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A comparison of grass production and utilisation in sodic and crest patches on a semi-arid granitic savanna catena in the southern Kruger National Park, South Africa

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Johannesburg, October 2009

DECLARATION

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

_____

Glynn Frank Alard

(Signature of candidate)

_____ Day of _____2009

ABSTRACT

Grass biomass productivity was measured in sodic and crest patches in the semi-arid (581.8 mm per annum) savanna of the southern Kruger National Park, straddling an herbivory exclosure located on the northern bank of the Sabie River. Sodic and crest patches are ubiquitous landscape elements within the undulating granitic terrain of the Lowveld region of north-eastern South Africa. Sodic patches consistently occupy footslope positions on the catena and are characterised by a sparse cover of woody shrubs, lower herbaceous standing crop and a higher concentration of large mammalian herbivores relative to adjacent crest patches. These characteristics imply that sodic patches possibly make a substantial contribution to the landscape in terms of high quantity or quality forage production. The long-term use of standing crop indices for grassland productivity assessment in the region are from areas subject to natural herbivory, and has created an impression of low grass biomass productivity on sodic patches. The crest and sodic patches were compared for grass biomass productivity, forage quality and utilisation, and were sampled in the growing season (November to May) from 2002 to 2005. Sequential monthly clippings were conducted in permanently located 1 m^2 plots inside the exclosure to determine monthly productivity and outside the exclosure to determine utilisation. Clippings of grass standing biomass were simultaneously collected from 1 m^2 once-off plots inside the exclosure to determine the effects of defoliation on productivity. Sodic productivity was 8.74 ± 2.37 g dry matter m^{-2} $month^{-1}$ where mammalian herbivory was excluded and did not differ significantly from crest productivity both inside or outside the exclosure ($p>0.05$), but was significantly higher than sodic forage yields of 0.15 ± 2.82 g m^{-2} $month^{-1}$ in the presence of sustained mammalian herbivory ($p<0.05$). This indicates that sodic forage is more heavily utilised than crest forage. Productivity was significantly higher in plots clipped once-off than in sequentially clipped plots ($p<0.05$). The patch utilisation differential was investigated by analysing dried productivity clippings for total nitrogen, sodium, carbon and phosphorus. Significantly higher ($p<0.05$) foliar nitrogen (>2% N) and sodium (>0.5% Na) in sodic forage both account for higher sodic utilisation, though relationships are not linear. Mixed and single species grass foliar samples from the study area were analysed for

stable natural abundance nitrogen and carbon isotopes to investigate nitrogen availability and cycling, and water availability, respectively. Relatively higher $\delta^{15}N$ ranges in sodic samples concur with higher sodic soil nitrogen availability and infer relatively higher rates of nitrogen cycling. Relatively higher $\delta^{13}C$ ranges in crest samples concur with lower crest water availability and that crest grass species are more water use efficient. Compared to the sodic patch, crest patches are relatively water and nitrogen limited environments resulting in less fertile grass forage which is less utilised.

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CHAPTER 1: INTRODUCTION

This study was set in the Kruger National Park (KNP), which lies within the semi-arid savanna biome, in the Lowveld region of South Africa (Cowling *et al*. 1997; Low and Rebelo 1998). Savannas make up 12.5% of the earth's land area and are found in the drier tropical areas. They are characterised by a continuous layer of grass cover with a discontinuous tree canopy (Scholes and Walker 1993). The contribution that savannas make to terrestrial primary production is second only to tropical forests (Chapin *et al*. 2002). Primary productivity is affected by many factors including climate, fire, herbivory and man (Knapp *et al*. 1998). The great diversity and abundance of large herbivores, conspicuous in African savannas, makes herbivory particularly important (Scholes and Walker 1993).

The evolution of many species of savanna herbivores (including megaherbivores) is inseparable from savanna evolution. Herbivory, together with water and nutrient availability are key factors determining the composition, structure and functioning of savannas, and indeed grass biomass production (Scholes and Walker 1993). Herbivory and/or mortality accounts for as much as 40% of total net primary productivity (NPP) in some systems (Chapin *et al*. 2002). When the utilised component of production is overlooked, assessing productivity in grazing ecosystems is often problematic (McNaughton *et al*. 1996). This could lead to misjudgements of the environment under investigation, specifically in terms of how much forage is produced and how much is utilised (Naiman *et al*. 2003).

