Die tyd wat springbokke, blesbokke en swart wildebeeste aan wei spandeer het, het ‘n noue assosiasie getoon met voorkeur grasspesies (soos bo vermeld).

Ten einde die gesimuleerde invloed van Tipe I spesies op die struktuur van die graslaag te bepaal, is die gras met ‘n grassnyer gesny. Twee eksperimentele persele is op ‘n hoogte van 5 cm gesny en nog twee op ‘n hoogte van 15 cm. Elke snybehandeling het ‘n perseel met smaaklike en onsmaaklike grasspesies ingesluit. Observasies was uitgevoer soos voorheen beskryf. Die gesimuleerde invloed van Tipe I spesies op die grasstruktuur (gras gesny op 5 cm) van onderbenutte grasveld kan die okkupasie daarvan deur kortgrasvreters, spesifiek blesbokke, wat vroeër die area vermy het, fasiliteer. Oor die algemeen was daar geen merkwaardige veranderinge in die aktiwiteit van springbokke en swart wildebeest nie.

Dit word aanbeveel dat die wildbelading in die wildkamp verminder en gehandhaaf word by onderhoubare vlakke ten einde dit moontlik te maak vir die plantegroei om te herstel en om verdere degradasie te voorkom. Herhaalde evaluerings van die plantegroei is noodsaaklik om verdere veranderinge in die graslaag te monitor, asook om die langtermyn volhoubaarheid van die wildkamp te monitor. Soortgelyke monitering word aanbeveel vir alle klein omheinde wildsplase.

Sleutelwoorde: Grasland, grond, plantegroei, herbivooor wildspesies, wildkamp, voeding, habitat voorkeure, seisoene.

REFERENCES

Abule E., Smit G.N. & Snyman H.A. 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. *Journal of Arid Environments* 60: 343-358.

Acocks J.P.H. 1988. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 57. 146 pp.

Agassi M., Shainberg I. & Morin J. 1981. Effect of electrolyte concentration and soil sodicity on infiltration rate and crust information. *Soil Science Society of America Journal* 45: 848-851.

Allden W.G. & Whittaker I.A. 1970. The determinants of herbage intake by grazing sheep: The interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* 21: 755-766.

Alfaro M.A., Jarvis S.C. & Gregory P.J. 2004. Factors affecting potassium leaching in different soils. *Soil Use and Management* 20: 182-189.

Andere D.K. 1981. Wildebeest *Connochaetes taurinus* (Burchek) and its food supply in Amboseli Basin. *African Journal of Ecology* 19: 239-250.

Anderson G.D. & Talbot L.M. 1965. Soil factors affecting the distribution of the grassland types and their utilisation by wild animals on the Serengeti Plains, Tanganyika. *Journal of Ecology* 53: 33-56.

Anderson T.M., Dong Y. & McNaughton S.J. 2006. Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture and grazing. *Journal of Ecology* 94: 1164-1175.

Anderson T.M. & Frank D.A. 2003. Defoliation effects on reproductive biomass:

Importance of scale and timing. *Journal of Range Management* 56: 501-516.

Anderson T.M., McNaughton S.J. & Ritchie M.E. 2004. Scale-dependent relationships between the spatial distribution of a limiting resource and plant species diversity in an African grassland ecosystem. *Oecologia* 139: 277-287.

Arnold J.F. 1955. Plant life-form classification and its use in evaluating range conditions and trend. *Journal of Range Management* 8: 176-181.

Arnold G.W. 1960. Selective grazing by sheep of two forage species at different stages of growth. *Australian Journal of Agricultural Research* 11: 1026-1033.

Arnold G.W. 1981. Grazing behavior. In: Morely F.H.W. (ed.). *Grazing animals*. Elsevier Scientific Publishing Company, Amsterdam.

Arnold G.W. & Dudzinski M.L. 1978. *Ethology of free-ranging domestic animals*. Elsevier Scientific Publishing Company, Amsterdam.

Arsenault R. & Owen-Smith N. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97: 313-318.

Augustine D.J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* 40: 137-149.

Austin M.P. 1980. An exploratory analysis of grassland dynamics: An example of a lawn succession. *Vegetatio* 43: 87-94.

Austin M.P. & Smith T.M. 1989. A new model for the continuum concept. *Vegetatio* 83: 35-47.

Baharav D. & Rosenzweig M.L. 1985. Optimal foraging in dorcas gazelles. *Journal of Arid Environments* 9: 167-171.

Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M. & Sims P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386-400.

Bailey D.W., Rittenhouse L.R., Hart R.H., Swift D.M. & Richards R.W. 1989. Association of relative food availabilities and locations by cattle. *Journal of Range Management* 42: 480-482.

Bakker J.P., De Leeuw J. & Van Wieren S.E. 1983. Micro-patterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio* 55: 153-161.

Barbour M.G., Burk J.H., Pitts W.D., Gillian F.S. & Schwartz C.C. 1998. *Terrestrial Plant Ecology*. Benjamin & Cummings, Menlo Park, California.

Barnes D.L. 1989. Reaction of three veld grasses to different schedules of grazing and resting. 2. Residual effects on vigour. *South African Journal of Plant and Soil* 6: 8-13.

Barnes D.L., Beukes B.H. & Kotze G.D. 1985. A study of variations in floristic composition of Highveld in the eastern Transvaal. *Journal of the Grassland Society of South Africa* 2: 23-27.

Barnes D.L., Odendaal J.J. & Beukes B.H. 1982. Use of the dry-weight-rank method of botanical analysis in the eastern Transvaal Highveld. *Proceedings of the Grassland Society of southern Africa* 17: 79-82.

Barnes D.L., Rethman N.F.G., Beukes B.H. & Kotze G.D. 1984. Veld composition in relation to grazing capacity. *Journal of the Grassland Society of Southern Africa* 1: 16-19.

Barnes T.G., Heitschmidt R.K. & Varner L.W. 1991. Wildlife. In: Heitschmidt R.K. & Stuth J.W. (eds.) *Grazing management: An ecological perspective*. Timber Press, Portland, Oregon. pp. 179-189.

Bauder J.W. & Brock T.A. 1992. Crop species, amendment, and water quality effects on selected soil physical properties. *Journal of the Soil Science Society of America* 56: 1292-1298.

Behr J. 1988. *Ekonomiese aspekte van wildboerdery in Suid-Afrika*. M.Sc. thesis, University of Pretoria, Pretoria.

Behr J. & Groenewald J.A. 1990. Profit potentials of game farming. *Agrekon* 29: 59-65.

Bell R.H.V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A. (ed.). *Animal populations in relation to their food resources*. Blackwell, Oxford. pp. 111-124.

Bell R.H.V. 1971. A grazing ecosystem in the Serengeti. *Scientific American* 225: 86-93.

Bell R.H.V. 1981. An outline of a management plan for Kasunga National Park, Malawi. In: Jewel P.A., Holt S. & Hart D. (eds.) *Problems in management of locally abundant wild mammals*. Academic Press, New York. pp. 69-89.

Bell R.H.V. 1982. The effect of soil nutrient availability on community structure in African eco-systems. In: Huntley B.J. & Walker B.H. (eds.). *Ecological studies 42: Ecology of tropical savannas*. Springer-Verlag, Berlin. pp. 193-216.

Bell R.H.V. 1984. Soil-plant-herbivore interactions. In: Bell R.H.V. & McShane-Caluzi E. (eds.). *Conservation and Wildlife Management in Africa*. US Peace Corps, Washington D.C.

Belovsky G.E. 1978. Diet optimization in a generalist herbivore: The moose. *Theoretical Population Biology* 14: 105-134.

Belovsky G.E. 1981a. Food plant selection by a generalist herbivore: The moose.

Ecology 62: 1020-1030.

Belovsky G.E. 1981b. Optimal activity times and habitat choice of moose. *Oecologia* (Berlin) 48: 22-30.

Belovsky G.E. 1986a. Generalist herbivore foraging and its role in competitive interactions. *American Zoology* 26: 51-69.

Belovsky G.E. 1986b. Optimal foraging and community structure: Implications for a guild of generalist grassland herbivores. *Oecologia* (Berlin) 70: 35-52.

Belovsky G.E. & Slade J.B. 1986. Time budgets of grassland herbivores: Body size similarities. *Oecologia* (Berlin) 70: 53-62.

Belsky A.J. 1986. Population and community processes in a mosaic grassland in the Serengeti, Tanzania. *Journal of Ecology* 74: 841-856.

Ben-Shahar R. 1991. Selectivity in large generalist herbivores: Feeding patterns of African ungulates in a semi-arid habitat. *African Journal of Ecology* 29: 302-315.

Ben-Shahar R. & Fairall N. 1987. Comparison of the diurnal activity patterns of blue wildebeest and red hartebeest. *South African Journal of Wildlife Research* 17: 49-54.

Berendse F. 1985. The effect of grazing on the outcome of competition between plant species with different nutrient requirements. *Oikos* 44: 35-39.

Berendse F. 1994. Litter decomposability – a neglected component of plant fitness. *Journal of Ecology* 82: 187-190.

Berendse F., Bobbink R. & Rouwenhorst G. 1989. A comparative study on nutrient cycling in wet heathland ecosystems II: Litter decomposition and nutrient mineralization. *Oecologia* 78: 338-348.

Bigalke R.C. 1972. Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *Zoologica Africana* 7: 333-359.

Binkley D. & Valentine D. 1991. Fifty-year biogeochemical effects on green ash, white pine, and Norway spruce in a replicated experiment. *Forest Ecology and Management* 40: 13-25.

Black J.L. & Kenney P.A. 1984. Factors affecting diet selection by sheep II. Height and density of pasture. *Australian Journal of Agricultural Research* 35: 565-578.

Blankenship L.A. & Qvortrup S.A. 1974. Resource management on a Kenya game ranch. *Journal of South African Wildlife Management Association* 4: 185-190.

Bonser S.P. & Reader R.J. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* 76: 2176-2183.

Booysen J. 1983. *Twee metodes vir die kwantitatiewe simulering van groeitoestande van klimaksgras*. M.Sc.(Agric) thesis, University of the Orange Free State, Bloemfontein.

Bosch O.J.H. 1989. Degradation of the semi-arid grasslands of southern Africa. *Journal of Arid Environments* 16: 143-147.

Bosch O.J.H. & Gauch H.G. 1991. The use of degradation gradients for the assessment and ecological interpretation of range condition. *Journal of the Grassland Society of Southern Africa* 8: 138-146.

Bosch O.J.H. & Janse van Rensburg F.P. 1987. Ecological status of species on grazing gradients on the shallow soils of the western grassland biome in South Africa. *Journal of the Grassland Society of South Africa* 4: 143-147.

Bosch O.J.H., Janse van Rensburg F.P. & Truter S. du T. 1987. Identification and selection of benchmark sites on Litholitic soils of the western grassland biome of South Africa. *Journal of the Grassland Society of South Africa* 4: 59-62.

Bosch O.J.H. & Kellner K. 1991. The use of degradation gradients in the ecological interpretation of veld condition assessment. *Journal of Arid Environments* 21: 21-29.

Bosch O.J.H., Kellner K. & Scheepers S.H.E. 1989. Degradation models and their use in detecting the condition of southern African grasslands. *Proceedings of the XVI International Grasslands Congress, October, Nice, France.*

Bosch O.J.H. & Van Rensburg F.P.J. 1987. Ecological status of species on grazing gradients on the shallow soils of the western grassland biome in South Africa. *Journal of the Grassland Society of South Africa* 4: 143-147.

Bothma J. du P. 1995. Graduate training in wildlife management in southern Africa. In: Bissonette J.A. & Krausman P.R. (eds.). *Integrating people and wildlife for a sustainable future*. *Proceedings of the First International Wildlife Management Congress.* The Wildlife Society, Bethesda. pp. 152-155.

Bothma J. du. P. 2000. *Wildplaas bestuur (3rd edition)*. Van Schaik Publishers, Pretoria.

Bothma J. du P., Van Rooyen N. & Du Toit J.G. 2000. Geskikte wildsoorte. In: Bothma J. du P. (ed.). *Wildplaas bestuur* (*3rd edition*). Van Schaik Publishers, Pretoria. pp. 137-151.

Bredenkamp G.H., Van Rooyen N. & Lubke R.A. 1996. Dry Sandy Highveld Grassland (37). In: Low A.B. & Rebelo A.G. (eds.). *Vegetation of South Africa, Lesotho, and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria. pp. 41-42.

Bredenkamp G.J. 1985. An evaluation of the relative importance of certain habitat factors that influence the distribution of the plant species in the Manyeleti Game Reserve. *South African Journal of Botany* 51: 194-196.

Bredenkamp G.J., Theron G.K. & Van Vuuren D.R.J. 1983. Ecological interpretation of plant communities by classification and ordination of quantitative soil characteristics. *Bothalia* 14: 691-699.

Briske D.D. 1991. Developmental morphology and physiology of grasses. In: Heitschmidt R.K. & Stuth J.W. (eds.). *Grazing management: An ecological perspective*. Timber Press, Portland, Oregon.

Bromilow C. 2001. *Problem Plants of South Africa (Revised edition)*. Briza Publications, Pretoria.

Buckman H.O. & Brady N.C. 1967. *The nature and properties of soils*. The MacMillan Company, New York.

Burke I.C., Laurenroth W.K., Riggle R., Brannen P., Madigan B. & Beard S. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems* 2: 422-438

Burke I.C., Lauenroth W.K., Vinton M.A., Hook P.B., Kelly R.H., Epstein H.E., Aguiar M.R., Robles M.D., Aguilera M.O., Murphy K.L. & Gill R.A. 1998. Plant-Soil interactions in temperate grasslands. *Biogeochemistry* 42: 121-143.

Burke I.C., Lauenroth W.K. & Coffin D.P. 1995. Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. *Ecological Applications* 793-801.

Burkey T.V. & Reed D.H. 2004. The effects of habitat fragmentation on extinction risk: Mechanisms and synthesis. *Journal of Scientific Technology* 28: 9-37.

Caldwell M.M., Osmond C.B. & Not D.L. 1977. C_4 pathway photosyntheses at low temperatures in cold-tolerant *Atriplex* species. *Plant Physiology* 60: 157-164.

Campling R.C. & Lean I.J. 1983. Food characteristics that limit voluntary intake. In: Rook J.F. & Thomas P.C. (eds.). *Nutritional physiology of farm animals*. Longman, New York, USA.

Canfield R.H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *Journal of Range Management* 10: 199-203.

Chacon E.A. & Stobbs T.H. 1976. Influence of progressive defoliation of a grass sward on the eating behavior of cattle. *Australian Journal of Agricultural Research* 27: 709-727.

Chapin F.S. 1991. Effects of multiple environmental stresses on nutrient availability and use. In: Mooney H.A., Winner W.E. & Pell E.J. (eds.). *Responses of plants to multiple stresses*. Academic Press, San Diego. pp. 67-88.

Chapman H.D. 1966. *Diagnostic criteria for plants and soils*. University of California, Riverside, USA.

Chaneton E.J., Lemcoff J.H. & Lavado R.S. 1996. Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate sub-humid grassland in Argentina. *Journal of Applied Ecology* 33: 291-302.

Charnov E.L. 1976. Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9: 129-136.

Christie E.K. 1981. Biomass and nutrient dynamics in a C_4 semi-arid Australian grassland community. *Journal of Applied Ecology* 18: 907-918.

Cihacek L.J., Anderson W.L. & Barak P.W. 1996. Linkages between soil quality and plant, animal and human health. In: Doran J.W. & Jones A.J. (eds.). *Methods for* *assessing soil quality*. Soil Society of America Inc., USA. pp. 9-23.

Cillié B. 2000. *Die soogdier-gids van suider-Afrika*. Briza Publishers, Pretoria, South Africa. 224 pp.

Cilliers J.W., Van Biljon P.L., Tolmay E. & Coertze C. 1997. Effects of different levels of fertilizer application to veld on growth of steers and chemical composition of the herbage. *Grass and Forage Science* 52: 242-248.

Collinson R.F.H. & Goodman P.S. 1982. An assessment of range condition and large herbivore carrying capacity of the Pilansberg Game Reserve, with guidelines and recommendations for management. *Inkwe* 1: 1-54.

Collinson W.B., Urness P.J. & Austin D.D. 1978. Elk diets and activities on different lodge pole pine habitat segments. *Journal of Wildlife Management* 42: 799-810.

Cook G.D. & Muller W.J 1997. Is exchangeable sodium content a better index of soil sodicity than exchangeable sodium percentage?: A reassessment of published data. *Soil Science* 162: 343-349.

Coombes P.J. & Mentis M.T. 1992. A procedure for defining conservation management objectives and goals. In: Ebedes H. (ed.). *Proceedings of the 3rd International Wildlife Ranching Symposium, Pretoria.*

Cooper S.M. & Owen-Smith N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67: 142-146.

Cooper S.M. & Owen-Smith N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68: 446-455.

Cooper S.M., Owen-Smith & Bryant J.P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75: 336-342.

Coughenour M.B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *Journal of Range Management* 44: 530-542.

Crampton E.W. 1964. Nutrient-to-caloric ratios in applied nutrition. *Journal of Nutrition* 82: 353-365.

Crawley M.J. 1983. *Herbivory: The dynamics of plant-animal interactions*. Blackwell Scientific Publishers, Oxford.

Cumming D.H.M. 1982. The influence of large herbivores on savanna structure in Africa. In: Huntley B.J. & Walker B.H. (eds.). *Ecology of tropical savannas*, Volume 42. Springer-Verlag, Berlin. pp. 217-245.

Cumming D.H.M. & Cumming G.S. 2003. Ungulate community structure and ecological processes: Body size, hoof area and trampling in African savannas. *Oecologia* 134: 560-568.

Danckwerts J.E. 1984. *Towards improved livestock production off sweet grassveld*. Ph.D thesis, University of Natal, Pietermaritzburg.

Danckwerts J.E. & Stuart-Hill G.C. 1987. Adaptation of a Decreaser and an Increaser grass species to defoliation in semi-arid grassveld. *Journal of the Grassland Society of South Africa* 4: 68-73.

Dasmann R.F. 1981. *Wildlife biology*. John Wiley, New York.

Day T. & Detling J.K. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71: 180-189.

De Boer W.F. & Prins H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82: 264-274.

Dekker B. 1997. Calculating stocking rates for game ranches: Substitution ratios for use in the Mopani Veld. *African Journal of Range and Forage Science* 14: 62-67.

Dekker B., Van Rooyen N. & Bothma J. du. P. 1996. Habitat partitioning by ungulates on a game ranch in the Mopani veld. *South African Journal of Wildlife Research* 26: 117-122.

Demment M.W. & van Soest P.J. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *American Naturalist* 125: 641-672.

Dontsova K. & Norton L.D. 2001. Effects of exchangeable Ca:Mg ratio on soil clay flocculation, infiltration and erosion. In: Stott D.E., Mohtar R.H. & Steinhardt G.C. (eds.). *Sustaining the Global Farm*. Purdue University, West Lafayette. pp. 580-585.

Dörgeloh W.G. 2001. Relationship between distribution of kudu and woody plant structure. *South African Journal of Wildlife Research* 31: 85-91.

Dormaar J.F., Smoliak S. & Willms W.D. 1990. Distribution of nitrogen fractions in grazed and ungrazed fescue grassland Ah horizons. *Journal of Range Management* 43: 6-9.

Draper N. & Smith H. 1981. *Applied regression analysis*. Wiley & Sons, New York.

Drawe D.L. 1999. Vegetation changes on the Welder Wildlife Refuge, Texas. In: *Proceedings of the VI International Rangeland Congress*. VI International Rangeland Congress Inc., Australia. pp. 256-258.

Du Plessis S.S. 1968. *Ecology of blesbok (Damaliscus dorcas phillipsi) on the Van Riebeeck Nature Reserve, Pretoria, with special reference to productivity*. Ph.D thesis, University of Pretoria, Pretoria, South Africa.

Du Plessis S.S. 1972. Ecology of blesbok with special reference to productivity. *Wildlife Monographs* 30.

Du Preez C.C. & Snyman H.A. 1993. Organic matter content of a soil in a semi-arid climate with three long-standing veld conditions. *African Journal of Range and Forage Science* 10: 108-110.

Du Toit P.V.C. 1995. The grazing index method of range condition assessment. *African Journal of Range and Forest Science* 12: 61-67.

Du Toit M.E., Du Preez C.C., Hensley M. & Bennie A.T.P. 1994. Effek van bewerking op die organiese materiaalinhoud van geselekteerde droëlandgronde in Suid-Afrika. *South African Journal of Plant and Soil* 11: 71-79.

Dye P.J. & Spear P.T. 1982. The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. *Zimbabwean Journal of Agricultural Research* 20: 103-118.

Dyksterhuis E.J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2: 104-115.

Dyne G.M., Brockington N.R., Szocs Z., Duek J. & Ribic C.A. 1980. Large herbivore subsystem. In: Breymeyer A.I. & Van Dyne G.M. (eds.). *Grassland systems analysis and man*. pp. 269-537.

Eckhardt H.C., Van Rooyen N. & Bredenkamp G.J. 1993. Use of Braun-Blanquet data for the assessment of veld condition and grazing capacity in grassland. *African Journal of Range and Forest Science* 10: 41-46.

Elberse W.T. & Berendse F. 1993. A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. *Functional Ecology* 7: 223-229.

Ellis J. 1995. Climate variability and complex ecosystem dynamics: Implications for pastoral development. In: Scoones I. (ed.). *Living with Uncertainty: new directions in pastoral development in Africa*. Intermediate Technology Publications, London, UK.

Eloff T. 1996. Farming with a future. *SA Game & Hunt* 2: 21-24.

Eltringham S.K. 1974. Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. *Journal of Applied Ecology* 11: 855-865.

Emmans G.C. 1991. Diet selection by animals: Theory and experimental design. *Proceedings of Nutritional Society* 50: 59-64.

Epstein H.E., Lauenroth W.K. & Burke I.C. 1997. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* 78: 2628-2631.

Esler K.J. & Rundel P.W. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: The succulent Karoo and Mojave Desert ecosystems. *Plant Ecology* 142: 97-104.

Estes R.D. 1969. Territorial behaviour of the wildebeest (*Connochaetes taurinus* Burchell 1823). *Zoologische Tier-psychologische* 26: 284-370.

Everett P.S., Perrin M.R. & Rowe-Rowe D.T. 1991. Responses by oribi to different range management practices in Natal. *South African Journal of Wildlife Research* 21: 114-118.

Fahrig L. 2002. Effect of habitat fragmentation of the extinction threshold: A synthesis. *Ecological Applications* 12: 346-353.

Fairburn J.W. & Suwal P.N. 1961. The alkaloids of hemlock (*Conium maculatum* L) II-evidence for a rapid turnover of the major alkaloids. *Phytochemistry* 1: 38-46.

Falkena H. & Van Hoven W. 2003. *Game ranch profitability in South Africa (3rd edition).* ABSA Economic Reasearch, South Africa.

Feller C., Fritsch E., Ross R. & Valentin C. 1991. Effects of the texture on the storage and dynamics of organic matter in some low activity clay soils (West Africa, particularly). *Cah. ORSTOM, Serie Pedologia* 26: 25-36.

Fernandez-Illescas C.P., Porporato A., Liao F. & Rodiguez-Iturbe L. 2001. The ecohydrological role of soil texture in a water-limited ecosystem. *Water Resources Research* 37: 2863-2872.

Ferraro D.O. & Oesterheld M. 2002. Effect of defoliation on grass growth. A quantitative review. *Oikos* 98: 125-133.

Field C.R. 1976. Palatability factors and nutritive values of the food of buffaloes (*Syncerus caffer*) in Uganda. *East African Wildlife Journal* 14: 181-201.

Foran B.D. 1976. *The development and testing of methods for assessing the condition of three grassveld types in Natal*. M.Sc.Agric thesis, University of Natal, Pietermaritzburg.

Foran B.D., Tainton N.M. & Booysen P. de V. 1987. The development of a method for assessing veld condition in three grassveld types in Natal. *Proceedings of the Grassland Society of Southern Africa* 15: 37-42.

Forbes J.M. 1986. *Voluntary food intake and diet selection in farm animals*. Butterworths, London.

Forbes J.M. 1995. *Voluntary food intake and diet selection in farm animals*. CAB International, Wallingford, UK.

Forbes T.D.A., Smith E.M., Razor R.B., Dougherty C.J., Allen V.G., Erlinger L.L., Moore J.E. & Rouquette Jr. F.M. 1985. The plant-animal interface. In: Watson

V.H. & Wells C.M. Jr. (eds.). *Simulation of forage and beef production in the Southern Region*. USDA – Southern Cooperative Series Bulletin 308. pp. 95-116.

Foster H.L. 1981. The basic factors which determine inherent soil fertility in Uganda. *Journal of Soil Fertility* 32: 149-190.

Foth H.D. & Ellis B.G. 1997. *Soil fertility (2nd edition).* CRC Press LLC, Florida, USA.

Fouché 1984. *Ondersoek na die gebruik van die Putu II simulasie model en Palmerindeks vir die karakterisering van droogtetoestande*. M.Sc(Agric) thesis, University of the Orange Free State, Bloemfontein.

Fourie J.H. & Du Toit P.F. 1983. Weidingstudies in die Vrystaatstreek: Die bepaling van veldtoestand. *Glen Agriculture* 12: 5-9

Fourie J.H., Engels E.A.N. & De Bruyn H.L.H.C. 1986. The influence of stocking rate and grazing system on the crude protein content and digestibility of *Tarcoanthus* veld in the Northern Cape. *Journal of the Grassland Society of South Africa* 3: 62-69.

Frank D.A., McNaughton S.J. & Tracy B.F. 1998. The ecology of the earth's grazing ecosystems. *BioScience* 48: 513-521.

Freeland W.J. & Janzen D.H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *American Naturalist* 108: 269-289.

French M.H. 1957. Nutritional value of tropical grasses and fodders. *Herbaceous Abstracts* 27: 1-9.

French N.R. 1985. Herbivore overlap and competition in Kenya rangelands. *African Journal of Ecology* 23: 259-268.

Frenkel G.S. 1969. The raison d'etre of secondary plant substances. *Science* 1929: 1466-1470.

Frenkel H., Goertzen J.O. & Rhoades J.D. 1978. Effect of clay type and content, exchangeable sodium percentage, and electrolyte concentration on clay dispersion and soil hydraulic conductivity. *Journal of the Soil Science Society of America* 142: 32-39.

Friedel M.M. 1991. Range condition assessment and the concept of thresholds: A viewpoint. *Journal of Range Management* 44: 422-426.

Fritz H. 1997. Low ungulate biomass in west African savannas: Primary production or missing megaherbivores or large predator species? *Ecography* 20: 417-421.

Fritz H., Duncan P., Gordon I.J. 2002. Megaherbivores influence trophic guild structure in African ungulate communities. *Oecologia* 131: 620-625.

Frost P., Medina E., Menaut J.C., Solbrig O., Swift M. & Walker B. 1996. Responses of savannas to stress and disturbance. *Biology International* 10: 38-41.

Fryxell J.M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138: 478-498.

F.S.S.A. 2003. *Fertilizer Handbook (5th edition)*. Fertilizer Society of South Africa, Pretoria.

Furstenburg D. 2002a. "White-tailed Gnu", *Connochaetes gnou* (Zimmermann, 1780). *Game & Hunt* Vol 8/6 June 2002.

Furstenburg D. 2002b. Springbok *Antidorcas marsupialis* (Zimmermann, 1780). *Game & Hunt* Vol 8/5 May 2002.

Galston A.W., Davies P.J. & Satter R.L. 1980. *The life of the green plant* (3rd edition).

Prentice-Hall Inc., New Jersey.

Gammon D.M. & Roberts B.R. 1978. Patterns of defoliation during continuous and rotational grazing of the Matopos sandveld of Rhodesia. 3. Frequency of defoliation. *Rhodesian Journal of Agricultural Research* 16: 147-164.

Georgiadis N.J. & McNaughton S.J. 1990. Elemental and fiber contents of savanna grasses: Variation with grazing, soil type, season and species. *Journal of Applied Ecology* 27: 623-634.

Georgiadis N.J., Ruess R.W., McNaughton S.J. & Western D. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81: 316-322.

Giest V. 1974. On the relationship of social evolution and ecology in ungulates. *American Zoologist* 14: 205-220.

Gordon I.J. 1989. Vegetation community selection by ungulates on the Isle of Rhum. *Journal of Applied Ecology* 26: 35-51.

Gordon I.J. & Illius A.W. 1996. The nutritional ecology of African ruminants: A reinterpretation. *Journal of Animal Ecology* 65: 18-28.

Gouws A. 1995. Wild bestendig skaapboerdery. *Landbouweekblad* 915, 3 November.

GraphPad 1997. *GraphPad Instat®. Version 3.0.* GraphPad Software, Inc.

Gregorich E.G., Monreal C.M., Ellert B.H., Angers D.A. & Carter M.R. 1993. Evaluating changes in soil organic matter. In: Acton D.F. (ed.) *A program to assess and monitor soil quality in Canada*. Agriculture Canada, Ottawa.

Grobler J.H. 1983. Feeding habits of the Cape mountain zebra *Equus zebra zebra* Linn. 1758. *Koedoe* 26: 159-168.

Grossman D.H., Bourgeron P., Busch W.-D.N., Cleland D.T., Platts W., Ray. G. Robins C. & Roloff G. 1999. Principles of Ecological Classification. In: Szaro R.C., Johnson N.C., Sextion T. & Malk A.J. (eds.). *Ecological stewardship: a common reference for ecosystem management. Volume 2.* Elsevier Science, Oxford, UK. pp. 353-393.

Grossman D., Grunow J.O. & Theron G.K. 1980. Biomass cycles, accumulation rates and nutritional characteristics of grass layer plants in canopied and uncanopied subhabitats of *Burkea* savanna. *Proceedings of the Grassland Society of Southern Africa* 15: 141-161.

Grunow J.O. 1980. Feed and habitat preferences among some large herbivores on African veld. *Proceedings of the Grassland Society of Southern Africa* 15: 141-146.

Grunow J.O., Groenewald H.T. & Du Toit S.H.C. 1980. Above-ground dry matter dynamics of the grass layer of a South African tree savannah. *Journal of Applied Ecology* 68: 877-889.

Grunow J.O., Rabie J.W. & Grattarola L. 1977. Standing crop dry matter accumulation and quality patterns of certain subtropical grass species. *Proceedings of the Grassland Society of Southern Africa* 12: 37-44.

Hacker R.B., Hodgkinson K.C., Bean J. & Melville G.J. 1999. Response to intensity and duration of grazing in a semi-arid wooded grassland. In: *Proceedings of the VI International Rangeland Congress*. VI International Rangeland Congress, Australia. pp. 458-459.

Haila Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications* 12: 321-334.

Hamilton C.L. 1971. Food intake and temperature stress in the monkey. *Proceedings of the Society of Experimental Biology and Medicine* 136: 207-209.

Hamilton III E.W., McNaughton S.J. & Coleman J.S. 2001. Molecular, physiological, and growth responses to sodium stress in C_4 grasses from a soil salinity gradient in the Serengeti ecosystem. *American Journal of Botany* 88: 1258-1265.

Hanley T.A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35: 146-151.

Hanley T.A. & Hanley K.A. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangelands. *Journal of Range Management* 35: 152-158.

Hardy M.B. & Hurt C.R. 1989. An evaluation of veld condition assessment techniques in Highland Sourveld. *Journal of the Grassland Society of Southern Africa* 6: 51-58.

Hardy M.B., Hurt C.R. & Bosch O.J.H. 1999. Veld condition assessment - grassveld. In: Tainton N. (ed.). *Veld management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 195-207.

Hardy M.B. & Walker R.S. 1991. Determining sample size for assessing species composition in grassland. *Journal of the Grassland Society of Southern Africa* 8: 70-73.

Hardy N., Shainberg I., Gal M. & Keren R. 1983. The effect of water quality and storm sequence upon infiltration rate and crust formation. *Journal of Soil Science* 34: 665-676.

Hatch G.P. & Tainton N.M. 1990. A preliminary investigation of area-selective grazing in the Southern Tall Grassveld of Natal. *Journal of the Grassland Society of South Africa* 7: 238-242.

Heard C.A.H., Tainton N.M., Clayton J. & Hardy M.B. 1986. A comparison of five methods for assessing veld condition in Natal Midlands. *Journal of the Grassland Society of Southern Africa* 3: 70-76.

Heitkönig I.M.A. & Owen-Smith 1998. Foraging site selection by roan antelope. *African Journal of Ecology* 36: 57-70.

Hillel D. 2004. *Introduction to environmental soil physics*. Elsevier Academic Press, Amsterdam.

Hirst S.M. 1975. Ungulate-habitat relationships in a South African woodland/savanna. *Wildlife Monographs No. 44*, 60 pp.

Hixon M.A. 1982. Energy maximizers and time minimizers: Theory and reality. *American Naturalist* 119: 596-599.

Hobbs N.T., Baker D.L. & Gill R.B. 1983. Comparative nutritional ecology of montane ungulates during winter. *Journal of Wildlife Management* 47: 1-16.

Hobbs N.T., Schimel D.S., Owensby C.E. & Ojima D.S. 1991. Fire and grazing in the tall grass prairie: Contingent effects on nitrogen budgets. *Ecology* 72: 1374-1383.

Hodgson J. 1981. Variations in the surface characteristics of the sward and the short-term rate of herbage intake by calves and lambs. *Grass and Forage Science* 36: 49-57.

Hofmann R.R. 1973. The ruminant stomach. *East African Monographs in Biology* 2: 1-354.

Hofmann R.R. & Stewart D.R.M. 1972. Grazer or browser: A classification based on the stomach structure and feeding habits of east African ruminants. *Mammalia* 36: 226-240.

Hudson R.J. & Christofferson R.J. 1985. Maintenance metabolism. In: Hudson R.J. & White R.G. (eds.). *Bioenergetics of wild herbivores*. CRC Press, Florida. pp. 121-142.

Hudson R.H. & Nietfeld M.T. 1985. Effect of forage depletion on the feeding rate of wapiti. *Journal of Range Management* 38: 80-82.

Huenneke L.F., Hamburg S.P., Koide R., Mooney H.A. & Vitousek P.M. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478-491.

Huisman J. & Olff H. 1998. Competition and facilitation in multispecies plant-herbivore systems of productive environments. *Ecological Letters* 1: 25-29.

Hurt C.R. & Bosch O.J.H. 1991. A comparison of some range condition assessment techniques used in southern African grasslands. *Journal of the Grassland Society of Southern Africa* 8: 131-137.

Hurt C.R. & Hardy M.B. 1989. A weighted key species method for monitoring changes in species composition of Highland Sourveld. *Journal of the Grassland Society of Southern Africa* 6: 109-113.

Huston J.E. & Pinchak W.E. 1991. Range Animal Nutrition. In: Heitschmidt R.K. & Stuth J.W. (eds.). *Grazing Management: An Ecological Perspective*. Timber Press, Portland, Oregon. pp. 27-64.

Illius A.W., Clark D.A. & Hodgson J. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. *Journal of Animal Ecology* 61: 183-194.

Illius A.W. & Gordon I.J. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56: 989-999.

Illius A.W. & Gordon I.J. 1992. Modelling the nutritional ecology of ungulate herbivores: Evolution of body size and competitive interactions. *Oecologia* 89: 428-434.

Inglis J.M.1985. *Wildlife management and IBMS*. Texas Agricultural Experimental

Station Bulletin B-1493. College Station, USA.

Irby L.R. 1981. Mountain reedbuck activity patterns in the Loskop Dam Nature Reserve. *South African Journal of Wildlife Research* 11: 115-120.

Janis C.M. & Ehrhardt D. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnaeus Society* 92: 267-284.

Janse van Rensburg F.P. & Bosch O.J.H. 1990. Influence of habitat differences on the ecological grouping of grass species on a grazing gradient. *Journal of the Grassland Society of South Africa* 7: 11-15.

Jarman M.V. & Jarman P.J. 1973. Daily activity of impala. *East African Wildlife Journal* 11: 75-92.

Jarman P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.

Jeltsch F., Milton, S.J., Dean W.R.J. & van Rooyen N. 1997. Analysing shrub encroachment in the southern Kalahari: A grid-based modeling approach. *Journal of Applied Ecology* 34: 1497-1508.

Jenkins K.J. & Wright R.G. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. *Canadian Journal of Zoology* 65: 1397-1401.

Johnson K.G. & Strack R. 1989. Adaptive behavior of laboratory rats feeding in hot conditions. *Comparative Biochemistry and Physiology A - Physiology* 94: 69-72.

Johnson L.C. & Damman A.W.H. 1991. Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos* 61: 234-242.

Jones D.I.H. & Wilson A.D. 1987. Nutritive quality of forage. In: Hacker J.B. & Ternouth J.H. (eds.). *The nutrition of herbivores*. Academic Press, Australia. pp. 65-89.

Jones M.J. 1973. The organic matter content of the savanna soils of West Africa. *European Journal of Soil Science* 24: 42-53.

Joubert S.C.J. 2000. Dieregedrag. In: Bothma J. du. P. (ed). *Wildplaas bestuur (3rd edition)*. Van Schaik Publishers, Pretoria. pp. 152-158.

Kabigumila J. 1993. Feeding-habits of elephants in Ngorongoro crater, Tanzania. *African Journal of Ecology* 31: 156-164.

Kahurananga J. & Silkiluwasha F. 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania, in 1972 and recent trends. *African Journal of Ecology* 35: 179-185.

Kalemera M.C. 1987. Dry season diurnal activity of elephant in Lake Manyara National Park, Tanzania. *African Journal of Ecology* 25: 255-263.

Kayser M. & Isselstein J. 2005. Potassium cycling and losses in grassland systems: a review. *Grass and Forage Science* 60: 213-224.

Kelley W.P. 1962. Sodium carbonate and adsorbed sodium in semiarid soils. *Soil Science* 94: 1-5.

Kenny P.A. & Black J.L. 1984. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Australian Journal of Agricultural Research* 35: 551-563.

Kettlitz W.K. 1962. The blesbok (*Damaliscus dorcas phillipsi*) with special reference to the herd in the Percy Fyfe Nature Reserve. *Fauna & Flora* 18: 36-46.

Kirkman K. & Carvalho P.C.F. 2003. Management interventions to overcome seasonal quantity and quality deficits of natural rangelands. In: Palmer, A.R. (org.). *Rangelands in the New Millenium*. Proceedings of the VII International Rangeland Congress, Durban. pp. 1289-1297.

Kiss A. 2004. Is community-based ecotourism a good use of biodiversity conservation funds? *Trends in Ecology and Evolution* 19: 232-237.

Kleiber M. 1961. *The fire of life: An introduction to animal energetics*. John Wiley & Sons, New York.

Klein D.R. & Fairall N. 1986. Comparative foraging behaviour and associated energetics of impala and blesbok. *Journal of Applied Ecology* 23: 489-502.

Kotlier N.B. & Wiens J.D. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.

Krebs J.R. & Davies J.B. 1978. *Behavioral ecology: An evolutionary approach*. Sinauer Associates Inc., Sunderland, Massachusetts.

Laca E.A., Distel R.A., Griggs T.C. & Demment M.W. 1994. Effects of canopy structure on patch depression by grazers. *Ecology* 75: 706-716.

Langvatn R. & Hanley T.A. 1993. Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia* 95: 164-170.

Lavado R.S., Sierra J.O. & Hashimoto P.N. 1996. Impact of grazing on soil nutrients in a *Pampean* grassland. *Journal of Range Management* 49: 452-457.

Laws R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1-15.

Ledgard S.F., Steele K.W. & Saunders W.H.M. 1982. Effects of cow urine and its major constituents on pasture properties. *New Zealand Journal of Agricultural Research* 25: 61-68.

Le Houérou H.N. 1984. Rain use efficiency: A unifying concept in arid-land ecology. *Journal of Arid Environments* 7: 213-247.

Leuthold B.M. & Leuthold W. 1978. Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. *East African Wildlife Journal* 16: 231-243.

Leuthold W. 1977. *African ungulates: A comparative review of their ethology and behavioural ecology*. Springer-Verlag, Berlin.

Levin D.A. 1976. The chemical defenses of plants to pathogens and herbivores. *Annual Review of Ecological Systems* 7: 121-159.

Levy G.J., Rosenthal A., Torchitzky J., Shainberg I & Cehn Y. 1999. Soil hydraulic conductivity changes caused by irrigation with reclaimed waste waters. *Journal of Environmental Quality* 28: 1658-1664.

Lewis J.G. 1977. Game domestication for animal production in Kenya: Activity patterns of eland, oryx, buffalo and zebu cattle. *Journal of Agricultural Science* 89: 551-563.

Loide V. 2004. About the effect of the contents and ratios of soil's available calcium, potassium and magnesium in liming of acid soils. *Agronomy Research* 2: 71-82.

Louw G.N., Steenkamp C.W.P. & Steenkamp E.L. 1967. Die verwantskap tussen die eterekstrak inhoud van Karoo bossies en hul smaaklikheid vir skape. *South African Journal for Agricultural Science* 10: 867-873.

Low A.B. & Rebelo A.T.G. 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria. 83 pp.

Low W.A., Tweedie R.L., Edwards C.B.H., Hodder R.M., Malafant K.W.J. & Cunnigham R.B. 1981. The influence of environment on daily maintenance behavior of free-ranging Shorthorn cows in central Australia. I. General introduction and descriptive analysis of day-long activities. *Applied Animal Ethol*ogy 7: 11-26.

Ludlow M.M. 1976. Ecophysiology of C_4 grasses. In: Lange O.L., Kappen L. & Schulze E.D. (eds.). *Water and plant life: problems and modern approaches*. Ecological Studies No. 19. Springer Verlag, Berlin. pp. 364-386.

Lütge B.U., Hardy M.B. & Hatch G.P. 1996. Plant and sward response to patch grazing in the Highland Sourveld. *African Journal of Range and Forage Science* 13: 94-99.

Magdoff F. 1992. *Building soils for better crops: Organic matter management*. University of Nebraska Press, Lincoln. 176 pp.

Magurran A. (1988). *Ecological diversity and its measurement*. Chapman & Hall, London.

Malavolta E. 1985. Potassium status of tropical and subtropical region soils. In: Munson R.D. (ed.) *Potassium in agriculture*. Madison, Wis.: American Society of Agronomy, USA. pp. 163-200.

Maloney S.K., Moss G., Cartmell T. & Mitchell D. 2005. Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *Journal of Comparative Physiology A* 191: 1055-1064.

Manley J.F., Schuman G.E., Reeder J.D. & Hart R.H. 1995. Rangeland soil carbon and nitrogen responses to grazing. *Journal of Soil and Water Conservation* 50: 294-298.

Marten G.C. 1978. The animal-plant complex in forage palatability phenomena. *Journal* *of Animal Science* 46: 1470-1477.

Martens J.C., Danckwerts J.E. & Zacharias P.J.K. 1996. Species responses to grazing in the Smaldeel area of the Eastern Cape. *African Journal of Range and Forage Science* 13: 29-36.

Matson P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia* 85: 241-246.

Mbatha K.R. & Ward D.M. 2006. Determining spatial and temporal variability in quantity and quality of vegetation for estimating the predictable sustainable stocking rate in the semi-arid savanna. *41st Annual Congress of the Grassland Society of South Africa, Bela Bela, Limpopo Province, South Africa.* p. 55.

McDonald P., Edwards R.A., Greenhalgh J.F.D. & Morgan C.A. 2002. *Animal Nutrition* (6th edition). Pearson Prentice Hall, Gosport, Britain.

McGarigal K. & Cushman S.A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12: 335-345.

McIntyre S. & Tongway D. 2005. Grassland structure in native pastures: links to soil surface condition. *Ecological Management and Restoration* 6: 43-50.

McKay A.D. & Frandsen P.E. 1969. Chemical and floristic components of the diet of Zebu cattle (*Bos indicus*) in browse and grass range pastures in a semi-arid upland area of Kenya. 1. Crude protein. *Tropical Agriculture, Trinidad* 46: 279-292.

McNaughton S.J. 1976. Serengeti migratory wildebeest: Facilitation of energy flow by grazing. *Science* 1991: 92-94.

McNaughton S.J. 1979. Grazing as an optimization process: Grass-Ungulate relationships in the Serengeti. *American Naturalist* 113: 691-703.

McNaughton S.J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40: 329-336.

McNaughton S.J. 1984. Grazing lawns: Animals in herds, plant form, and co-evolution. *American Naturalist* 124: 863-886.

McNaughton S.J. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* 55: 259-294.

McNaughton S.J. 1987. Adaptation of herbivores to seasonal changes in nutrient supply. In: Hacker J.B. & Ternought J.H. (eds.). *The nutrition of herbivores*. Academic Press, Sydney, Australia. pp. 391-408.

McNaughton S.J. & Chapin F.S. III 1985. Effects of phosphorus nutrition and defoliation of C_4 graminoids from the Serengeti plains. *Ecology* 66: 1617-1629.

McNaughton S.J., Ruess R.W. & Seagle S.W. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* 38: 794-800.

Mduma S.A.R., Sinclair A.R.E. & Hilbron R. 1999. Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology* 68: 1101-1122.

Meadows M.E. & Hoffman M.T. 2002. The nature, extent and causes of land degradation in South Africa: legacy of the past, lessons for the future? *Area* 34: 428-437.

Meissner H.H. 1976. A note on the energy requirements of young growing blesbok. *South African Journal of Wildlife Research* 6: 51-54.

Meissner H.H. 1982. Theory and application of a method to calculate forage intake of wild southern African ungulates for purposes of estimating carrying capacity. *South African Journal of Wildlife Research* 12: 41-47.

Meissner H.H. & Paulsmeier D.V. 1995. Plant compositional constituents affecting between-plant and animal species prediction of forage intake. *Journal of Animal Science* 73: 2447-2457.

Meissner H.H., Pieterse E. & Potgieter J.H.J. 1996. Seasonal food selection and intake by male impala *Aepyceros melampus* in two habitats. *South African Journal of Wildlife Research* 26: 56-63.

Meissner H.H., Zacharias P.J.K. & O′Reagain P.J. 1999. Forage quality (feed value). In: Tainton N.M. (ed.). *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 139-168.

Melillo J.M., Aber J.D. & Muratore J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.

Melton D.A. 1987. Habitat selection and resource scarcity. *South African Journal of Science* 83: 646-651.

Melton D.A. & Heard D. 1991. Ungulate behaviour and habitat quality: Insights from Africa and the Artic. *Ongules/Ungulates 91 - Proceedings of the International Symposium*. pp. 185-188.

Mentis M.T. 1980. The effect of animal size and adaptation on defoliation, selective defoliation, animal production and veld condition. *Proceedings of the Grassland Society of Southern Africa* 15: 147-151.

Mentis M.T. 1981. Acceptability and palatability. In: Tainton N.M. (ed.). *Veld and pasture management in South Africa*. Shuter & Shooter and University of Natal Press, Pietermartizburg. pp. 186-191.

Mentis M.T. & Duke R.R. 1976. Carrying capacity of natural veld in Natal for large wild herbivores. *South African Journal of Wildlife Research* 6: 65-74.

Microsoft 2003. *Microsoft Excel Software, Version 2003.* Microsoft Corporation.

Milchunas D.G. & Lauenroth W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327-366.

Miller R.W. & Donahue R.L. 1995. *Soils in our environment (7th edition).* Prudence Hall, Englewood Cliffs, New York.

Miller R.W., Donahue R.L. & Miller J.U. 1990. *Soils: An introduction to soils and plant growth (6th edition).* Prentice-Hall International, New Jersey, USA.

Miller R.W. & Gardiner D.T. 1998. *Soils in our environment (8th edition).* Prentice-Hall Inc., New Jersey, USA.

Mills A.J. & Fey M.V. 2002. Farming with goats alters vegetation and leads to major transformations in soil quality in Xeric Succulent Thicket of the Eastern Cape, South Africa. In: *Proceedings VIII International Congress of Ecology, Seoul*.

Mills A.J. & Fey M.V. 2003. Declining soil quality in South Africa: Effects of land use on soil organic matter and surface crusting. *South African Journal of Science* 99: 429-436.

Milne J.A. 1991. Diet selection by grazing animals. *Proceedings of the Nutritional Society* 50: 77-85.

Minson D.J. 1971. The digestibility and voluntary intake of six varieties of *Panicum*. *Australian Journal of Experimental Agriculture and Animal Husbandry* 11: 18-25.

Minson D.J. 1990. *Forage in Ruminant Nutrition*. Academic Press, San Diego, USA.

Mitchell B.B., Staines B.W. & Welch D. 1977. *Ecology of red deer, a research review* *relevant to their management in Scotland.* Institute of Terrestrial Ecology. 74pp.

Moffett R. 1997. *Grasses of the Eastern Free State*. Uniqwa, University of the North, Qwa-Qwa.

Moleele N.M. & Perkins J.S. 1998. Encroaching woody plant species and boreholes: Is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana. *Journal of Arid Environments* 40: 245-253.

Moore A. 1989. *Die ekologie en ekofisiologie van Rhigozum trichotonum (Driedoring)*. Ph.D thesis, University of Port Elizabeth, Port Elizabeth.

Moore A. & Odendaal A. 1987. Die ekonomiese implikasies van bosverdigting en bosbeheer soos van toepassing op ‘n speenkalfproduksiestelsel in die doringbosveld van die Molopogebied . *Journal of the Grassland Society of South Africa* 4: 139-142.

Moore A., Van Niekerk J.P., Knight I.W. & Wessels H. 1985. The effect of Tebuthiuron on the vegetation of the thorn bushveld of the northern Cape: A preliminary report. *Journal of the Grassland Society of South Africa* 2: 7-10.

Moretto A.S. & Distel R.A. 2002. Soil nitrogen availability under grasses of different palatability in a temperate semi-arid rangeland of central Argentina. *Austral Ecology* 27: 509-514.

Morris C.D., Tainton N.M. & Hardy M.B. 1992. Plant species dynamics in the Southern Tall Grassveld under grazing, resting and fire. *Journal of the Grassland Society of Southern Africa* 9: 90-95.

Morse D.H. 1974. Niche breadth as a function of social dominance. *American Naturalist* 108: 818-830.

Mosley J.C. 1999. Influence of social dominance on habitat selection by free-ranging ungulates. In: Launchbaugh K.L., Sanders K.D. & Mosley J.C. (eds.). *Grazing behavior of livestock and wildlife*. Idaho Forest, Wildlife & Range Experimental Station Bulletin No. 7, University of Idaho, Moscow. pp. 109-118.

Mostert J.W.C., Roberts B.R., Heslinga C.F. & Coetzee P.G.F. 1971. *Veldbestuur in die O.V.S.-streek*. Bulletin of the Department of Agricultural Technology Services of South Africa No. 391.

Mott J.J. 1985. Mosaic grazing – animal selectivity in tropical savannas of northern Australia. *Proceedings of the 15th International Grassland Congress, Kyoto, Japan*. pp. 1129-1130.

Mowat D.N., Fulkerson R.S., Tossell W.E. & Winch I.E. 1965. The *in vitro* digestibility and protein content of leaf and stem portions of forages. *Canadian Journal of Plant Science* 45: 321-331.

Moyo C.S. & Campbell B.M. 1998. Grass species composition, yield and quality under and outside tree crowns in a semi-arid rangeland in southwestern Zimbabwe. *African Journal of Range and Forage Science* 15: 23-24.

Murray M.G. & Illius A.W. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos* 89: 501-508.

Myklestad A. 2004. Soil, site and management components of variation in species composition of agricultural grasslands in western Norway. *Grass and Forage Science* 59: 136-143.

Mysterud A. 1998. The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113: 442-446.

Nagy K.A. 1994. Seasonal water, energy and food use by free-living, arid habitat mammals. *Australian Journal of Zoology* 42: 55-63.

Nagy K.A. & Knight M.H. 1994. Energy, water and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *Journal of Mammalogy* 75: 860-872.

Nash M.S., Whitford W.G., de Soyza A. & van Zee J. 1999. Livestock activity and Chihuahuan desert annual plant communities: Boundary analysis of disturbance gradients. *Ecological Applications* 9: 814-823.

Norman M.J. & Green J.O. 1958. Local influence of cattle dung and urine upon yield and botanical composition of a permanent pasture. *Journal of the British Grassland Society* 13: 39-45.

Novellie P.A. 1975. *Comparative social behaviour of springbok and blesbok on the Jack Scott Nature Reserve, Transvaal*. M.Sc thesis, University of Pretoria, Pretoria, South Africa.

Novellie P.A. 1978. Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. *South African Journal of Wildlife Research* 8: 137-144.

Novellie P.A. 1989. *Management plan for the Mountain Zebra National Park*. Unpublished report, Mountain Zebra National Park, South Africa.

Novellie P.A 1990. Habitat use by indigenous grazing ungulates in relation to sward structure and veld condition. *Journal of Grassland Society South Africa* 7: 16-23.

Noy-Meir I., Gutman M. &. Kaplan Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77: 290-310.

Noy-Meir I. & Walker B.H. 1986. Stability and resilience in rangelands. In: Joss P.J., Lynch P.W. & Williams 0.B. (eds.). *Rangelands: A resource under siege.* Australian Academic Science, Canberra. pp. 21-25.

O′Connor T.G. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology* 31: 155-171.

O’Connor T.G. 1995. Transformation of savanna grassland by drought and grazing. *African Journal of Range and Forage Science* 12: 53-60.

O′Connor T.G. & Bredenkamp G.J. 1997. Grassland. In: Cowling R.M., Richardson D.M. & Pierce S.M. (eds.). *Vegetation of southern Africa*. Cambridge University Press, Cambridge.

O′Connor T.G. & Roux P.W. 1995. Vegetation changes (1949-71) in semi-arid, grassy dwarf shrubland in the Karoo, South Africa: Influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* 32: 612-626.

Oesterheld M. & McNaughton S.J. 2000. Herbivory in terrestrial ecosystems. In: Sala O.E., Jackson R.B., Mooney H.A. & Howarth R. (eds.) *Methods in ecosystem science*. Springer-Verlag, New York. pp. 151-157.

Olivier R.C.D. & Laurie W.A. 1974. Habitat utilization of the hippopotamus in the Mara River. *East African Wildlife Journal* 12: 249-272.

Olubajo F.O, Van Soest P.J. & Oyenuga V.A. 1974. Comparison and digestibility of four tropical grasses grown in Nigeria. *Journal of Animal Science* 38: 149-153.

O' Reagain P.J. 1993. Plant structure and the acceptability of different grasses to sheep. *Journal of Range Management* 46: 232-236.

O’Reagain P.J. 1994. *The effect of sward structure and species composition on dietary quality and intake in cattle and sheep grazing the Dohne Sourveld*. Ph.D thesis, University of the Witwatersrand, Johannesburg.

O' Reagain P.J. & Mentis M.T. 1989. Sequence and process of species selection by cattle in relation to optimal foraging theory on an old land in the Natal sour sandveld. *Journal of the Grassland Society of South Africa* 6: 71-76.

O'Reagain P.J. & Schwartz J. 1995. Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. In: *Proceedings of the International Symposium on the Nutrition of Herbivores, 4, 1995, Paris: INRA*. pp. 407-423.

Ottichilo W.K. De Leeuw J., Skidmore A.K., Prins H.H.T. & Said M.Y. 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology* 38: 202-216.

Owen-Smith N. 1977. On territoriality in ungulates and an evolutionary model. *Quarterly Review of Biology* 52: 1-38.

Owen-Smith N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. *South African Journal of Wildlife Research* 9: 102-110.

Owen-Smith N. 1985. Niche separation among African ungulates. In: Vrba E.S. (ed.) *Species and Speciation*. Transvaal Museum Monograph No.4, Transvaal Museum, Pretoria.

Owen-Smith N. 1988. *Megaherbivores: The influence of very large body size on Ecology*. Cambridge University Press, Cambridge.

Owen-Smith N. 1989. Morphological factors and their consequences for resource partitioning among African savanna ungulates: A simulation modeling approach. In: Morris D.W., Abramsky Z., Fox B.J. & Willig M.R. (eds.). *Patterns and structure of mammalian communities*. Texas Tech University Press, Texas. pp. 155-165.

Owen-Smith N. 1992. Grazers and browsers: Ecological and social contrasts among African ruminants. In: Spitz F., Janeau G., Gonzales G. & Aulagnier S. (eds.)

Ongulés/Ungulates 91. S.F.E.P.M.-I.R.G.M., Paris, Toulouse. pp. 175-181.

Owen-Smith N. 1993. Woody Plants, browsers and tannins in southern African savannas. *South African Journal of Science* 39: 505-510.

Owen-Smith N. 1994. Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. *Ecology* 75: 1050-1062.

Owen-Smith N. 1999. The animal factor in veld management. In: Tainton N.M. (ed.) *Veld Management in South Africa*, University of Natal Press, Pietermaritzburg. pp. 117-138.

Owen-Smith N. & Novellie P. 1982. What should a clever ungulate eat? *American Naturalist* 119: 151-178.

Owen-Smith N. & Cooper S.M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology* 68: 319-331.

Owen-Smith N. & Cooper S.M. 1988. Plant palatability assessment and its implications for plant-herbivore relations. *Journal of the Grassland Society of southern Africa* 5: 72-75.

Owen-Smith N. & Novellie P. 1982. What should a clever ungulate eat? *American Naturalist* 119: 151-178.

Page B.R. & Walker B.H. 1978. Feeding niches of four large herbivores in the Hluhluwe Game Reserve, Natal. *Proceedings of the Grassland Society of southern Africa* 13: 117-122.

Pagot J. 1992. *Animal Production in the Tropics and Subtropics*. MacMillan, London, UK.

Pal Y., Wong T. & Gilkes R. 1999. The forms of potassium and potassium adsorption in some virgin soils from south western Australia. *Australian Journal of Soil Research* 37: 695-709.

Parker I.S.C. 1983. The Tsavo story: An ecological case history. In: Owen-Smith N (ed.). *Mammals in African conservation areas*. Haun, Pretoria. pp. 37-50.

Pastor J., Aber J.D., McClaugherty C.A. & Melillo J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.

Pastor J. & Post W.M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycle. *Biogeochemistry* 2: 3-27.

Pearcy R.W., Bjorkman O.P., Caldwell M.M., Keeley J.E., Monson R.K. & Strain B.R. 1987. Carbon gained by plants in natural environments. *Biosciences* 37: 21-29.

Peel M.J.S. & Smith D.C. 1994. Determinants of herbaceous plant species composition on a number of ranches in the North-Western Transvaal. *Wildlife Ranching a celebration of diversity, Proceedings of the third international wildlife ranching symposium (1992)*. pp. 131-135.

Petrides G.A. 1975. Principal foods versus preferred foods and their relation to stocking rate and range condition. *Biological Conservation* 7: 161-169.

Pettifer H.L. & Stumpf R.H. 1981. An approach to the calculation of habitat preference data: Impala on Loskop Dam Nature Reserve. *South African Journal of Wildlife Research* 11: 5-13.

Pienaar U. du V. 1974. Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 7: 185-195.

Pieterse P.A. & Grunow J.O. 1985. Produksie en kwaliteit van ‘n aantal grasspesies in die *Combretum*-veld van Noord-Transvaal. *Joernaal van die Weidingsvereniging* *van Suid-Afrika* 2: 26-30.

Pietersen L.M., Meissner H.H. & Pietersen E.W. 1993. Food selection and intake by male impalas in the Timbavati area. *South African Journal of Wildlife Research* 23: 6-11.

Poppitt S.D., Speakman J.R. & Racey P.A. 1994. Energetics of reproduction in the lesser hedgehog tenrec, *Echinops telfairi* (Martin). *Physiological Zoology* 67: 976-994.

Prache S., Gordon I.J. & Rook A.J. 1998. Foraging behaviour and diet selection in domestic herbivores. *Annales de Zootechnie* 47: 335-345.

Prins H.H.T. & Olff H. 1998. Species richness of African grazer assemblages: Towards a functional explanation. In: Prins D., Prins H.H.T. & Brown N.D. (eds.). *Dynamics of tropical communities*. Blackwell Publishers, Oxford. pp. 449-490.

Provenza F.D. & Balph D.F. 1987. Diet learning by domestic ruminants: Theory evidence and practical implications. *Applied Animal Behavior Science* 18: 211-232.

Pyke G.H., Pulliam H.R. & Charnov E.C. 1977. Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 55: 137-154.

Redfern J.V., Grant R., Biggs G. & Getz W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84: 2092-2107.

Reid R.S., Thornton P.K. & Kruska R.L. 2004. Fragmentation and loss of habitat for pastoral people and wildlife in East Africa: concepts and issues. *African Journal of Range and Forage Science* 21: 171-181.

Renecker L.A. & Valdez R. 1994. The wildlife ranching symposium: History, Structure, Achievements, Goals, and Implications for wildlife management. In: Van Hoven

W., Ebedes H. & Conroy A. (eds.). *Wildlife Ranching a celebration of diversity - Proceedings of the third international wildlife ranching symposium 1992*. pp. 27-32.

Renvoize S.A., Cope T.A., Cook F.E.M., Clayton W.D. & Wickens G.E. 1992. Distribution and utilisation of grasses in arid and semi-arid regions. In: Chapman G.P. (ed.). *Desertified grasslands, their biology and management*. Academic Press, London. pp. 3-16.

Rhoades D.F. 1979. Evolution of plant chemical defense against herbivores. In: Rosenthal G.A. & Janzen D.H. (eds.). *Herbivores, their interaction with secondary plant metabolites*. Academic Press, New York. pp. 3-54.

Rhodes B.D. & Sharrow S.H. 1990. Effect of grazing by sheep on the quantity and quality of forage available to big game in Oregon's Coast Range. *Journal of Range Management* 43: 235-237.

Ring C.B., Nicholson R.A. & Launchbaugh J.L. 1985. Vegetational traits of patch grazed rangeland in west-central Kansas. *Journal of Range Management* 38: 51-55.

Roberts B.R. 1963. Ondersoek in die plantegroei van die Willem Pretorius Wildtuin. *Koedoe* 6: 137-166.

Roberts B.R. 1970. Assessment of veld condition and trend. *Proceedings of the Grassland Society of Southern Africa* 5: 137-139.

Roberts B.R. 1973. *Common grasses of the Orange Free State*. Nature Conservation Miscellaneous Publication No. 3, Provincial Administration, Bloemfontein. 127 pp.

Roberts B.R. & Scott J.D. 1968. The nutritive value, yield and botanical composition of irrigated pastures as influenced by nitrogen fertilization. *Proceedings of the*

Grassland Society of Southern Africa 3: 83-90.

Rogers P.J. & Blundell J.E. 1991. Mechanisms of diet selection: the translation of needs into behaviour. *Proceedings of the Nutritional Society* 50: 65-70.

Rogerson A. 1968. Energy utilisation by the eland and wildebeest. In: Crawford M.A. (ed.). *Comparative nutrition of wild animals - Symposium of the Zoological Society,* London 21:153-161.

Roos J.H., Rethman N.F.G. & Kotze G.D. 1973. Preliminary results on species selection by animals on sour grassland. *Proceedings of the Grassland Society of southern Africa* 8: 77-81.

Rosenzweig M.L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.

Rothauge A. 2000. New ecological perceptions of arid rangelands. *Agricola* 11: 49-56.

Rowe-Rowe D.T. 1983. Habitat preferences of five Drakensberg antelopes. *South African Journal of Wildlife Research* 13: 1-8.

Ruess R.W. & McNaughton S.J. 1984. Urea as a pro-motive coupler of plant–herbivore interactions. *Oecologia* 63: 331-337.

Ruess R.W. & McNaughton S.J. 1988. Ammonia volatilization and the effects of large grazing mammals on nutrient loss from East African grasslands. *Oecologia* 77: 382-386.

Rutherford M.C. & Westfall R.H. 1994. *Biomes of southern Africa: An objective categorization*. National Botanical Institute, Pretoria. pp. 4-50.

Ruyle G.B. & Dwyer D.D. 1985. Feeding stations of sheep as an indicator of diminished forage supply. *Journal of Animal Science* 61: 349-353.

Sala O.E., Parton W.J., Joyce L.A. & Lauenroth W.K. 1988. Primary production of the central grassland region of the United States. *Ecology* 69: 40-45.

Salter P.J. & Williams J.B. 1965. The influence of texture on the moisture characteristics of soils. I. A critical comparison of techniques for determining the available water capacity and moisture characteristic curve of a soil. *Journal of Soil Science* 16: 1-15.

SAS (1990) SAS/STAT User's Guide, version 6, (4th edition), volume 2. SAS Institute, Cary, N.C.

Savory A. 1988. *Holistic resource management*. Island Press, Covelo, California.

Scanlan J.C. & Burrows W.H. 1990. Woody over-story impact on herbaceous understory in *Eucalyptus* spp. communities in central Queensland. *Australian Journal of Ecology* 15: 191-197.

Schlesinger W.H., Raikes J.A., Hartley A.E. & Cross A.F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364-374.

Schlesinger W.H., Reynolds J.F., Cunningham G.L., Huenneke L.F., Jarrell W.M., Virginia R.A. & Whitford W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1047.

Schmidt-Nielsen K. 1997. *Animal physiology adaptation and environment (5th edition).* Cambridge University Press, United Kingdom.

Schmutz E.M., Holt G.A. & Michaels C.C. 1963. Grazed-class method of estimating forage utilization. *Journal of Range Management* 16: 54-60.

Schoener T.W. 1971. Theory of feeding strategies. *Annual Review of Ecological Systems* 2: 369-403.

Scholes R.J. 1991. The influence of soil fertility on the ecology of south African dry savannas. In: Werner P.A. (ed.). *Savanna ecology and management - Australian perspectives and intercontinental comparisons*. Blackwell Scientific Publications, London. pp. 71-76.

Schulte E.E. & Kelling K.A. 1993. *Soil calcium to magnesium ratios – Should you be concerned?* Manual A2986. Cooperative Extension Publications, University of Wisconsin. 4 pp.

Schwartz C.C. & Hobbs N.T. 1985. Forage and range evaluation. In: Hudson R.J. & White R.G. (eds.). *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA. pp. 25-51.

Scotcher J.S.B. 1979. A review of faecal analysis techniques for determining the diet of wild grazing herbivores. *Proceedings of the Grassland Society of South Africa* 14: 131-136.

Scott D. 1974. Description of relationships between plants and environment. In: Billings W.D. & Strain R.R. (eds.). *Vegetation and Environment. Handbook of Vegetation Science, part 6.* Junk, The Hague. pp. 49-69.

Scott J.T. 1974. Correlation of vegetation with environment: A test of the continuum and community-type hypotheses. In: Billings W.D. & Strain R.R. (eds.). *Vegetation and Environment. Handbook of Vegetation Science, part 6.* Junk, The Hague. pp. 89-109.

Scriven L. & Eloff T. 2003. Markets derived from nature tourism in South Africa and KwaZulu-Natal: a survey of the sale of live game. In: Aylward B. & Lutz E. (eds.). *Nature tourism, conservation, and development in KwaZulu-Natal, South Africa*. The International Bank for Reconstruction and Development / The World Bank, Washington DC. pp. 245-286.

Seagle S.W. & McNaughton S.J. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology* 7: 229-241.

Seagle S.W., McNaughton S.J. & Ruess R.W. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. *Ecology* 73: 1105-1123.

Senft R.L. 1989. Hierarchical foraging models: Effects of stocking and landscape composition on simulated resource use by cattle. *Ecological Modeling* 46: 283-303.

Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E. & Swift D.M. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37: 789-799.

Senft R.L., Rittenhouse L.R. & Woodmansee R.G. 1985. Factors influencing patterns of grazing behavior on shortgrass steppe. *Journal of Range Management* 38: 81-87.

Serneels S. & Lambin E.F. 2001. Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. *Journal of Biogeography* 28: 391-407.

Shackleton C.M. 1992. Area and species selection by wild ungulates in coastal sour grasslands of Mkambati Game Reserve, Transkei, southern Africa. *African Journal of Ecology* 30: 189-202.

Shackleton C.M. & M.T. Mentis 1992. Seasonal changes in nutrient content in three coastal grassland communities in Transkei. *Journal of the Grassland Society of Southern Africa* 9: 30-37.

Shainberg I. & Letey J. 1984. Response of soils to sodic and saline conditions. *Hilgardia* 61: 21-57

Shewmaker G.E., Mayland H.F., Rosenau R.C. & Asay K.H. 1989. Silica in C_3-grasses: Effects on forage quality and sheep preference. *Journal of Range Management* 42: 122-127.

Shipley L.A. 1999. Grazers and Browsers: How digestive morphology affects diet selection. In: Launchbaugh K.L., Sanders K.D. & Mosley J.C. (eds.). *Grazing behavior of livestock and wildlife*. University of Idaho, Moscow. pp. 20-27.

Short J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* 22: 435-447.

Sikora L.J. & Stott D.E. 1996. Soil organic carbon and nitrogen. In: Doran J.W. & Jones A.J. (eds.) *Methods for assessing soil quality*. Soil Society of America Inc., USA. pp. 157-167.

Sinclair A.R.E. 1983. The adaptations of African ungulates and their effects on community function. In: Bourlier F. (ed.). *Ecosystems of the World 13: Tropical Savannas*. Elsevier, Amsterdam. pp. 401-426.

Sinclair A.R.E. & Norton-Griffiths M. 1982. Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia* 53: 364-369.

Simons A.B. & Marten G.C. 1971. Relationship indole alkaloids to palatability of *Phalaris arundinacea*. *Agronomic Journal* 63: 915-919.

Skead C.J. 1958. Mammals of the Uitenhage and Cradock C.P. districts in recent times. *Koedoe* 1: 19-59.

Skinner J.D. 2005. *The mammals of the southern African sub-region (3rd edition).* Cambridge University Press, Cambridge.

Smit G. N. 1994. *The influence of intensity of tree thinning on Mopani veld.* Ph.D-thesis, University of Pretoria, Pretoria.

Smit G.N. 2003a. *Resource evaluation and game ranch management for sustainable game production and conservation*. Unpublished report, Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein. 5 pp.

Smit G.N. 2003b. *Critical periods and the seasonal growth cycle of grazing plants*. Unpublished report, Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein. 7 pp.

Smit G.N. (undated). *Calculation of grazing capacity and browse capacity for game species*. Unpublished report, Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein. 3 pp.

Smit G.N. & Rethman N.F.G. 1992. Inter-related floristic changes associates with different long-term grazing treatments in Sourish Mixed Bushveld. *Journal of the Grassland Society of Southern Africa* 9: 76-82.

Smith D. 1973. The nonstructural carbohydrates. In: Butler G.W. & Bailey R.W. (eds.). *Chemistry and Biochemistry of herbage*. Academic Press, London. pp. 106-151.

Smith E.L. 1989. Range condition and secondary succession: A critique. In: Lauenroth W.K. & Laycock W.A. (eds.). *Secondary succession and the evaluation of range condition*. Westview Press, Boulder, Colorado. pp. 103-141.

Smith J.L. & Doran J.W. 1996. Measurement and use of pH and electrical conductivity for soil quality analysis. In: Doran J.W. & Jones A.J. (eds.). *Methods for assessing soil quality*. Soil Science Society of America, Special Publication 49. Soil Science Society of America, Madison, Wisconsin.

Snyman H.A. 1988. Bepaling van waterverbruiksdoeltreffendheid van veld in die Sentrale Oranje-Vrystaat vanaf evapotranspirasiemetings. *Water South Africa*

14: 153-158.

Snyman H.A. 1993a. Streef na optimale veldtoestand en weidingkapasiteit. *Suid Afrikaanse Koöperasie* 9: 25-28.

Snyman H.A. 1993b. The effect of defoliation during wilting on the production of *Themeda triandra* and *Eragrostis lehmanniana* in semi-arid grassland. *African Journal of Range and Forage Science* 10: 113-117.

Snyman H.A. 1997. The influence of range condition on the hydrological characteristics in a semi-arid rangeland. In: Winnipeg M. (ed.). *XVIII International Grassland Congress*, Saskatoon, Saskatchewan, Canada. pp. 231-232.

Snyman H.A. 1998a. Dynamics and sustainable utilisation of rangeland ecosystems in arid and semi-arid climates of southern Africa. *Journal of Arid Environments* 39: 645-666.

Snyman H.A. 1998b. Short-term effects of soil water, defoliation and rangeland condition on productivity of a semi-arid rangeland in South Africa. *Journal of Arid Environments* 43: 47-62.

Snyman H.A. 1999. Quantification of the soil-water balance under different veld condition classes in a semi-arid climate. *African Journal of Range and Forage Science* 16: 108-117.

Snyman H.A. 2000. Soil-water utilisation and sustainability in a semi-arid grassland. *Water South Africa* 26: 333-341.

Snyman H.A. & Du Preez C.C. 2005. Rangeland degradation in a semi-arid South Africa – II: Influence on soil quality. *Journal of Arid Environments* 60: 483-507.

Snyman H.A. & Fouché H.J. 1993. Estimating seasonal herbage production of a semi-arid grassland based on veld condition rainfall, and evapotranspiration.

African Journal of Range and Forage Science 10: 21-24.

Spain A. 1990. Influence of environmental conditions and some soil chemical properties on the carbon and nitrogen contents of some tropical Australian rain-forest soils. *Australian Journal of Soil Sciences* 28: 825-839.

Spalinger D.E., Hanley T.A. & Robbins C.T. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology* 69: 1166-1175.

Sponheimer M., Lee-Thorp J.A., DeRuiter D.J., Smith J.M., Van der Merwe N.J., Reed K., Grant C.C., Ayliffe L.K., Robinson T.F., Heidelberger C. & Marcus W. 2003. Diets of southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy* 84: 471-479.

Squires V.R. 1982. Behavior of free-ranging livestock on native grasslands and shrublands. *Tropical Grasslands* 16: 161-170

Standard Bank AgriReview 2000. *The game industry: Delicately poised*. Standard Bank's May 2000 quarterly agricultural review states.

Stephens D.W. & Krebs J.R. 1986. *Foraging Theory*. Princeton University Press, New Jersey, USA.

Stockdale E.A., Shepherd M.A., Fortune S. & Cuttle S.P. 2002. Soil fertility in organic farming systems – fundamentally different? *Soil Use and Management* 18: 301-308.

Stoddart L.A. & Smith A.D. 1955. *Range management (2nd edition).* McGraw-Hill, New York.

Stoddart L.A., Smith A.D. & Box T.W. 1975. *Range management (3rd edition)*. McGraw-Hill Book Company, New York, New York.

Strahler A. & Strahler A. 1998. *Introducing physical geography (2nd edition)*. Von Hoffmann Press Inc., USA.

Stuart C.T. & Stuart M.D. 2000. *Field guide to the larger mammals of Africa*. Struik Publishers, Cape Town, South Africa.

Stuart-Hill G.C. & Mentis M.T. 1982. Coevolution of African grasses and large herbivores. *Proceedings of the Grassland Society of Southern Africa* 17: 122-128.

Stuth J.W. 1991. Foraging Behavior. In: Heitschmidt R.K. & Stuth J.W. (eds.). *Grazing Management: An ecological perspective*. Timber Press, Portland, Oregon. pp. 65-83.

Stuth J.W., Lyons R.K. & Kreuter U.P. 1993. Animal-plant interactions: Nutrient acquisition and use by ruminants. In: Powell J.M., Fernandez-Rivera S., Williams T.O. & Renard C. (eds.). *Proceedings: Livestock and sustainable Nutrient cycling in mixed farming systems of Sub-Saharan Africa Technical papers Vol. 2*. Addis Ababa, Ethiopia. pp. 63-82.

Stuth J.W. & Searcy S. 1987. A new electronic approach to monitoring ingestive behavior of cattle. In: *Proceedings of the Second International Symposium of Nutrition of Herbivores*. Brisbane, Australia. pp. 81-82.

Sullivan S. & Rohde R. 2002. On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography* 29: 1595-1618.

Swartz C.C. & Hobbs N.T. 1985. Forage and range evaluation. In: Hudson R.J. & White R.G. (eds.). *Bioenergetics of Wild Herbivores*. pp. 25-51.

Swenson M.J. 1977. Duke's physiology of domestic animals. In: Duke H.H. & Swenson M.J. (eds.). *Physiology of domestic animals (9th edition)*. Ithaca, Cornstock.

Tainton N.M. 1981. The ecology of the main grazing lands of South Africa. In: Tainton N.M. (ed.). *Veld and pasture management in South Africa*. Shuter and Shooter and University of Natal Press, Pietermaritzburg. pp. 25-56.

Tainton N.M. 1982. Veld evaluation and sweetveld observation. *Proceedings of the Beef and Game on Sweetveld Symposium*, October 1982, Hlabisa Soil Conservation Committee. pp. 24-30.

Tainton N.M. 1988. A consideration of veld condition assessment techniques for commercial livestock production in South Africa. *Journal of the Grassland Society of South Africa* 5: 76-79.

Tainton N.M. 1999. The ecology of the main grazing lands of South Africa, the grassland biome. In: Tanton N.M. (ed.). *Veld management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 25-33.

Tainton N.M., Edwards P.J. & Mentis M.T. 1980. A revised method for assessing veld condition. *Proceedings of the Grassland Society of Southern Africa* 15: 37-42.

Tainton N.M., Fourie J.H. & Vorster M. (undated). *Die bepaling van veldtoestande en weidingskapasiteit vir die doeleindes van hulpbronklassifikasie*. (Unpublished).

Tainton N.M. & Hardy M.B. 1999. Introduction to the concepts of development of vegetation. In: Tainton N.M (ed.). *Veld management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 1-22.

Tan K.H. 1994. *Environmental soil science*. Marcel Dekker Inc., New York.

Teague W.R. & Danckwerts J.E. 1989. The concept of vegetation change and veld condition. In: Danckwerts J.E. & Teague W.R. (eds.). *Veld management in the Eastern Cape*. Agriculture & Water Supply, Eastern Cape Region.

Teague W.R. & Smit G.N. 1992. Relations between woody and herbaceous components and the effect of bush-clearing in southern African savannas. *Journal of the Grassland Society of Southern Africa* 9: 60-71.

Ter Braak C.J.F. 1988. *Canoco – a FORTAN program for canonical community ordination by (partial) (deterended) (canonical) correspondence analysis, principal component analysis, and redundancy analysis (Version 2.1).* Technical report LWA-88-02. Agricultural Mathematics Group, Wageningen.

The Non-affiliated Soil Analyses Work Committee of 1990. Handbook of standard soil testing methods for advisory purposes. Soil Science Society of South Africa, Pretoria.

Theron E.P. & Booysen P. de V. 1966. Palatability in grasses. *Proceedings of the Grassland Society of southern Africa* 1: 111-120.

Tidmarsh C.E.M. & Havenga C.M. 1955. The wheel-point method of survey and measurement of semi-open grasslands and Karoo vegetation in South Africa. *Memoirs of the Botanical Survey of South Africa No. 29*.

Toft N.L., McNaughton S.J. & Georgiadis N.J. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an east African grass, *Eustachys paspaloides*. *Australian Journal of Plant Physiology* 14: 211-226

Tolsma D.J., Ernst W.H.O. & Verwey R.A. 1987. Nutrients in soil and vegetation around two artificial water points in Eastern Botswana. *Journal of Applied Ecology* 24: 991-1000.

Tolsma D.J., Ernst W.H.O., Verwey R.A. & Vooijs R. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *Journal of Ecology* 75: 755-770.

Torres-Contreras H. & Bozinovic F. 1997. Food selection in an herbivorous rodent: Balancing nutrition with thermoregulation. *Ecology* 78: 2230-2237.

Troeh F.R. & Thompson L.M. 1993. *Soils and soil fertility (5th edition)*. Oxford University Press, Oxford.

Trollope W.S.W. 1990. Veld management with specific reference to game ranching in the grassland and savanna areas of South Africa. *Koedoe* 33: 77-86.

Trollope W.S.W. 1999. Veld burning. In: Tainton N.M. (ed.). *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 217-245.

Trollope W.S.W. & Tainton N.M. 1986. Effect of fire intensity on the grass and bush components of the Eastern Cape Thornveld. *Journal of the Grassland Society of Southern Africa* 7: 52-61.

Trollope W.S.W., Trollope L.A. & Bosch O.J.H. 1990. Veld and pasture management terminology in southern Africa. *Journal of the Grassland Society of South Africa* 7: 52-61.

Underwood R. 1982. Vigilance behaviour in grazing African ungulates. *Behaviour* 79: 82-107.

Ungar E.D., Genizi A. & Demment M.W. 1991. Bite dimensions and herbage intake by cattle grazing short hand-constructed swards. *Agronomical Journal* 83: 973-978.

Van Aswegen C.H.J. 1944. *Aktiwiteitspatrone van die blesbok (Damaliscus dorcas phillipsi Harper, 1939) in die sentrale Oranje-Vrystaat*. M.Sc-thesis, University of the Free State, Bloemfontein.

Van den Berg J.A. 1983. Die verwantskap tussen die langtermyn gemiddelde reënval en die weidingkapasiteit van natuurlike veld in droë dele van Suid-Afrika. *Proceedings of the Grassland Society of Southern Africa* 18: 165-167.

Van der Merwe F.J. & Smith W.A. 1991. *Dierevoeding* (2nd edition). Animal Science, Pinelands, South Africa.

Van der Waal C. & Dekker B. 2000. Game ranching in the Northern Province of South Africa. *South African Journal of Wildlife Research* 30: 151-156.

Van der Wal R., Egas M., Van der Veen A. & Bakker J. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* 88: 317-330.

Van der Westhuizen H.C. 1994. *Die kwantifisering van veldtoestand in die sentrale Vrystaat*. M.Sc.Agric.-thesis, University of the Free State, Bloemfontein.

Van Dyne G.M., Brockington N.R., Szocs Z., Duek J. & Ribic A. Large herbivore subsystem. In: Breymeyer A.I. & Van Dyne G.M. (eds.). *Grassland systems analysis and man*. Cambridge University Press, Cambridge. pp. 269-537.

Van Hoven W. 2000. Wildvoeding in die natuur. In: Bothma J. du P. (ed.). *Wildplaas bestuur (3rd edition)*. Van Schaik Uitgewers, Pretoria. pp.168-182.

Van Hoven W. & Boomker E.A. 1981. Feed utilisation and digestion in the black wildebeest (*Connochaetes gnou*, Zimmerman, 1780) in the Golden Gate Highlands National Park. *South African Journal of Wildlife Research* 11: 35-40.

Van Oudtshoorn F. 1999. *Guide to the grasses of southern Africa*. Briza Publications, Pretoria.

Van Rooyen N., Bredenkamp G.J. & Theron G.K. 2000. Weiveldbestuur. In: Bothma J. du. P. (ed.). *Wildplaasbestuur (3rd edition)*. Van Schaik Publishers, Pretoria. pp. 515-546.

Van Rooyen N. & Theron G.K. 2000a. Biome, veldtipes en wildboerderystreke van Suid-Afrika. In: Bothma J. du. P. (ed.) *Wildplaasbestuur* (3rd edition). Van Schaik Publishers, Pretoria. pp. 33-40.

Van Rooyen N. & Theron G.K. 2000b. Habitatontleding. In: Bothma J. du. P. (ed.)

Wildplaasbestuur (3rdedition). Van Schaik Publishers, Pretoria. pp. 70-73.

Van Soest P.J. 1967. Development of a comprehensive system of feed analyses and its application to forages. *Journal of Animal Science* 26: 119-128.

Van Soest P.J. 1982. *Nutritional ecology of the ruminant*. O & B Books, Corvallis, Oregon. 374 pp.

Van Soest P.J. 1994. *Nutritional Ecology of the Ruminan*t (2nd edition). Cornell University Press, London, UK 476 pp.

Van Sumere C.F., Albrecht J. Dedonder A., Depooter H. & Pé I. 1975. Plant proteins and phenolics. In: Harborne J.B. & Van Sumere C.F. (eds.) *Annual Proceedings of the Phytochemical Society* Vol 11. pp. 211-264.

Van Wieren S.E. 1992. Factors limiting food intake in ruminants and non-ruminants in the temperate zone. *Ongules/Ungulates 91 - Proceedings of the International Symposium*. pp. 139-145.

Van Zyl J.H.M. 1965. The vegetation of the S.A. Lombard Nature Reserve and its utilization by certain antelope. *Zoologica Africana* 1: 55-71.

Venter J. 1994. An integrated monitoring system for large herbivore and veld management on an Eastern Transvaal game ranch. In: Van Hoven W., Ebedes H. & Conroy A. (eds.) *Wildlife ranching, a celebration of diversity, proceedings of the third international wildlife ranching symposium (1992)*. pp. 27-32.

Vesey-Fitzgerald D.F. 1960. Grazing succession among East African game animals. *Journal of Mammology* 41: 161-172.

Vetter S., Nikolic D. & Palmer J. 2006. *How productive are blesbok grazing patches, and what contribution do they make to blesbok diets?* 41st Annual Congress of the Grassland Society of South Africa, Bela Bela, Limpopo Province, South

Africa. p.101.

Villard M.A. 2002. Habitat fragmentation: Major conservation issue or intellectual attractor? *Ecological Applications* 12: 319-320.

Vinton M.A. & Burke I.C. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* 76: 1116-1133.

Vitousek P.M., Walker L.R., Whiteaker L.D., Mueller-Dombois D. & Matson P.A. 1987. Biological invasion by Myrica faya alters ecosystem development in Hawaii. *Science* 238: 802-804.

Von Richter W. 1974. *Connochaetes gnou*. Mammalian Species 50: 1-6.

Voster M. 1982. The development of the ecological index method for assessing veld condition in the Karoo. *Proceedings of the Grassland Society of Southern Africa* 17: 84-89

Vrahimis S. & Kok O.B. 1993. Daily activity of black wildebeest in a semi-arid environment. *African Journal of Ecology* 31: 328-336.

Waller S.S. & Lewis J.K. 1979. Occurrence of C_3 and C_4 photosynthetic pathways in North American grasses. *Journal of Range Management* 32: 12-28.

Warren R.G. & Johnston A.E. 1962. The accumulation and loss of soil potassium in long-term experiments, Rothamsted and Woburn. *Proceedings of the London Fertilizer Society* 72: 5-24.

Wedin D.A. 1995. Species, nitrogen, and grassland dynamics: The constraints of stuff. In: Jones C.G. & Lawton J.H. (eds.) *Linking species and Ecosystems*. Chapman and Hall, New York. pp. 253-262.

Wedin D.A. & Tilman D. 1990. Species effects on nitrogen cycling: A test with perennial grasses. *Oecologia* 84: 433-441.

Welch J.G. & Hooper A.P. 1988. Ingestion of feed and water. In: Church D.C. (ed.) *The ruminant animal digestive physiology and nutrition*. Prentice Hall, USA. pp. 5-116.

Westoby M. 1974. An analysis of diet selection by large generalist herbivores. *The American Naturalist* 108: 290-304.

Westoby M., Walker B. & Noy-Meir I. 1989. Opportunistic management for rangelands not as equilibrium. *Journal of Range Management* 42: 266-274.

Wheeler J.L. 1958. The effect of sheep excreta and nitrogen fertilizer on botanical composition and production of a hey. *Journal of British Grasslands Society* 13: 196-202.

Wiegand T., Snyman H.A., Kellner K. & Paruelo J.M. 2004. Do grassland have a memory: Modeling phytomass production of a semi-arid South African grassland. *Ecosystems* 7: 243-258.

Wickstrom M.L., Robbins C.T., Hanley T.A., Spalinger D.E. & Parish S.M. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48: 1285-1301.

Williams P.H. & Haynes R.J. 1992. Transformations and plant uptake of urine-sulphate in urine-affected areas of pasture soil. *Plant and Soil* 145: 167-175.

Willms W.D., Dormaar J.F. & Schaalje G.B. 1988. Stability of grazed patches on rough fescue grasslands. *Journal of Range Management* 41: 503-508.

Wilson J.R. 1981. Environmental and nutritional factors affecting herbage quality. In: Hacker J.B. (ed.) Nutritional limits to animal production from pastures. **CAB**. pp. 111-129.

Wise M.J. & Abrahamson W.G. 2005. Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos* 109: 417-428.

Withers P.J.A., Clay S.D. & Breeze V.C. 2001. Phosphorus transfer in runoff following application of fertilizer, manure and sewage sludge. *Journal of Environmental Quality* 30: 180-188.

Wolfson M.M. 1999. The morphology and physiology of the major forage plants. Grasses. In: Tainton N.M. (ed.) *Veld management in South Africa*. University of Natal Press, Pietermaritzburg. pp. 91-101.

Wolfson M.M. & Tainton N.M. 1999. The morphology and physiology of the major forage plants. In: Tainton N.M. (ed.) *Veld management in South Africa*. University of Natal Press, Pietermaritzburg, South Africa. pp. 54-90.

Wright W. & Illius A.W. 1995. A comparative study of the fracture properties of five grasses. *Functional Ecology* 9: 269-278.

Young B.A. 1988. Effect of environmental stress on nutrient needs. In: Church D.C. (ed.) *The ruminant animal digestive physiology and nutrition*. Prentice Hall, USA. pp. 456-467.

Appendix A_1: Composition of the soil samples taken from each experimental plot.

Plot	% Contribution		
	Sand (coarse, medium and fine)	Silt coarse and fine	Clay
A1	32	16	52
A2	32	18	50
A3	24	16	60
A4	32	16	52
B1	44	20	36
B2	52	16	32
B3	27	22	51
B4	27	22	51
C1	28	16	56
C2	36	18	46
C3	59	13	28
C4	31	16	53
D1	34	16	50
D2	40	18	42
D3	37	18	45
D4	46	14	40
E1	46	24	30
E2	50	22	28
E3	43	20	37
E4	44	20	36

Appendix B_1

Ecological group classification of herbaceous species according to the Ecological Index Method (EIM) of Vorster (1982) revised by Tainton *et al*. (undated) as cited by Heard *et al*. (1986).

Decreasers

Decreaser species are those which dominate in veld in good/excellent condition, i.e. that community which is considered to be the most productive for that site and one which is stable if well managed. They decrease in abundance when veld is under- or over-utilised.

Increaser Ia

This species increase in abundance with moderate under-utilisation. These grasses are usually unpalatable climax species that can crow without any defoliation.

Increaser IIa

Species in this group are rare in veld in excellent condition, but increase when veld is moderately over-grazed in the long-term. Their relative occurrence usually increases when that of Decreaser species declines. The sub-climax and dis-climax grasses, as well as the more palatable Karoo bushes and taller shrubs, belong to this group. When these species dominate, the veld may be agro-ecologically classified as being in a good to fair condition.

Increaser IIb

Members of this group are rare in veld in excellent condition, but increase as veld is heavily over-grazed for an extended period. An increase in their relative abundance is coupled with a decrease of the species of the Increaser IIa category. Species which belong to this group as the perennial pioneer grasses and the moderately hardy and less palatable Karoo bushes and taller shrubs. Dominance of this group is generally a sign of veld in an ago-ecologically fair to poor condition.

Increaser IIc

Members of this group are rare in veld in excellent condition and increase when veld is over-grazed for an extended period. Their numbers increase when the abundance of Increaser IIb species decline. This group is represented mainly by rain-dependant annual grasses, ephemerals, hardy unpalatable Karoo bushes and taller shrubs, as well as a number of poisonous plants. Dominance of this group signifies that the veld is in an agro-ecological poor to very poor condition.

Appendix B$_2$: Percentage occurrence of plant species in the herbaceous layer of plot A1, A2, A3 and A4, for the 2003/04 and 2004/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of 2003/04 season's occurrence.

Species	**Occurrence (%)**											
	2003/04				**2004/05**							
	Experimental plots											
	A1	**A2**	**A3**	**A4**	**A1**	**% (*)**	**A2**	**% (*)**	**A3**	**% (*)**	**A4**	**% (*)**
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	0.5 (9)	♦	0.5 (7)	♦	-	-	-	-
Asteraceae												
Berkheya onopordifolia	2.0 (4)	-	0.5 (6)	1.0 (5)	-	♦	-	-	-	♦	-	♦
Felicia muricata muricata	0.5 (7)	-	-	-	-	♦	0.5 (7)	♦	-	-	-	-
Pentzia incana	1.5 (5)	3.0 (3)	2.0 (4)	1.0 (5)	2.5 (5)	+66.7	1.0 (6)	–66.7	-	♦	1.5 (6)	+50.0
Schkuhria pinnata	0.5 (7)	-	-	-	-	♦	-	-	-	-	-	-
Cactaceae												
Opuntia ficus indica	-	0.5 (7)	-	-	-	-	-	♦	-	-	-	-
Chenopodiaceae												
Salsola glabrescens	1.0 (6)	0.5 (7)	-	-	1.5 (7)	+50.0	-	♦	-	-	-	-
Cyperaceae												
Cyperus rupestris	-	-	-	-	2.0 (6)	♦	0.5 (7)	♦	-	-	-	-
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	6.0 (3)	♦	4.0 (3)	♦	3.0 (3)	♦	3.5 (4)	♦
Lamiaceae												
Salvia verbenaca	6.0 (3)	1.5 (5)	3.0 (3)	5.0 (3)	0.5 (9)	–91.7	-	♦	-	♦	1.5 (6)	–70.0
Nyctaginaceae												
Commicarpus pentandrus	-	-	-	-	1.5 (7)	♦	1.0 (6)	♦	-	-	-	-
Poaceae												
Aristida adscensionis	-	-	-	-	-	-	0.5 (7)	♦	-	-	-	-
Aristida bipartita	44.0 (1)	34.0 (2)	30.0 (2)	40.0 (2)	33.0 (1)	–25.0	39.5 (2)	+16.2	51.0 (1)	+70.0	54.5 (1)	+36.3
Brachiaria eruciformis	1.0 (6)	-	1.0 (5)	1.0 (5)	9.0 (2)	+800.0	2.5 (4)	♦	1.0 (5)	0.0	5.5 (3)	+450.0
Chloris virgata	1.0 (6)	-	1.0 (5)	-	1.0 (8)	0.0	-	-	-	♦	-	-
Cynodon dactylon	-	-	-	1.0 (5)	-	-	-	-	1.0 (5)	♦	1.0 (7)	0.0
Eragrostis chloromelas	34.5 (2)	56.0 (1)	58.0 (1)	45.5 (1)	33.0 (1)	–4.3	46.0 (1)	–17.9	40.0 (2)	–31.0	27.0 (2)	–40.7

…Table continues

Appendix B$_2$ continued...

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	A1	**A2**	**A3**	**A4**	**A1**	**% (*)**	**A2**	**% (*)**	**A3**	**% (*)**	**A4**	**% (*)**
Panicum stapfianum	1.0 (6)	1.0 (6)	1.0 (5)	1.0 (5)	-	♦	1.0 (6)	0.0	1.0 (5)	0.0	1.5 (6)	+50.0
Setaria incrassata	6.0 (3)	2.5 (4)	3.0 (3)	2.0 (4)	5.0 (4)	–16.7	2.0 (5)	–20.0	2.0 (4)	–33.3	2.0 (5)	0.0
Themeda triandra	-	1.0 (6)	-	1.0 (5)	-	-	1.0 (6)	0.0	-	-	1.0 (7)	0.0
Tragus berteronianus	1.0 (6)	-	-	-	1.0 (1)	0.0	-	-	-	-	-	-
Solanaceae												
Lycium horridum	-	-	-	1.0 (5)	2.0 (6)	♦	-	-	-	-	-	♦
Bare patch	-	-	0.5 (6)	0.5 (6)	1.5 (7)	-	-	-	1.0 (5)	+100.0	1.0 (7)	+100.0

Appendix B3: Percentage occurrence of plant species in the herbaceous layer of plot B1, B2, B3 and B4, for the 2003/04 and 2004/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of 2003/04 season's occurrence.

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	B1	B2	B3	B4	B1	% (*)	B2	% (*)	B3	% (*)	B4	% (*)
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	0.5 (11)	♦	-	-	-	-	-	-
Asteraceae												
Berkheya onopordifolia	-	0.5 (10)	0.5 (9)	-	-	-	-	♦	0.5 (10)		-	-
Felicia muricata muricata	7.0 (4)	4.0 (7)	3.0 (6)	1.0 (5)	2.5 (9)	–64.3	2.0 (10)	–50.0	4.0 (6)	–33.3	-	♦
Pentzia incana	6.5 (5)	5.0 (6)	5.0 (4)	0.5 (6)	3.0 (8)	–53.8	5.5 (7)	+10.0	4.0 (6)	–20.0	5.5 (5)	+1 000.0
Schkuhria pinnata	0.5 (11)	-	-	-	0.5 (11)	0.0	0.5 (12)	♦	-	-	-	-
Taraxacum officinale	0.5 (11)	-	-	-	-	♦	-	-	-	-	-	-
Cactaceae												
Opuntia ficus indica	-	-	-	-	-	-	-	♦	0.5 (10)	♦	0.5 (8)	♦
Caryophyllaceae												
Stellaria media	-	-	-	-	-	-	0.5 (12)	♦	0.5 (10)	♦	-	-
Chenopodiaceae												
Salsola glabrescens	3.0 (9)	-	-	-	3.0 (8)	0.0	0.5 (12)	♦	-	-	-	-
Cyperaceae												
Cyperus rupestris	7.0 (4)	6.0 (5)	3.0 (6)	-	13.0 (3)	+85.7	20.5 (1)	+241.7	7.5 (4)	+150.0	-	-
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	1.5 (10)	♦	1.0 (11)	♦	8.0 (3)	♦	5.0 (6)	♦
Chamaesyce inaequilatera	-	-	-	-	0.5 (11)	♦	-	-	-	-	-	-
Lamiaceae												
Salvia verbenaca	3.0 (9)	1.0 (9)	2.0 (7)	2.0 (4)	3.0 (8)	0.0	1.0 (11)	♦	-	♦	0.5 (8)	–75.0
Nyctaginaceae												
Commicarpus pentandrus	1.0 (10)	1.0 (9)	1.0 (8)	-	-	♦	-	♦	-	♦	-	-
Poaceae												
Aristida adscensionis	1.0 (10)	1.0 (9)	1.0 (8)	-	0.5 (11)	–50.0	2.0 (10)	+100.0	-	♦	0.5 (8)	♦

…Table continues

Appendix B3 continued…

Species	**Occurrence (%)**											
	2003/04				**2004/05**							
	Experimental plots											
	B1	**B2**	**B3**	**B4**	**B1**	**% (*)**	**B2**	**% (*)**	**B3**	**% (*)**	**B4**	**% (*)**
Aristida bipartita	4.0 (8)	9.0 (4)	20.0 (2)	39.0 (2)	3.5 (7)	–12.5	4.5 (9)	–50.0	17.5 (2)	–12.5	42.0 (1)	+7.7
Brachiaria eruciformis	3.0 (9)	1.0 (9)	1.0 (8)	1.0 (5)	8.5 (4)	+183.3	6.0 (6)	+500.0	6.5 (5)	+550.0	7.0 (4)	+600.0
Chloris virgata	1.0 (10)	-	-	-	3.5 (7)	+250.0	1.0 (11)	♦	-	-	0.5 (8)	♦
Cynodon dactylon	1.0 (10)	0.5 (10)	-	1.0 (5)	-	♦	-	♦	-	-	-	♦
Eragrostis chloromelas	18.0 (1)	23.0 (1)	45.5 (1)	46.5 (1)	10.5 (2)	–41.7	19.0 (2)	–17.4	36.0 (1)	+20.9	26.0 (2)	–44.1
Eragrostis obtusa	8.0 (3)	17.0 (2)	8.0 (3)	-	5.5 (5)	–31.3	6.5 (5)	– 61.8	1.5 (8)	–81.3	-	-
Eragrostis plana	1.0 (10)	1.0 (9)	-	-	-	♦	-	♦	-	-	-	-
Panicum stapfianum	1.0 (10)	5.0 (6)	1.0 (8)	1.0 (5)	5.0 (6)	+400.0	5.0 (8)	0.0	7.5 (4)	+650.0	1.0 (7)	0.0
Setaria incrassata	15.0 (2)	6.0 (5)	2.0 (7)	4.0 (3)	5.5 (5)	–63.3	7.5 (4)	+25.0	1.5 (8)	–25.0	10.0 (3)	+150.0
Themeda triandra	5.5 (7)	16.0 (3)	4.0 (5)	1.0 (5)	2.5 (9)	–54.5	11.0 (3)	–31.3	2.0 (7)	–50.0	-	♦
Tragus berteronianus	6.0 (6)	1.0 (9)	-	-	25.5 (1)	+325.0	5.5 (7)	+450.0	1.0 (9)	♦	-	-
Solanaceae												
Lycium horridum	-	-	1.0 (8)	1.0 (5)	0.5 (11)	♦	-	-	0.5 (10)	–50.0	1.0 (7)	0.0
Bare patch	7.0 (4)	2.0 (8)	2.0 (7)	2.0 (4)	1.5 (10)	–78.6	-	♦	1.0 (9)	–50.0	0.5 (8)	–75.0

Appendix B4: Percentage occurrence of plant species in the herbaceous layer of plot C1, C2, C3 and C4, for the 2003/04 and 2004/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of 2003/04 season's occurrence.

Species	**Occurrence (%)**											
	2003/04				**2004/05**							
	Experimental plots											
	C1	**C2**	**C3**	**C4**	**C1**	**% (*)**	**C2**	**% (*)**	**C3**	**% (*)**	**C4**	**% (*)**
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	0.5 (10)	♦	1.5 (8)	♦	-	-	-	-
Asteraceae												
Berkheya onopordifolia	1.0 (6)	-	-	0.5 (11)	1.0 (9)	0.0	-	-	-	-	-	♦
Felicia muricata muricata	1.0 (6)	2.5 (6)	7.0 (3)	9.5 (3)	1.0 (9)	0.0	1.0 (9)	–60.0	4.0 (5)	–42.9	6.0 (6)	–36.8
Pentzia incana	-	2.0 (7)	2.5 (6)	6.0 (4)	2.0 (8)	♦	2.5 (7)	+25.0	0.5 (9)	–80.0	5.0 (7)	–16.7
Schkuhria pinnata	0.5 (7)	-	-	-	0.5 (10)	0.0	-	-	-	-	-	-
Senecio consanguineus	-	0.5 (9)	-	-	-	-	-	♦	-	-	-	-
Cactaceae												
Opuntia ficus indica	-	-	-	-	0.5 (10)	♦	0.5 (10)	♦	-	-	0.5 (12)	♦
Chenopodiaceae												
Salsola glabrescens	-	0.5 (9)	-	-	-	-	1.0 (9)	+100.0	-	-	-	-
Cyperaceae												
Cyperus rupestris	-	1.0 (8)	3.5 (5)	2.5 (8)	-	-	5.5 (5)	+450.0	7.5 (3)	+114.3	8.0 (3)	+220.0
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	4.0 (6)	♦	1.5 (8)	♦	-	-	6.0 (6)	♦
Lamiaceae												
Salvia verbenaca	12.0 (4)	6.5 (5)	1.0 (7)	3.0 (7)	10.5 (4)	–12.5	4.0 (6)	–38.5	0.5 (9)	–50.0	1.5 (11)	–50.0
Nyctaginaceae												
Commicarpus pentandrus	-	-	0.5 (8)	0.5 (11)	-	-	0.5 (10)	♦	-	♦	-	♦
Poaceae												
Aristida adscensionis	-	-	1.0 (7)	1.0 (10)	-	-	-	-	4.0 (5)	+100.0	3.5 (9)	+250.0
Aristida bipartita	17.0 (2)	7.0 (4)	0.5 (8)	18.5 (2)	18.0 (2)	+5.9	7.5 (3)	+7.1	2.5 (6)	+400.0	22.5 (1)	+21.6
Brachiaria eruciformis	2.5 (5)	2.0 (7)	1.0 (7)	1.5 (9)	7.0 (5)	+180.0	6.5 (4)	+225.0	4.0 (5)	+100.0	7.0 (4)	+366.7
Chloris virgata	-	-	-	-	-	-	1.0 (9)	♦	-	-	0.5 (12)	♦

…Table continues

Appendix B4 continued…

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	C1	C2	C3	C4	C1	% (*)	C2	% (*)	C3	% (*)	C4	% (*)
Cymbopogon pospischilii	-	1.0 (8)	-	-	-	-	-	♦	-	-	-	-
Cynodon dactylon	-	-	1.0 (7)	0.5 (11)	-	-	-	-	-	♦	-	♦
Digitaria eriantha	-	-	1.0 (7)	-	-	-	-	-	1.0 (8)	0.0	-	-
Eragrostis chloromelas	14.0 (3)	21.5 (2)	4.0 (4)	37.0 (1)	13.0 (3)	–7.1	25.0 (2)	+16.3	2.5 (6)	– 37.5	16.0 (2)	–56.8
Eragrostis obtusa	1.0 (6)	1.0 (8)	7.0 (3)	1.0 (10)	-	♦	1.0 (9)	0.0	7.5 (3)	+7.1	2.5 (10)	+150.0
Eragrostis plana	1.0 (6)	1.0 (8)	1.0 (7)	-	-	♦	-	♦	1.5 (7)	+50.0	-	-
Panicum stapfianum	2.5 (5)	1.0 (8)	4.0 (4)	4.0 (6)	2.5 (7)	0.0	5.5 (5)	+450.0	4.5 (4)	+12.5	4.0 (8)	0.0
Setaria incrassata	45.5 (1)	43.0 (1)	38.0 (1)	6.0 (4)	38.5 (1)	–15.4	29.5 (1)	+31.4	32.5 (1)	–14.5	6.5 (5)	+8.3
Themeda triandra	1.0 (6)	7.5 (3)	26.0 (2)	2.5 (8)	-	♦	5.5 (5)	–26.7	26.0 (2)	0.0	6.0 (6)	+140.0
Tragus berteronianus	-	-	-	1.0 (10)	-	-	-	-	1.5 (7)	♦	3.5 (9)	+250.0
Solanaceae												
Lycium horridum	-	-	-	0.5 (11)	0.5 (10)	♦	-	-	-	-	0.5 (12)	0.0
Bare patch	1.0 (6)	2.0 (7)	1.0 (7)	4.5 (5)	0.5 (10)	–50.0	0.5 (10)	–75.0	-	♦	0.5 (12)	–88.9

Appendix B5: Percentage occurrence of plant species in the herbaceous layer of plot D1, D2, D3 and D4, for the 2003/04 and 2004/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of 2003/04 season's occurrence.

Species	**Occurrence (%)**											
	2003/04				**2004/05**							
	Experimental plots											
	D1	**D2**	**D3**	**D4**	**D1**	**% (*)**	**D2**	**% (*)**	**D3**	**% (*)**	**D4**	**% (*)**
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	0.5 (12)	♦	1.0 (8)	♦	-	-	-	-
Asteraceae												
Berkheya onopordifolia	-	0.5 (9)	0.5 (9)	-	0.5 (12)	♦	-	♦	0.5 (11)	0.0	-	-
Felicia muricata muricata	1.5 (10)	1.5 (7)	4.0 (6)	5.0 (6)	5.5 (5)	+266.7	5.5 (4)	+266.7	2.0 (8)	–50.0	4.5 (10)	–10.0
Pentzia incana	3.0 (8)	0.5 (9)	1.0 (8)	6.0 (5)	2.0 (10)	–33.3	2.5 (7)	+400.0	4.0 (6)	+300.0	9.0 (4)	+50.0
Schkuhria pinnata	1.0 (11)	1.0 (8)	-	-	-	♦	-	♦	-	-	0.5 (14)	♦
Senecio consanguineus	-	-	1.0 (8)	-	-	-	-	-	-	♦	-	-
Cactaceae												
Opuntia ficus indica	-	0.5 (8)	-	-	-	-	-	♦	0.5 (11)	♦	-	-
Cyperaceae												
Cyperus rupestris	-	1.0 (8)	3.0 (7)	3.0 (7)	1.0 (11)	♦	0.5 (9)	–50.0	3.0 (7)	0.0	5.0 (8)	+66.7
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	-	-	0.5 (9)	♦	-	-	1.0 (13)	♦
Lamiaceae												
Salvia verbenaca	11.0 (3)	11.0 (2)	9.0 (4)	5.0 (6)	5.5 (5)	–50.0	13.0 (2)	+18.2	8.0 (3)	–11.1	2.5 (12)	–50.0
Nyctaginaceae												
Commicarpus pentandrus	0.5 (12)	-	-	0.5 (10)	-	♦	-	-	-	-	0.5 (14)	0.0
Poaceae												
Aristida adscensionis	-	-	1.0 (8)	1.0 (9)	1.0 (11)	♦	0.5 (9)	♦	1.0 (10)	0.0	3.0 (11)	+200.0
Aristida bipartita	9.0 (4)	7.5 (3)	5.0 (5)	22.5 (2)	14.0 (2)	+55.6	7.5 (3)	0.0	5.0 (5)	0.0	22.5 (1)	0.0
Brachiaria eruciformis	1.0 (11)	1.0 (8)	1.0 (8)	1.0 (9)	4.0 (6)	+300.0	1.0 (8)	0.0	2.0 (8)	+100.0	8.0 (5)	+700.0
Cymbopogon pospischilii	1.0 (11)	1.0 (8)	0.5 (9)	-	-	♦	1.0 (8)	0.0	0.5 (11)	0.0	-	-
Cynodon dactylon	6.0 (5)	1.5 (7)	1.0 (8)	0.5 (10)	6.5 (4)	+8.3	1.0 (8)	–33.3	3.0 (7)	+200.0	-	♦
Digitaria eriantha	2.5 (9)	2.0 (6)	4.0 (6)	-	1.0 (11)	–60.0	-	♦	1.0 (10)	–75.0	-	-

…Table continues

Appendix B_5 continued…

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	D1	D2	D3	D4	D1	% (*)	D2	% (*)	D3	% (*)	D4	% (*)
Eragrostis chloromelas	5.0 (6)	5.0 (5)	1.0 (8)	26.5 (1)	3.0 (8)	–40.0	4.0 (5)	–20.0	0.5 (11)	–50.0	16.0 (2)	–39.6
Eragrostis obtusa	1.0 (11)	0.5 (9)	3.0 (7)	2.5 (8)	2.5 (9)	+150.0	-	♦	1.5 (9)	–50.0	4.0 (9)	+60.0
Eragrostis plana	3.0 (8)	2.0 (6)	4.0 (6)	0.5 (10)	3.5 (7)	+16.7	2.5 (7)	+25.0	6.0 (4)	+50.0	0.5 (14)	0.0
Panicum stapfianum	3.5 (7)	2.0 (6)	10.0 (3)	6.5 (4)	2.0 (10)	–42.9	3.5 (6)	+75.0	1.0 (10)	–90.0	6.0 (6)	–7.7
Setaria incrassata	34.0 (1)	54.0 (1)	34.0 (1)	3.0 (7)	33.0 (1)	–2.9	50.0 (1)	–7.4	45.0 (1)	+32.4	5.5 (7)	+83.3
Themeda triandra	16.5 (2)	6.5 (4)	17.0 (2)	15.5 (3)	12.0 (3)	–27.3	5.5 (4)	–15.4	14.5 (2)	–14.7	11.5 (3)	–25.8
Tragus berteronianus	-	-	-	-	-	-	-	-	0.5 (11)	♦	-	-
Solanaceae												
Lycium horridum	-	-	-	0.5 (10)	1.0 (11)	♦	-	-	-	-	-	♦
Bare patch	0.5 (12)	1.0 (8)	-	0.5 (10)	1.0 (11)	0.0	0.5 (9)	–50.0	0.5 (11)	♦	-	♦

Appendix B_6: Percentage occurrence of plant species in the herbaceous layer of plot E1, E2, E3 and E4, for the 2003/04 and 2004/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of 2003/04 season's occurrence.

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	E1	E2	E3	E4	E1	% (*)	E2	% (*)	E3	% (*)	E4	% (*)
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	-	-	-	-	0.5 (11)	♦	-	-
Asteraceae												
Berkheya onopordifolia	0.5 (11)	0.5 (12)	-	0.5 (11)	0.5 (12)	0.0	0.5 (12)	0.0	-	-	-	♦
Felicia muricata muricata	2.0 (8)	1.0 (11)	2.0 (9)	4.0 (8)	2.5 (10)	+25.0	3.0 (7)	+200.0	2.5 (9)	+25.0	6.5 (4)	+62.5
Pentzia incana	-	5.0 (6)	4.0 (6)	8.0 (4)	-	-	4.5 (5)	–10.0	7.5 (4)	+87.5	3.5 (6)	–56.3
Schkuhria pinnata	0.5 (11)	-	-	-	-	♦	-	-	-	-	-	-
Senecio consanguineus	0.5 (11)	0.5 (12)	-	1.0 (10)	-	♦	-	♦	-	-	-	♦
Cactaceae												
Opuntia ficus indica	-	-	-	-	-	-	-	-	0.5 (11)	♦	-	-
Chenopodiaceae												
Salsola glabrescens	-	-	-	1.0 (10)	-	-	-	-	-	-	-	♦
Cyperaceae												
Cyperus rupestris	2.0 (8)	2.0 (9)	0.5 (11)	0.5 (11)	0.5 (12)	–75.0	2.0 (9)	0.0	0.5 (11)	0.0	3.5 (6)	+600.0
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	-	-	0.5 (12)	♦	-	-	-	-
Chamaesyce inaequilatera	-	-	-	-	-	-	-	-	-	-	0.5 (10)	♦
Lamiaceae												
Salvia verbenaca	2.0 (8)	4.0 (7)	13.0 (3)	4.0 (8)	-	♦	2.0 (9)	–50.0	8.5 (3)	–34.6	-	♦
Nyctaginaceae												
Commicarpus pentandrus	0.5 (11)	-	-	1.0 (10)	-	♦	-	-	0.5 (11)	♦	0.5 (10)	–50.0
Poaceae												
Aristida adscensionis	1.0 (10)	1.0 (11)	1.0 (10)	2.0 (9)	6.0 (6)	+500.0	1.5 (10)	+50.0	1.5 (10)	+50.0	3.5 (6)	+75.5
Aristida bipartita	1.5 (9)	2.5 (8)	3.0 (8)	19.5 (2)	8.0 (4)	+433.0	5.0 (4)	+100.0	7.5 (4)	+150.0	24.0 (1)	+23.1
Brachiaria eruciformis	1.0 (10)	1.0 (10)	0.5 (11)	-	1.0 (11)	0.0	2.5 (8)	+100.0	3.5 (6)	+600.0	3.5 (6)	♦

…Table continues

Appendix B$_6$ continued…

Species	Occurrence (%)											
	2003/04				2004/05							
	Experimental plots											
	E1	E2	E3	E4	E1	% (*)	E2	% (*)	E3	% (*)	E4	% (*)
Cymbopogon pospischilii	4.0 (5)	1.5 (10)	1.0 (10)	1.0 (10)	5.5 (7)	+37.5	5.0 (4)	+233.3	-	♦	1.0 (9)	0.0
Cynodon dactylon	7.0 (4)	0.5 (12)	1.0 (10)	-	7.0 (5)	0.0	-	♦	-	♦	-	-
Digitaria eriantha	4.0 (5)	4.0 (7)	6.5 (5)	0.5 (11)	3.5 (9)	–12.5	5.0 (4)	+25.0	3.0 (7)	–53.8	-	♦
Eragrostis chloromelas	11.5 (2)	18.0 (2)	4.0 (6)	7.0 (6)	11.5 (2)	0.0	17.0 (2)	–5.6	3.5 (6)	–12.5	6.5 (4)	–7.1
Eragrostis obtusa	2.5 (7)	1.5 (10)	1.0 (10)	7.5 (5)	4.5 (8)	+80.0	1.5 (10)	0.0	4.0 (5)	+300.0	8.0 (3)	+6.7
Eragrostis plana	8.5 (3)	7.5 (4)	3.5 (7)	1.0 (10)	9.5 (3)	+11.8	12.5 (3)	+66.7	8.5 (3)	+142.9	1.5 (8)	+50.0
Heteropogon contortus	-	2.0 (9)	-	1.0 (10)	-	-	-	♦	-	-	-	♦
Panicum stapfianum	1.0 (10)	5.5 (5)	7.5 (4)	10.5 (3)	2.5 (10)	+150.0	4.0 (6)	–27.3	3.0 (8)	–60.0	5.5 (5)	–47.6
Setaria incrassata	1.0 (10)	11.5 (3)	27.5 (1)	5.0 (7)	1.0 (11)	0.0	5.0 (5)	–56.5	22.0 (2)	–20.0	6.5 (4)	–30.0
Themeda triandra	44.0 (1)	29.5 (1)	23.5 (2)	24.5 (1)	34.5 (1)	–21.6	27.0 (1)	–8.5	22.5 (1)	–4.3	23.0 (2)	–6.1
Tragus berteronianus	1.0 (10)	0.5 (12)	-	-	1.0 (11)	♦	1.0 (11)	–50.0	-	-	2.0 (7)	♦
Solanaceae												
Lycium horridum	1.0 (10)	-	-	-	1.0 (12)	0.0	0.5 (12)	♦	-	-	-	-
Bare patch	3.0 (6)	0.5 (12)	0.5 (11)	0.5 (11)	-	♦	-	♦	0.5 (11)	0.0	0.5 (10)	0.0

Appendix B$_7$: Average percentage occurrence of plant species in different succession classes, as well as non-grasses (Karoo bushes and forbs) in the 2003/04 and 2004/05 growing seasons.

Species	Average occurrence (%)									
	2003/04					2004/05				
	Climax	Sub-climax	Pioneer	Karoo bushes	Forbs	Climax	Sub-climax	Pioneer	Karoo bushes	Forbs
Amaranthaceae										
Amaranthus thunbergii	-	-	-	-	-	-	-	-	-	0.3
Asteraceae										
Berkheya onopordifolia	-	-	-	-	0.4	-	-	-	-	0.2
Felicia muricata muricata	-	-	-	4.1	-	-	-	-	2.6	-
Pentzia incana	-	-	-	3.1	-	-	-	-	3.3	-
Schkuhria pinnata	-	-	-	-	0.2	-	-	-	-	0.1
Senecio consanguineus	-	-	-	-	0.2	-	-	-	-	-
Taraxacum officinale	-	-	-	-	0.0	-	-	-	-	-
Cactaceae										
Opuntia ficus indica	-	-	-	-	0.1	-	-	-	-	0.2
Caryophyllaceae										
Stellaria media	-	-	-	-		-	-	-	-	0.1
Chenopodiaceae										
Salsola glabrescens	-	-	-	0.3	-	-	-	-	0.3	-
Cyperaceae										
Cyperus rupestris	-	-	-	-	1.8	-	-	-	-	4.0
Euphorbiaceae										
Acalypha segetalis	-	-	-	-	-	-	-	-	-	2.2
Chamaesyce inaequilatera	-	-	-	-	-	-	-	-	-	0.1
Lamiaceae										
Salvia verbenaca	-	-	-	-	5.3	-	-	-	-	3.1
Nyctaginaceae										
Commicarpus pentandrus	-	-	-	-	0.3	-	-	-	-	0.2
Poaceae										
Aristida adscensionis	-	-	0.6	-	-	-	-	1.4	-	-
Aristida bipartita	16.7	-	-	-	-	-	19.5	-	-	-

…Table continues

Appendix B7 continued …

Species	Average occurrence (%)									
	2003/04					2004/05				
	Climax	**Sub-climax**	**Pioneer**	**Karoo bushes**	**Forbs**	**Climax**	**Sub-climax**	**Pioneer**	**Karoo bushes**	**Forbs**
Brachiaria eruciformis	-	-	1.1	-	-	-	-	4.8	-	-
Chloris virgata		-	0.2	-	-	-	-	1.0	-	-
Cymbopogon pospischilii	0.6	-	-	-	-	0.7	-	-	-	-
Cynodon dactylon	-	-	1.1	-	-	-	-	1.0	-	-
Digitaria eriantha	1.2	-	-	-	-	0.7	-	-	-	-
Eragrostis chloromelas	24.1	-	-	-	-	17.8	-	-	-	-
Eragrostis obtusa	-	3.1	-	-	-	-	2.5	-	-	-
Eragrostis plana	-	1.8	-	-	-	-	2.3	-	-	-
Heteropogon contortus	0.2	-	-	-	-	-	-	-	-	-
Panicum stapfianum	3.5	-	-	-	-	3.3	-	-	-	-
Setaria incrassata	17.2	-	-	-	-	15.5	-	-	-	-
Themeda triandra	12.1	-	-	-	-	10.3	-	-	-	-
Tragus berteronianus	-	-	0.5	-	-	-	-	2.1	-	-
Solanaceae			-	-	-	-	-	-	-	-
Lycium horridum	-	-	-	0.3	-	-	-	-	0.4	-
Total	58.7	21.8	3.5	7.7	8.3	48.3	24.3	10.3	6.6	10.5

Appendix B8: Above-ground dry matter (DM) production (kg ha$^{-1)}$ of plant species in plot A1, A2, A3 and A4, for the ¾ and 04/05 growing seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of ¾ season's production.

Species	Production (kg ha^{1})											
	2003/04				2004/05							
	Experimental plots											
	A1	A2	A3	A4	A1	% (*)	A2	% (*)	A3	% (*)	A4	% (*)
Asteraceae												
Berkheya onopordifolia	1.8 (7)	0.8 (7)	-	1.0 (7)	5.4 (11)	+200.0	1.5 (6)	+87.5	4.9 (6)	♦	-	♦
Schkuhria pinnata	1.4 (8)	-	-	-	-	♦	-	-	-	-	-	-
Felicia muricata muricata	-	-	-	-	-	-	-	-	-	-	0.2 (10)	♦
Pentzia incana	13.6 (5)	19.6 (4)	4.6 (4)	16.0 (5)	23.6 (6)	+73.5	-	♦	-	♦	5.8 (5)	–63.8
Tripteris aghillana	1.4 (8)	-	-	-	-	♦	-	-	-	-	-	-
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	3.0 (12)	♦	-	-	-	-	-	-
Chenopodiaceae												
Salsola glabrescens	-	-	-	-	46.1 (4)	♦	-	-	-	-	-	-
Cyperaceae												
Cyperus rupestris	1.8 (7)	-	-	-	24.1 (5)	+1 238.9	-	-	1.1 (9)	♦	-	-
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	-	-	-	-	1.5 (8)	♦	1.9 (9)	♦
Phyllanthus parvulus	-	-	-	-	1.6 (13)	♦	-	-	0.7 (10)	♦	-	-
Lamiaceae												
Salvia disermas	-	-	-	-	0.2 (16)	♦	-	-	0.7 (10)	♦	2.3 (8)	♦
Salvia verbenaca	18.4 (4)	15.8 (5)	2.8 (5)	62.0 (3)	-	♦	14.6 (3)	–7.6	0.4 (11)	–85.7	13.7 (3)	–77.9
Nyctaginaceae												
Commicarpus pentandrus	-	-	-	-	6.9 (9)	♦	-	-	-	-	-	-
Poaceae												
Aristida bipartita	439.6 (1)	307.2 (1)	369.2 (1)	249.8 (1)	192.1 (1)	–56.3	192.7 (2)	–37.3	285.2 (1)	–22.8	335.6 (1)	+34.3
Brachiaria eruciformis	1.6 (9)	2.6 (6)	0.2 (6)	3.0 (6)	82.1 (3)	+5 031.3	11.9 (4)	+357.7	48.0 (3)	+23 900.0	5.0 (6)	+66.7
Cynodon dactylon	-	-	-	0.2 (8)	-	-	-	-	1.8 (7)	♦	-	♦
Digitaria monodactyla	-	-	-	-	1.1 (14)	♦	-	-	-	-	-	-

…Table continues

Appendix B_8 continued…

Species	Production (kg ha^{1})											
	2003/04				2004/05							
	Experimental plots											
	A1	A2	A3	A4	A1	% (*)	A2	% (*)	A3	% (*)	A4	% (*)
Eragrostis chloromelas	242.0 (2)	138.2 (2)	222.8 (2)	203.0 (2)	190.7 (2)	–21.2	288.0 (1)	+108.4	86.6 (2)	–61.1	235.7 (2)	+16.0
Eragrostis plana	2.4 (6)	-	-	-	-	–100.0	-	-	-	-	-	-
Panicum stapfianum	-	-	-	-	-	-	-	-	-	-	2.5 (7)	♦
Setaria incrassata	101.6 (3)	90.8 (3)	47.8 (3)	-	1.0 (15)	–99.0	1.7 (5)	–58.8	35.9 (4)	–24.9	1.3 (9)	♦
Tragus berteronianus	-	-	-	-	8.1 (8)	♦	-	-	-	-	-	-
Solanaceae												
Lycium horridum	-	-	-	16.8 (4)	6.3 (10)	♦	-	-	6.4 (5)	♦	6.4 (4)	–61.9

Appendix B$_9$: Above-ground dry matter (DM) production (kg ha^{-1}) of plant species in plot B1, B2, B3 and B4, for the ¾ and 04/05 seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of ¾ season's production.

Species	**Production (kg ha^{-1})**											
	2003/04				**2004/05**							
	Experimental plots											
	B1	**B2**	**B3**	**B4**	**B1**	**% (*)**	**B2**	**% (*)**	**B3**	**% (*)**	**B4**	**% (*)**
Acanthaceae												
Blepharis integrifolia	1.8 (10)	12.8 (9)	2.4 (7)	-	3.7 (14)	+105.6	-	♦	-	♦	-	-
Apocynaceae												
Asclepias sp.	-	0.6 (14)	-	-	-	-	-	♦	-	-	-	-
Asteraceae												
Berkheya onopordifolia	0.8 (13)	-	-	1.0 (7)	-	♦	-	-	0.3 (11)	♦	-	♦
Schkuhria pinnata	-	-	-	-	2.0 (18)	♦	0.7 (16)	♦	-	-	-	-
Felicia muricata muricata	1.0 (12)	0.2 (10)	6.2 (5)	0.6 (8)	4.4 (12)	+340.0	25.4 (6)	+149.0	13.6 (7)	+119.4	-	♦
Pentzia incana	47.0 (4)	69.4 (2)	29.0 (3)	29.0 (4)	63.4 (4)	+34.9	35.9 (5)	–48.3	74.6 (3)	+157.2	9.7 (4)	–66.6
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	0.5 (20)	♦	-	-	-	-	0.9 (7)	-
Cactaceae												
Opuntia ficus indica	-	-	-	-	431.3 (1)	♦	-	-	-	-	-	-
Chenopodiaceae												
Salsola glabrescens	59.6 (2)	-	-	-	-	♦	4.3 (12)	♦	-	-	-	-
Cyperaceae												
Cyperus rupestris	27.8 (6)	16.6 (8)	-	-	33.1 (6)	+19.1	42.3 (3)	+154.8	29.9 (5)	♦	-	-
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	146.0 (3)	♦	2.9 (14)	♦	23.6 (6)	♦	2.6 (5)	♦
Phyllanthus parvulus	-	-	-	-	-	-	-	-	-	-	1.3 (6)	♦
Fabaceae												
Indigofera alternans	-	19.6 (7)	-	-	-	-	-	♦	-	-	-	-
Lamiaceae												
Salvia verbenaca	57.8 (3)	22.2 (6)	9.0 (4)	11.0 (5)	7.4 (10)	–87.2	24.0 (7)	+8.1	0.3 (11)	+99.7	-	♦
Malvaceae												
Hibiscus pusillus	-	-	-	-	0.8 (19)	♦	-	-	-	-	-	-

…Table continues

Appendix B9 continued…

Species	Production (kg ha^{-1})											
	2003/04				2004/05							
	Experimental plots											
	B1	B2	B3	B4	B1	% (*)	B2	% (*)	B3	% (*)	B4	% (*)
Nyctaginaceae												
Commicarpus pentandrus	-	-	-	4.0 (6)	-	-	-	-	-	-	-	♦
Poaceae												
Aristida adscensionis	2.2 (9)	2.0 (12)	-	-	0.2 (21)	+90.1	-	♦	-	-	-	-
Aristida bipartita	2.6 (8)	36.6 (4)	179.2 (1)	211.4 (1)	13.4 (9)	+415.4	36.3 (4)	–0.8	125.0 (2)	–30.2	226.3 (1)	+7.0
Brachiaria eruciformis	0.2 (14)	-	4.8 (6)	-	39.9 (5)	+19 850.0	22.1 (8)	♦	37.7 (4)	+685.4	61.0 (2)	♦
Chloris virgata	-	-	-	-	15.4 (8)	♦	-	-	-	-	-	-
Cynodon dactylon	-	1.4 (13)	-	1.0 (7)	-	-	-	♦	-	-	-	♦
Cynodon hirsutum	-	-	-	-	2.8 (16)	♦	-	-	-	-	-	-
Eragrostis chloromelas	2 9.8 (5)	176.8 (1)	100.0 (2)	154.6 (2)	28.4 (7)	+189.8	141.1 (1)	–20.2	146.3 (1)	+46.3	-	♦
Eragrostis obtusa	1.2 (11)	2.8 (11)	-	-	6.7 (11)	+458.3	17.1 (9)	+510.7	-	-	-	-
Panicum stapfianum	-	-	-	-	2.3 (17)	♦	5.2 (11)	♦	1.3 (9)	♦	-	-
Setaria incrassata	83.2 (1)	45.8 (3)	-	57.0 (3)	196.2 (2)	+6 031.3	62.1 (2)	+35.6	7.1 (8)	♦	20.9 (3)	+63.3
Themeda triandra	-	25.0 (5)	-	-	3.3 (15)	♦	3.8 (13)	–84.8	0.6 (10)	♦	-	-
Tragus berteronianus	2.8 (7)	0.2 (15)	-	-	3.8 (13)	+35.7	5.4 (10)	+2 600.0	-	-	-	-
Solanaceae												
Lycium harridum	-	-	-	-	-	-	2.2 (15)	♦	0.2 (12)	♦	-	-

Appendix B$_{10}$: Above-ground dry matter (DM) production (kg ha^{-1}) of plant species in plot C1, C2, C3 and C4, for the ¾ and 04/05 seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of ¾ season's production.

Species	**Production (kg ha^{1})**											
	2003/04				**2004/05**							
	Experimental plots											
	C1	**C2**	**C3**	**C4**	**C1**	**% (*)**	**C2**	**% (*)**	**C3**	**% (*)**	**C4**	**% (*)**
Acanthaceae												
Blepharis integrifolia	-	-	-	-	-	-	-	-	3.1 (12)	♦	-	-
Asteraceae												
Berkheya onopordifolia	1.4 (9)	-	-	0.2 (9)	9.8 (6)	+600.0	-	-	-	-	22.1 (5)	+10 950.0
Schkuhria pinnata	-	-	-	-	0.7 (12)	♦	-	-	-	-	-	-
Felicia muricata muricata	3.6 (7)	0.4 (8)	36.0 (3)	55.4 (3)	8.9 (7)	+147.2	6.6 (7)	+1 550.0	18.3 (6)	–49.2	8.3 (8)	–85.0
Pentzia incana	9.0 (6)	36.4 (3)	14.4 (4)	24.4 (5)	1.2 (11)	–86.7	16.7 (6)	–54.1	2.6 (13)	–81.9	21.7 (6)	–11.1
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	1.3 (10)	♦	6.0 (8)	♦	0.7 (16)	♦	-	-
Chenopodiaceae												
Chenopoduim album	-	-	-	-	-	-	0.5 (12)	♦	-	-	-	-
Cyperaceae												
Cyperus rupestris	-	-	-	0.6 (7)	3.1 (8)	♦	29.2 (5)	♦	10.8 (8)	♦	-	♦
Euphorbiaceae												
Acalypha segetalis	-	-	-	-	1.6 (9)	♦	4.0 (10)	♦	1.4 (14)	♦	18.6 (7)	♦
Euphorbia hirta	-	-	-	-	-	-	-	-	0.8 (15)	♦	-	-
Fabaceae												
Lotononis sp.	-	-	-	-	-	-	-	-	4.5 (11)	♦	-	-
Lamiaceae												
Salvia verbenaca	31.2 (3)	34.0 (4)	-	27.6 (4)	42.4 (3)	+35.9	1.8 (11)	–94.7	-	-	8.1 (9)	–70.7
Poaceae												
Aristida adscensionis	-	-	2.4 (8)	-	-	-	5.2 (9)	♦	22.8 (5)	+850.0	0.6 (12)	♦
Aristida bipartita	81.8 (2)	60.0 (2)	7.2 (6)	130.8 (1)	117.5 (2)	+43.6	93.2 (2)	+55.3	51.4 (3)	+613.9	102.6 (2)	–21.6
Brachiaria eruciformis	16.0 (5)	3.6 (7)	-	-	27.4 (4)	+71.3	29.8 (4)	+727.8	-	-	101.6 (3)	♦

…Table continues

Appendix B$_{10}$ continued…

Species	**Production (kg ha^{-1})**											
	2003/04				**2004/05**							
	Experimental plots											
	C1	**C2**	**C3**	**C4**	**C1**	**% (*)**	**C2**	**% (*)**	**C3**	**% (*)**	**C4**	**% (*)**
Eragrostis chloromelas	16.4 (4)	18.2 (6)	-	82.2 (2)	14.6 (*)	–11.0	31.4 (3)	+72.5	11.2 (7)	♦	146.3 (1)	+78.0
Eragrostis obtusa	0.6 (10)	-	-	-	-	♦	0.1 (13)	♦	7.2 (9)	♦	-	-
Panicum stapfianum	-	-	11.8 (5)	0.4 (8)	-	-	-	-	44.7 (4)	+278.8	-	♦
Setaria incrassata	274.6 (1)	256.0 (1)	218 (1)	19.8 (6)	289.7 (1)	+5.5	223.0 (1)	–12.9	156.1 (1)	–28.4	71.4 (4)	+259.1
Themeda triandra	-	23.8 (5)	114.2 (2)	-	-	-	-	♦	68.9 (2)	–39.7	5.9 (10)	♦
Tragus berteronianus	-	-	-	-	-	-	-	-	5.1 (10)	♦	4.0 (11)	♦
Solanaceae												
Lycium harridum	-	-	5.6 (7)	-	-	-	-	-	0.2 (17)	–96.4	-	-
Unknown	3.5 (8)	-	-	-	-	♦	-	-	-	-	-	-

Appendix B_{11}: Above-ground dry matter (DM) production (kg ha^{-1}) of plant species in plot D1, D2, D3 and D4, for the ¾ and 04/05 seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of ¾ season's production.

Species	**Production (kg ha^{1})**											
	2003/04				**2004/05**							
	Experimental plots											
	D1	**D2**	**D3**	**D4**	**D1**	**% (*)**	**D2**	**% (*)**	**D3**	**% (*)**	**D4**	**% (*)**
Acanthaceae												
Blepharis integrifolia	-	-	-	1.2 (11)	-	-	-	-	-	-	-	♦
Asteraceae												
Berkheya onopordifolia	4.6 (9)	-	-	-	0.2 (11)	–95.7	-	-	-	-	-	-
Schkuhria pinnata	-	-	-	2.0 (10)	-	-	-	-	-	-	-	♦
Felicia muricata muricata	33.6 (3)	4.4 (6)	26.0 (6)	19.8 (7)	0.1 (12)	–99.7	6.4 (7)	+45.5	6.5 (9)	–75.0	-	♦
Pentzia incana	15.8 (6)	5.6 (5)	18.8 (9)	38.6 (5)	15.7 (7)	–0.6	9.8 (6)	+75.0	17.7 (3)	–5.9	7.4 (9)	–80.8
Amaranthaceae												
Amaranthus thunbergii	-	-	-	-	-	-	-	-	2.4 (12)	♦	-	-
Convolvulaceae												
Convolvulus sagittatus	-	-	-	-	1.3 (9)	♦	-	-	-	-	-	-
Cyperaceae												
Cyperus rupestris	0.2 (12)	0.8 (8)	1.2 (12)	1.0 (12)	0.6 (10)	+200.0	2.3 (9)	+187.5	8.9 (5)	+641.7	3.5 (10)	+250.0
Lamiaceae												
Salvia verbenaca	25.2 (4)	6.4 (4)	39.4 (5)	59.0 (3)	44.5 (3)	+76.6	71.9 (3)	+1 023.4	69.4 (2)	+76.1	12.1 (7)	–79.5
Poaceae												
Aristida adscensionis	-	-	-	1.0 (12)	-	-	-	-	-	-	-	♦
Aristida bipartita	21.4 (5)	28.2 (3)	116.2 (2)	103.0 (2)	128.0 (2)	+498.1	79.7 (2)	+182.6	7.4 (6)	–93.6	165.9 (1)	+61.1
Brachiaria eruciformis	1.4 (10)	-	-	-	36.8 (4)	+2 528.6	61.8 (4)	♦	6.6 (8)	♦	70.6 (2)	♦
Cynodon dactylon	14.4 (7)	2.2 (7)	9.2 (10)	-	35.2 (5)	+144.4	-	♦	17.4 (4)	+89.1	-	-

…Table continues

Appendix B11 continued…

Species	Production (kg ha^{1})											
	2003/04				2004/05							
	Experimental plots											
	D1	D2	D3	D4	D1	% (*)	D2	% (*)	D3	% (*)	D4	% (*)
Digitaria eriantha	-	-	-	1.0 (12)	-	-	-	-	-	-	-	♦
Eragrostis chloromelas	-	31.6 (2)	19.6 (7)	32.2 (6)	5.6 (8)	♦	0.6 (10)	–98.1	0.2 (13)	–99.0	28.1 (4)	+12.7
Eragrostis obtusa	0.8 (11)	-	1.0 (13)	3.8 (9)	-	♦	-	-	4.5 (10)	+350.0	-	♦
Eragrostis plana	-	-	5.2 (11)	-	-	-	12.1 (5)	♦	3.6 (11)	–30.8	-	-
Heteropogon contortus	-	-	46.6 (3)	-	-	-	-	-	-	♦	-	-
Panicum stapfianum	9.0 (8)	-	19.6 (4)	8.8 (8)	-	♦	-	-	-	♦	7.5 (8)	–14.8
Setaria incrassata	217.4 (1)	417.0 (1)	287.8 (1)	133.8 (1)	332.4 (1)	+52.9	-	♦	352.3 (1)	+65.5	19.4 (6)	–85.5
Themeda triandra	40.6 (2)	-	19.2 (8)	39.0 (4)	20.1 (6)	–50.5	3.5 (8)	♦	6.7 (7)	–65.1	52.2 (3)	+33.8
Tragus berteronianus	-	-	-	-	-	-	-	-	-	-	0.3 (11)	♦

Appendix B12: Above-ground dry matter (DM) production (kg ha^{-1}) of plant species in plot E1, E2, E3 and E4, for the ¾ and 04/05 seasons. A – indicates the absence of a species, ♦ indicates that a species only occurred in one of the two seasons, and % (*) indicates the increase (+) or decrease (-) as a percentage of ¾ season's production.

Species	**Production (kg ha^{1})**											
	2003/04				**2004/05**							
	Experimental plots											
	E1	**E2**	**E3**	**E4**	**E1**	**% (*)**	**E2**	**% (*)**	**E3**	**% (*)**	**E4**	**% (*)**
Acanthaceae												
Blepharis integrifolia	0.2 (14)	2.4 (11)	-	5.0 (8)	-	♦	-	♦	-	-	5.1 (9)	♦
Asteraceae												
Berkheya onopordifolia	-	-	3.8 (10)	-	-	-	5.1 (12)	♦	8.9 (11)	+134.2	-	-
Schkuhria pinnata	-	-	-	-	-	-	-	-	-	-	-	-
Felicia muricata muricata	38.0 (4)	17.8 (8)	32.6 (4)	30.4 (4)	31.4 (6)	–17.4	9.1 (10)	–48.9	68.0 (5)	+108.6	2.3 (12)	–92.4
Pentzia incana	3.0 (12)	36.4 (5)	8.2 (7)	34.8 (3)	0.7 (15)	+76.7	40.2 (6)	+10.4	36.1 (6)	+340.2	21.6 (6)	–37.9
Cactaceae												
Opuntia ficus indica	-	-	-	-	1 204.9 (1)	♦	594.0 (1)	♦	171.2 (1)	♦	-	-
Convolvulaceae												
Convolvulus boedeckeriana	-	-	-	-	-	-	0.9 (14)	-	-	-	-	-
Cyperaceae												
Cyperus rupestris	-	2.2 (12)	-	-	-	-	10.0 (9)	+354.5	0.5 (5)	♦	18.6 (7)	♦
Lamiaceae												
Salvia verbenaca	3.8 (11)	27.2 (6)	66.2 (3)	25.0 (5)	-	-	7.1 (11)	–73.9	72.5 (3)	+9.5	4.0 (10)	–84.0
Nyctaginaceae												
Commicarpus pentandrus	-	-	-	-	3.5 (14)	♦	1.2 (13)	♦	-	-	-	-
Poaceae												
Aristida adscensionis	10.2 (8)	-	23.8 (5)	3.4 (9)	34.5 (5)	+238.2	18.2 (7)	♦	3.9 (12)	–83.6	0.1 (16)	+97.1
Aristida bipartita	28.6 (6)	46.8 (3)	-	110.2 (2)	19.9 (9)	–30.4	0.2 (17)	–99.6	26.8 (8)	♦	160.5 (2)	+45.6
Brachiaria eruciformis	-	-	-	-	11.3 (11)	♦	0.6 (15)	♦	-	-	0.6 (15)	♦
Cymbopogon pospischilii	29.2 (5)	-	-	-	21.0 (8)	–28.1	-	-	-	-	-	-
Cynodon dactylon	42.2 (3)	-	-	-	46.4 (4)	+10.0	-	-	-	-	-	-
Digitaria eriantha	26.8 (7)	-	-	0.4 (11)	-	♦	11.7 (8)	-	-	-	3.2 (11)	+700.0
Digitaria monodactyla	-	-	-	-	17.6 (10)	♦	-	-	-	-	-	-
Eragrostis chloromelas	96.2 (2)	50.0 (2)	16.6 (6)	9.6 (7)	57.8 (3)	–39.9	57.6 (4)	+15.2	28.1 (7)	+69.3	1.2 (13)	–87.5

…Table continues

Appendix B12 continued…

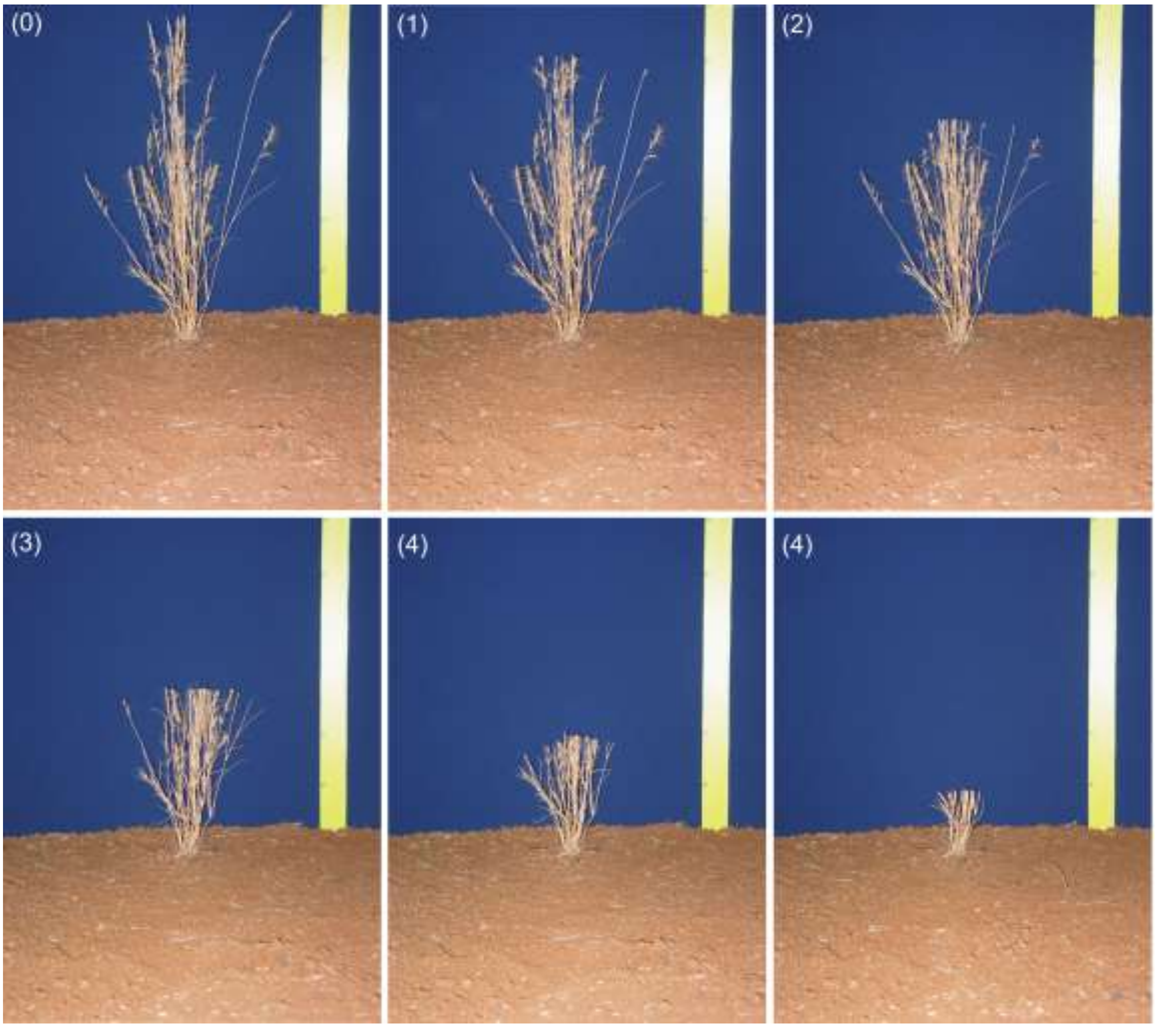
Species	Production (kg ha^{-1})											
	2003/04				2004/05							
	Experimental plots											
	E1	**E2**	**E3**	**E4**	**E1**	**% (*)**	**E2**	**% (*)**	**E3**	**% (*)**	**E4**	**% (*)**
Eragrostis obtusa	4.6 (9)	-	0.8 (11)	1.2 (10)	-	♦	-	-	9.1 (10)	+1 037.5	25.8 (5)	+2 050.0
Eragrostis plana	4.4 (10)	38.2 (4)	7.8 (8)	-	24.8 (7)	+463.6	42.2 (5)	+10.5	12.8 (9)	+64.1	-	-
Heteropogon contortus	-	-	-	-	5.5 (13)	♦	-	-	-	-	-	-
Panicum stapfianum	2.2 (13)	24.4 (7)	5.4 (9)	15.4 (6)	-	♦	0.5 (16)	–98.0	-	♦	44.8 (4)	+190.9
Setaria incrassata	-	15.4 (10)	114.2 (2)	-	-	-	122.9 (2)	+698.1	70.3 (4)	–38.4	71.9 (3)	♦
Themeda triandra	176.0 (1)	186.0 (1)	172.8 (1)	230.0 (1)	99.4 (2)	–43.5	111.0 (3)	–40.3	115.2 (2)	–33.3	250.9 (1)	+9.1
Solanaceae												
Lycium horridum	-	16.0 (9)	-	-	8.0 (12)	♦	-	♦	-	-	10.0 (8)	♦
Unknown	-	-	-	-	0.7 (15)	♦	-	-	-	-	-	-
Unknown	-	-	-	-	-	-	-	-	-	-	1.1 (14)	♦

Appendix B$_{13}$: Correlation coefficients of the grass species, Karoo bushes and forbs (grouped) between the species representing the five ecological groups. * indicates that the species was grouped according to personal observations.

Species	**Decreaser (*T. triandra*)**	**Increaser Ia (*C. pospischilii*)**	**Increaser IIa (*E. chloromelas*)**	**Increaser IIb (*A. bipartita*)**	**Increaser IIc (*B. eruciformis*)**	**Group**
Poaceae						
Digitaria eriantha	0.7142	0.6554	-0.4579	-0.5002	-0.3309	Decreaser
Panicum stapfianum	0.3813	0.0256	-0.4277	-0.4082	0.0134	Decreaser
Setaria incrassata	0.0377	-0.0941	-0.6123	-0.4988	-0.0971	Decreaser
Cynodon dactylon	0.4731	0.5298	-0.3303	-0.2472	-0.2615	Increaser Ia
Eragrostis plana	0.7514	0.8122	-0.4579	-0.5019	-0.2718	Increaser Ia
*Heteropogon contortus**	0.3174	0.1234	-0.0888	-0.1433	-0.1902	Increaser IIa
*Eragrostis obtusa**	0.3850	-0.0113	-0.2825	-0.4042	-0.0447	Increaser IIb
*A. adscensionis**	-0.3144	0.4338	-0.0818	0.0787	0.0711	Increaser IIc
Chloris virgata	-0.2914	-0.1930	0.0622	-0.0587	0.4850	Increaser IIc
Tragus berteronianus	-0.0977	-0.0675	-0.1299	-0.2230	0.4028	Increaser IIc
Karoo bushes	0.1586	-0.1137	-0.2516	-0.3401	0.1817	Increaser IIc
Forbs	-0.1789	-0.2752	-0.4025	-0.4330	0.4799	Increaser IIc

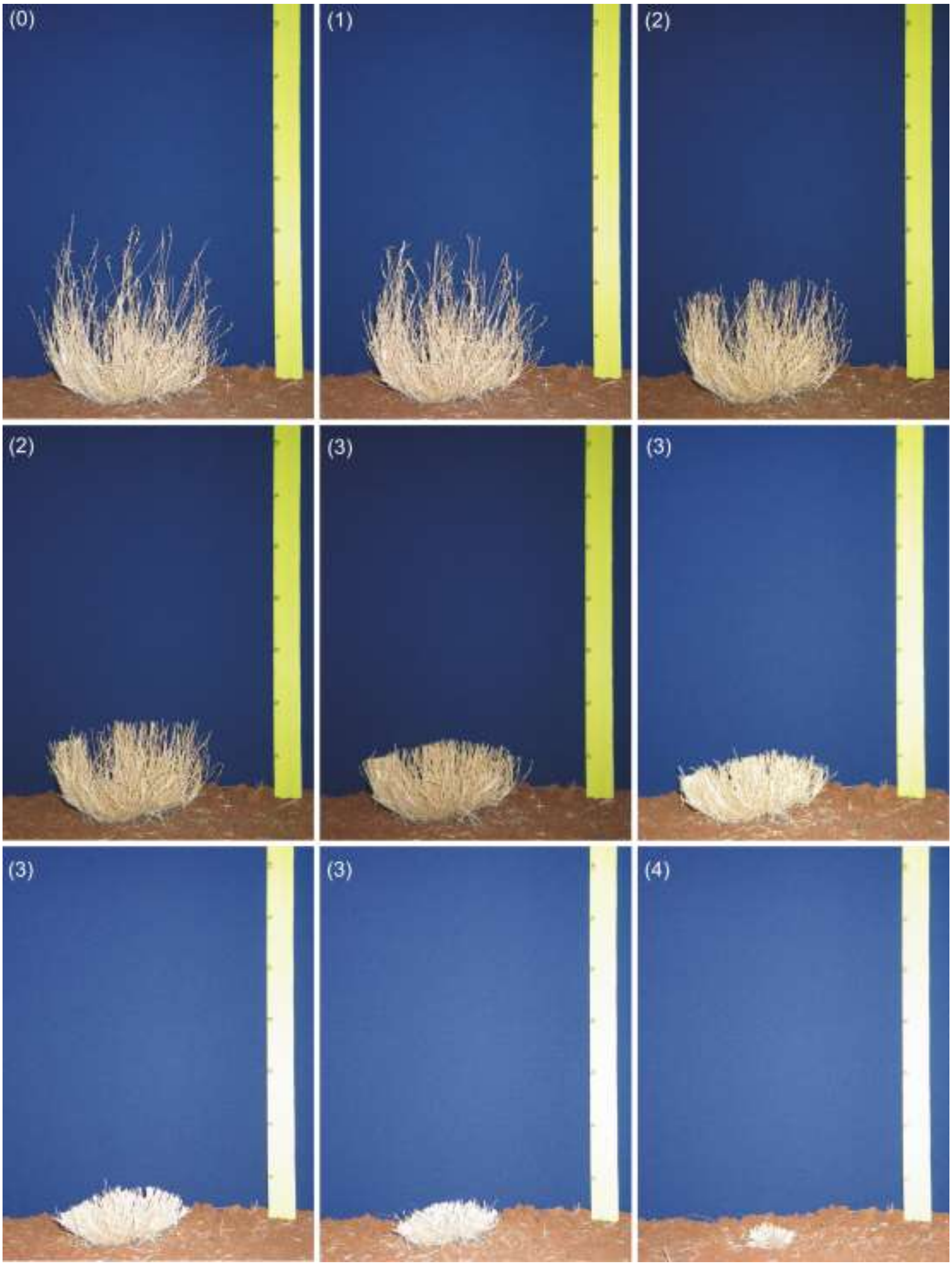
Appendix C1: Field reference guide

Aristida adscensionis L.

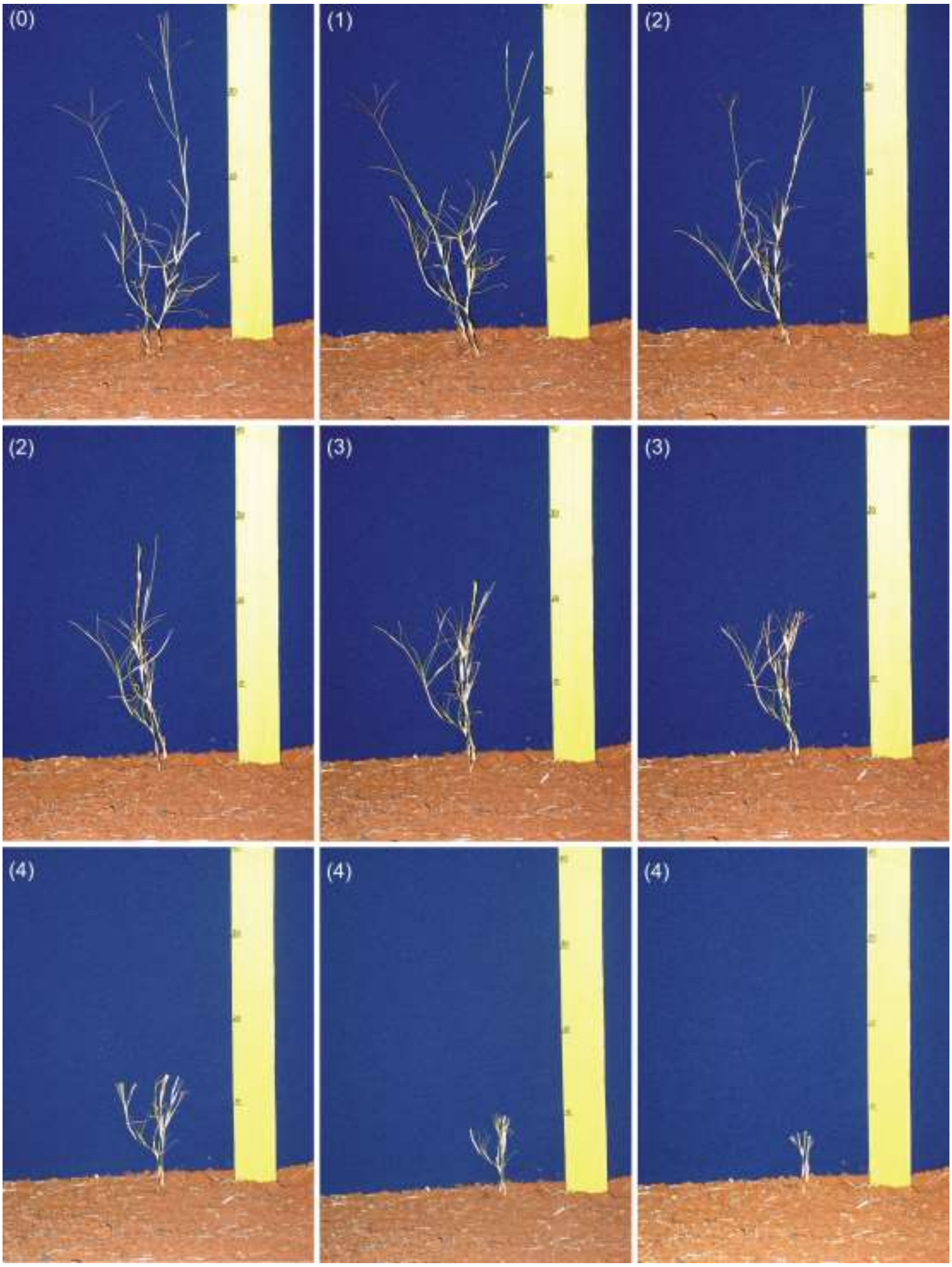


Aristida bipartita L.

Brachiaria eruciformis (Trin.)



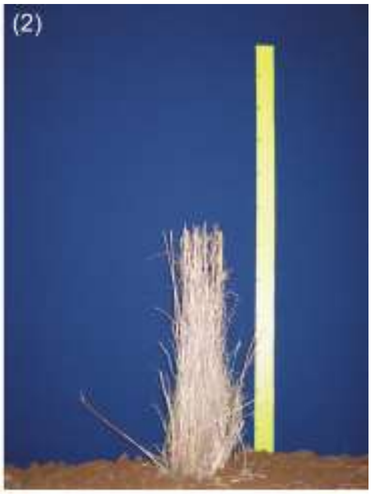
Cynodon dactylon Rich.



Cymbopogon pospischilii Spreng.


(0)


(1)

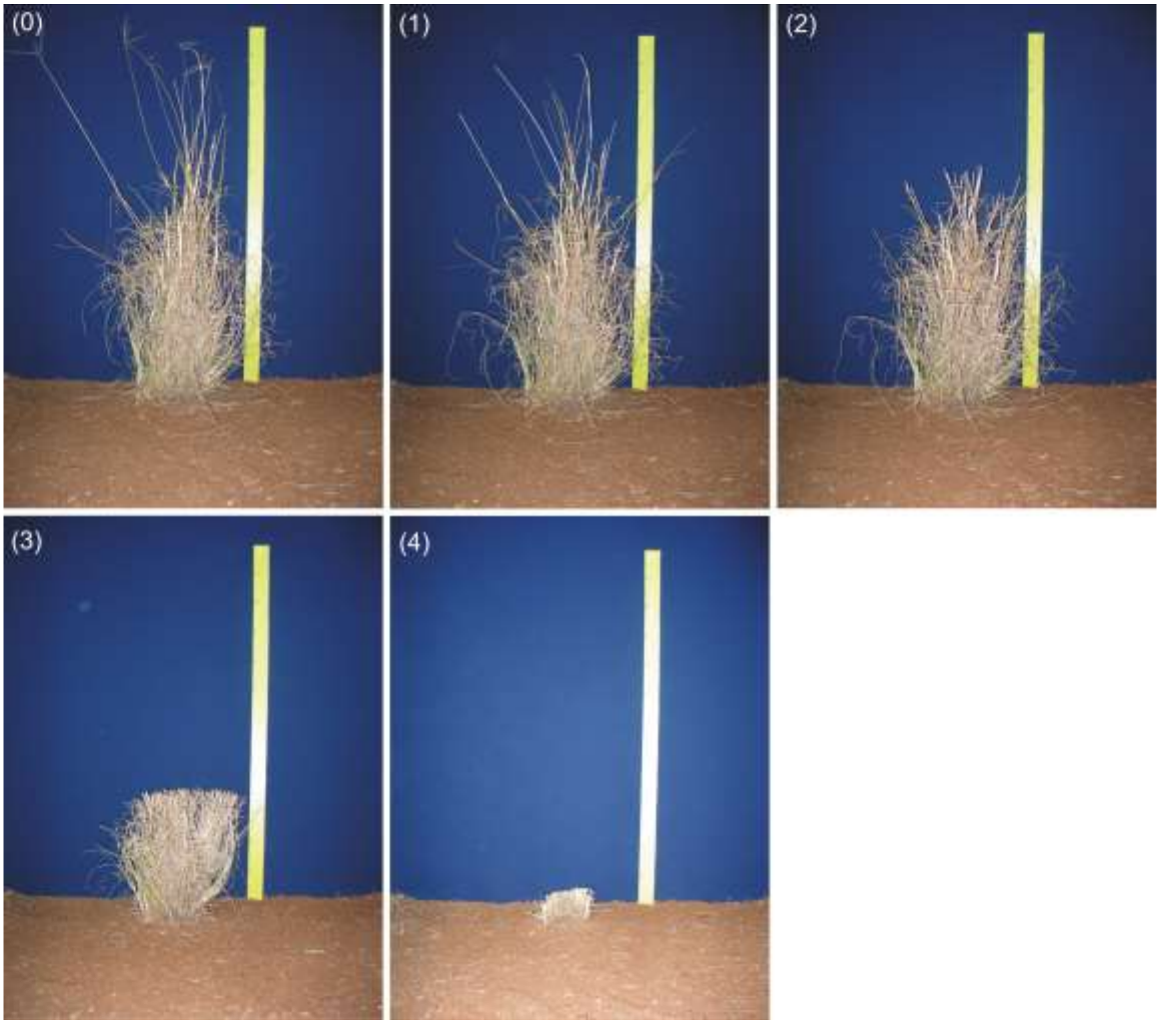

(2)


(3)

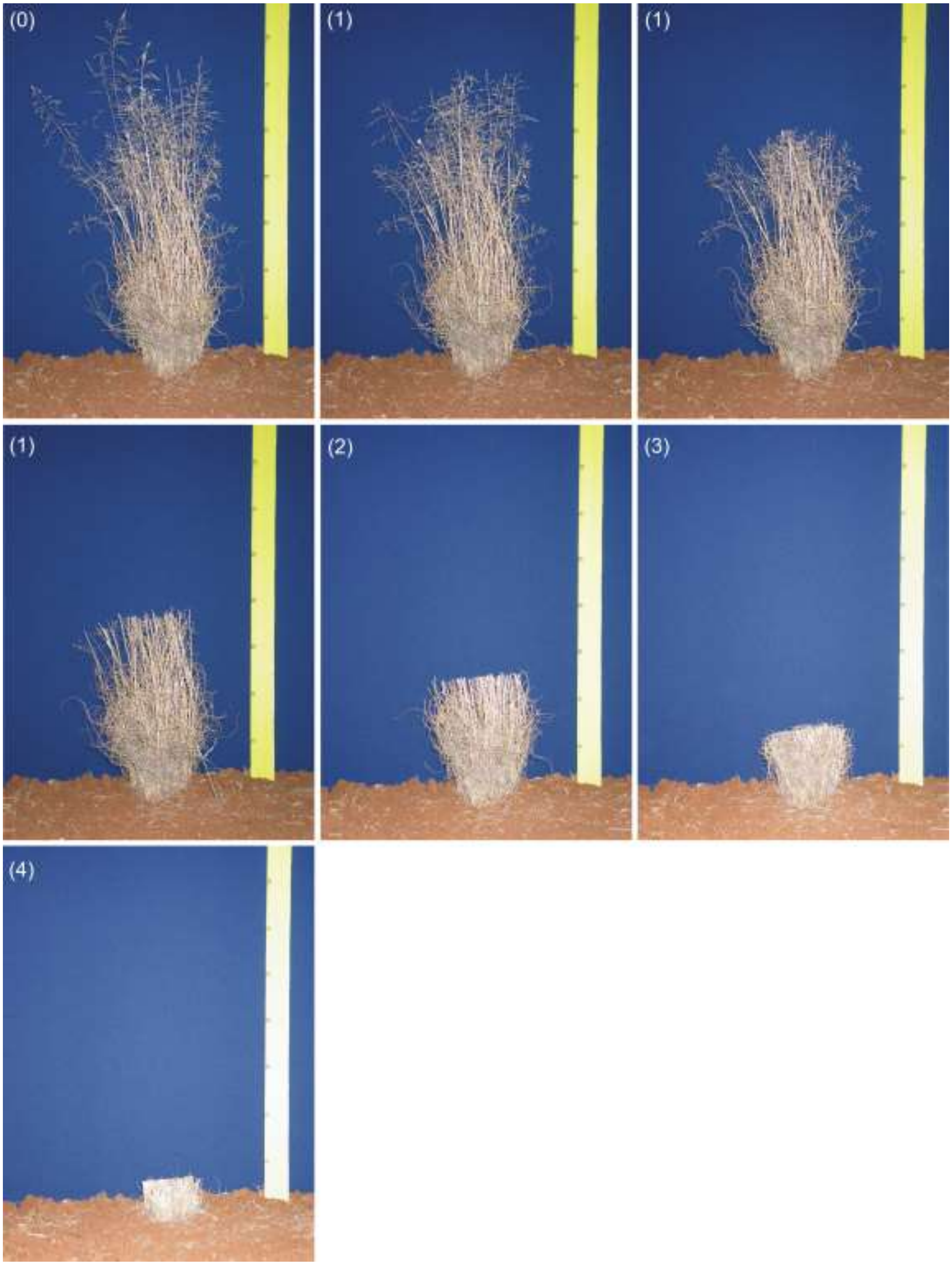

(4)

Chloris virgata Sw.

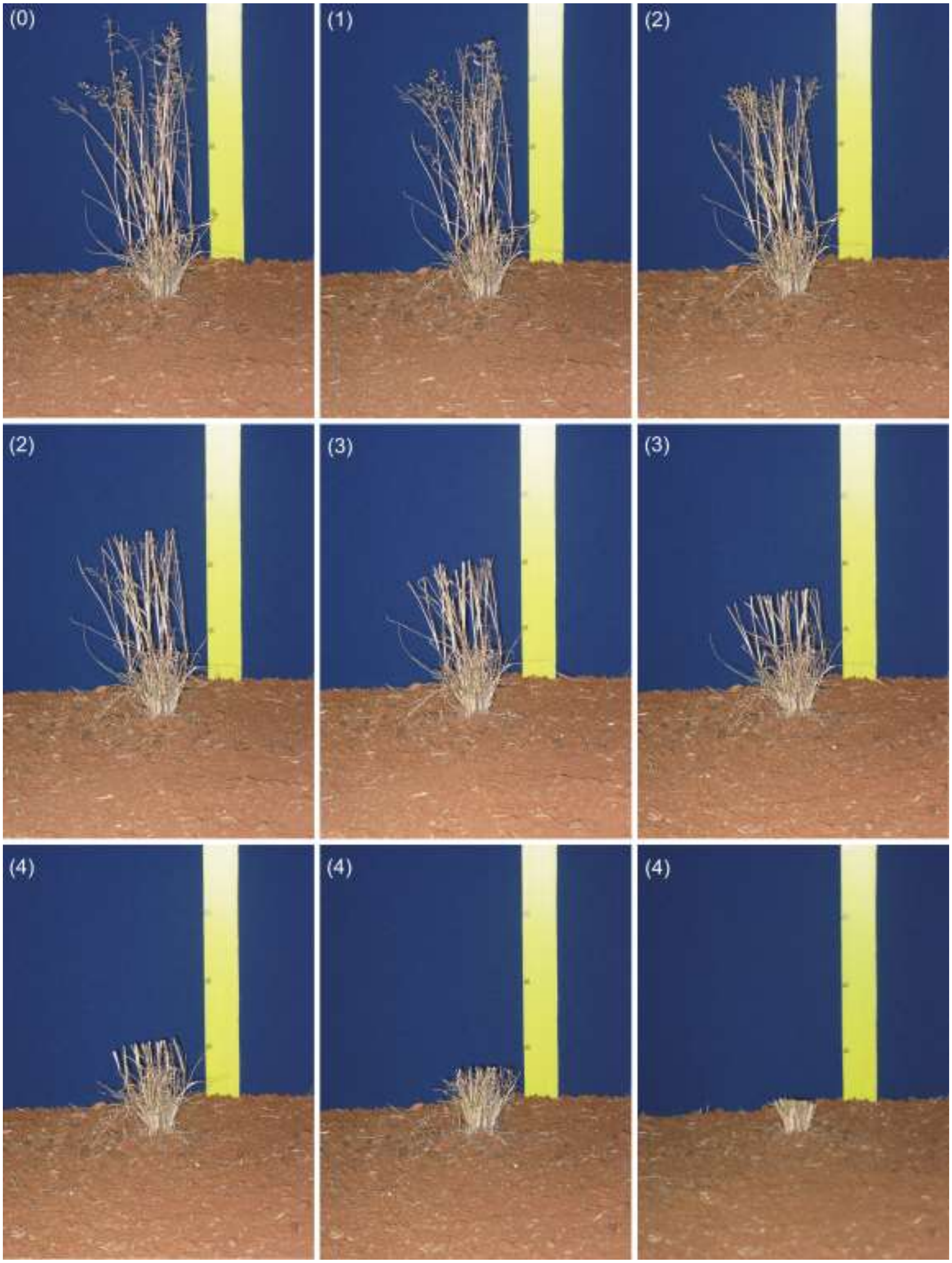
Digitaria eriantha Haller



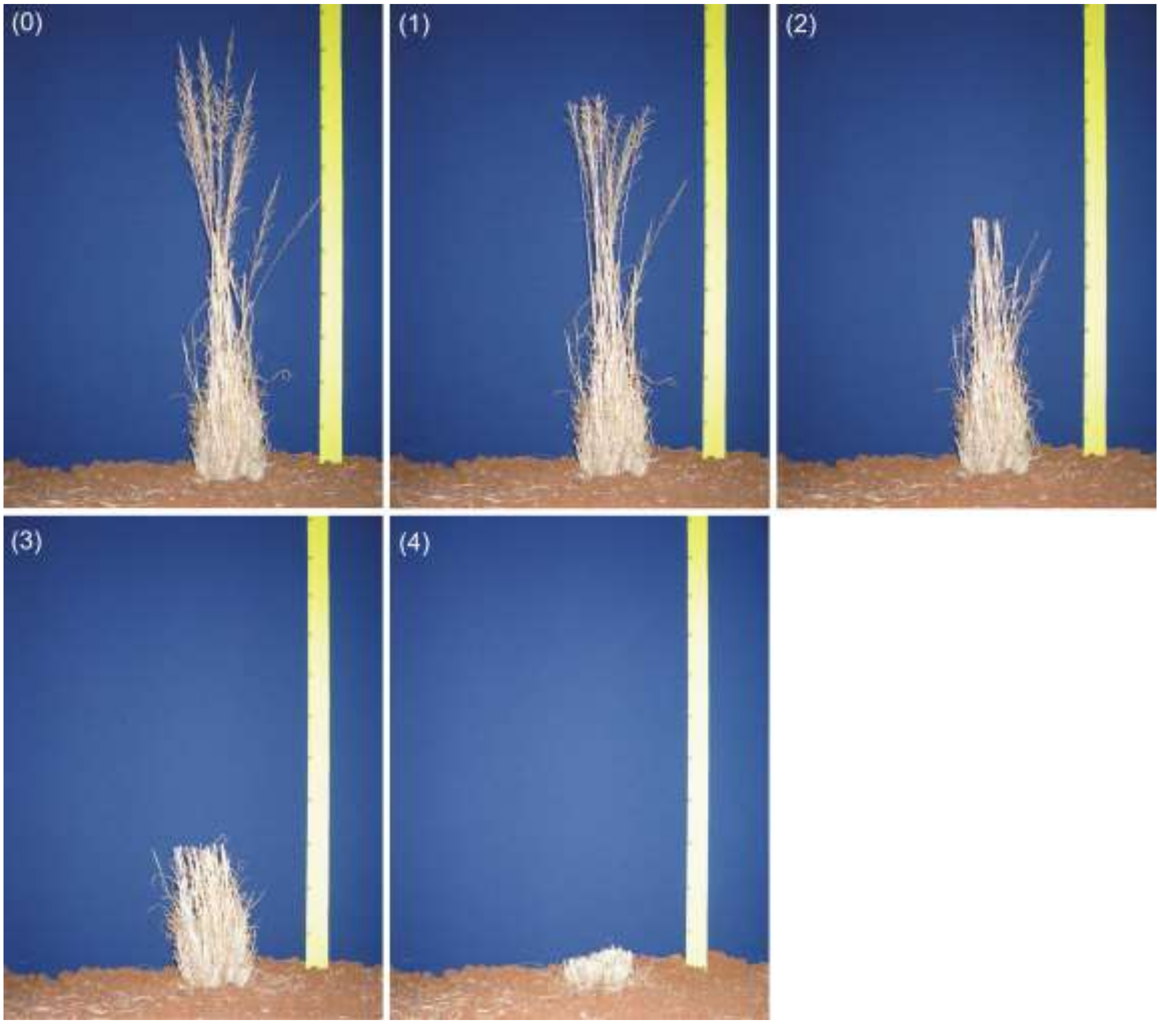
Eragrostis chloromelas Wolf.



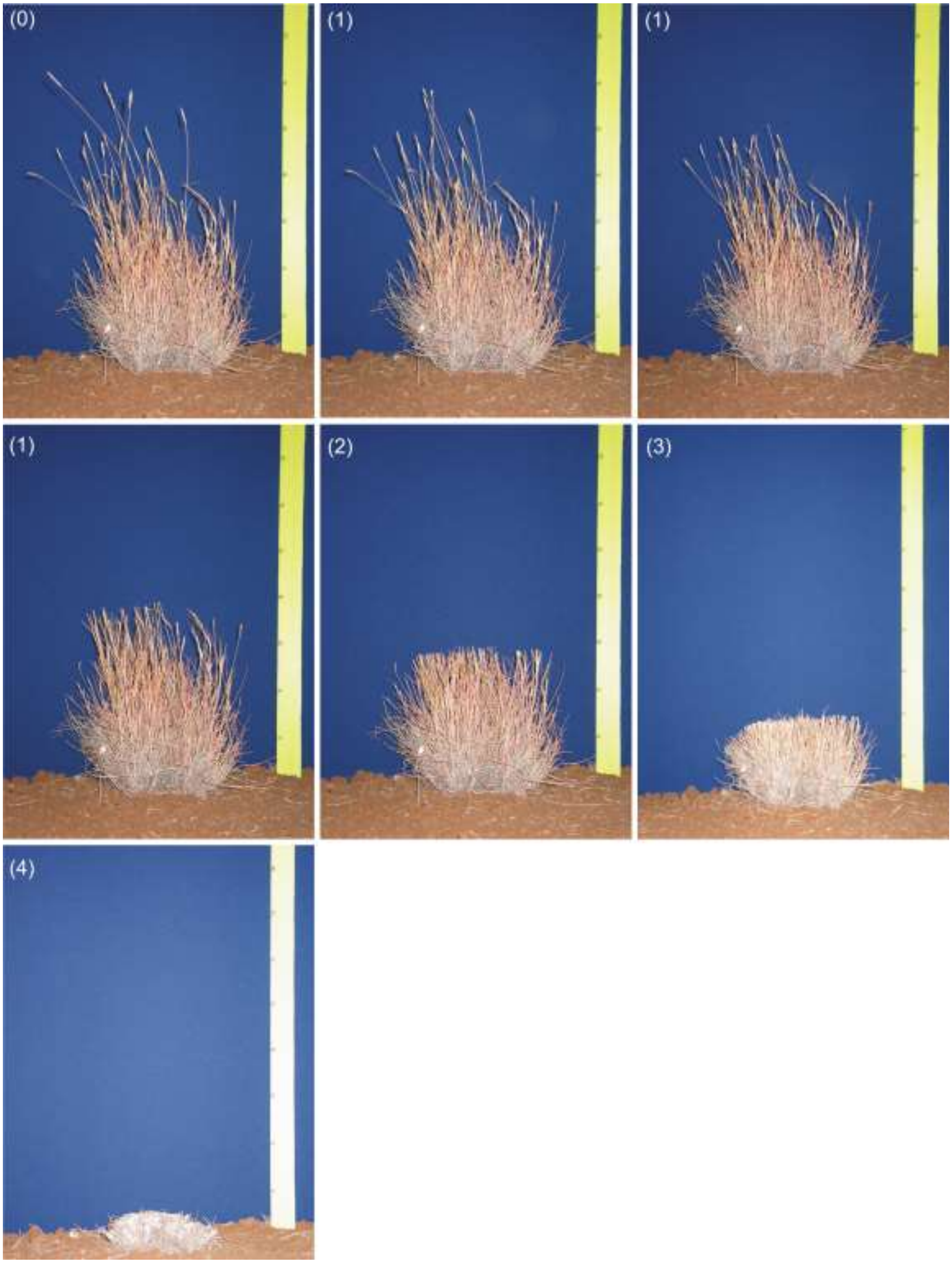
Eragrostis obtusa Steud.



Eragrostis plana Nees.

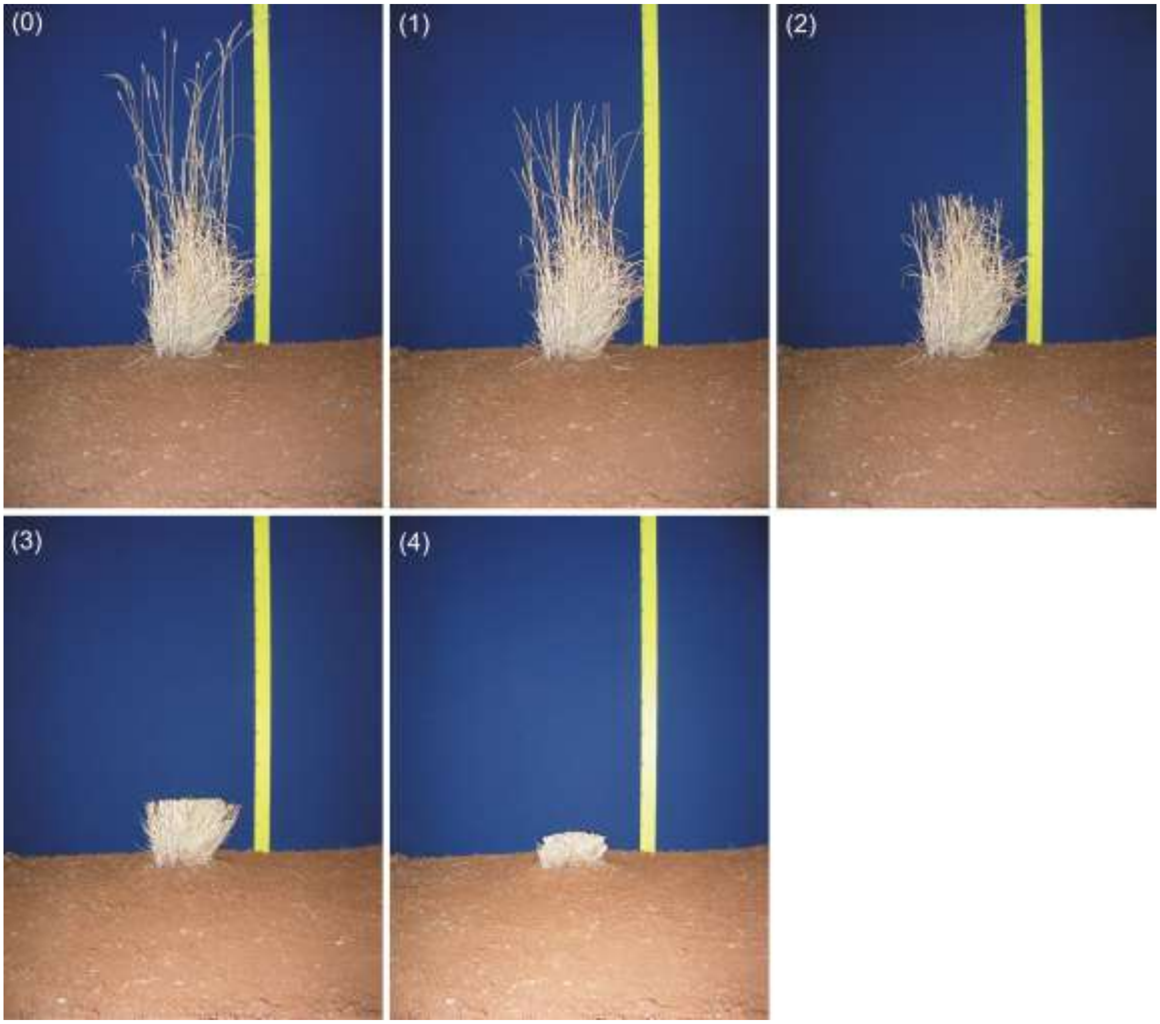


Heteropogon contortus Pers.



Panicum stapfianum L.

Setaria incrassata P.Beauv.



Themeda triandra Forssk.