In the history of the management of the KNP, vegetation data sets from crest patches have largely determined the classification of landscapes, and partly that of land types and land systems (Gertenbach 1983; Venter *et al*. 2003). Implicitly this has been translated into homogenous forage production potential values across the given landscapes. As a result, patchiness within these landscapes has been largely ignored, specifically patches where herbivory may be concentrated in the landscape. Much of the generated wisdom that links to existing long-term data sets (e.g. the KNP veld condition assessment (VCA)

network) is based on data generated from crests. For this reason, crest patches are used in this study, to link the results and recommendations closely to the management of the area and the knowledge which has been generated on crest-biased data sets. Past studies in and adjacent to the KNP indicated heavy herbivore utilisation of patches within landscapes, sodic patches being notable among these (Grant and Scholes 2006; Peel *et al* 1999). Sodic patches are open areas associated with footslopes and valley bottoms of catenas. They are characterised by duplex soils with a high pH and 15-20% exchangeable sodium percentage (ESP) associated with dispersed clays (Venter *et al*. 2003). Several studies have investigated soil characteristics, (specifically erosion), together with vegetation and environmental aspects of these patches in semi-arid southern African savannas (Chappel 1992; Dye and Walker 1980; Grant and Scholes 2006; Khomo and Rogers 2005; Scholes and Walker 1993; Venter *et al*. 2003). In the study on sodic patches by Chappell (1992), it is stated that, in the absence of "over-grazing" and erosion, a dense layer of grass cover is produced, but that these patches contribute little to the landscape herbage production, even though they are favoured by many grazing species. However, there is a paucity of data relating to the productivity of sodic patches as a contributor to grass production in the landscape. The established paradigm regarding sodic patches has been reinforced by the following: 1) perpetual low standing crop translating into putative low biomass productivity (Chappel 1992), 2) naturally highly erodable soils translating into "degraded" areas or "management problems" (Chappel 1992; Khomo and Rogers 2005) and, 3) high concentrations of large mammalian herbivores on these patches being attributed to the relative openness of sodic patches (i.e. an anti-predator strategy) (Chappel 1992). Biomass production on these patches has not been researched. Existing erosion of these patches in the region has largely been exacerbated by poor management practices (e.g. road and artificial water-point placement (Venter *et al*. 2003) and although the anti-predator hypothesis has been stated, little empirical evidence exists to substantiate these claims.

In the KNP, standing crop and increaser: decreaser grass species ratios have been used as an assessment of forage production and quality (Trollope *et al* 1989; Trollope 1990; van Oudtshoorn 1999). Increaser grass species increase in abundance with an increase in

utilisation, and decreaser grass species decrease in abundance with an increase in utilisation (van Oudtshoorn 1999). In the context of this study, it is suggested that this method alone is inadequate for understanding herbivore and forage dynamics. In this study it is hypothesised that grass standing crop (which is seemingly always higher on crests than sodic patches (Gertenbach 1983; Chappel 1992)) is removed by mammalian herbivores at a rate and intensity which gives sodic patches their characteristic bare appearance, but that productivity is higher on these sodic patches. The amount of primary production in an ecosystem is determined by temperature, precipitation, light, length of the growing season, nutrient availability, species diversity, herbivory, fire and edaphic features and their interactions (Haddad *et al* 2002; Briggs and Knapp 1995; McNaughton 1988). These are also important in differentiating sodic patches from crests.

Herbivory complicates the determination of grass biomass production. In the southern KNP, an herbivory exclosure which encloses an entire catena has been erected along the Sabie River. The Nkuhlu Research Exclosure, which excludes all mammalian herbivores larger than a hare, makes this study possible (O'Keefe and Alard 2002). Estimated large herbivore biomass in the Skukuza land system between 1980 and 1991 was 27 kg/ha (Naiman *et al*. 2003).

Hypotheses and Key Questions

The aim of this study is to investigate selected ecophysiological grass characteristics in sodic and crest patches within a granitic catenal sequence in relation to herbivory. To facilitate this investigation, I addressed the following hypotheses:

At a $1m^2$ spatial scale, the sodic patches produce significantly more grass than crests, but that at a broad landscape or regional scale crests produce more than sodic patches because sodic patches occupy a significantly smaller proportion of area than crests. In all the granitic land systems of the KNP, crests comprise a larger proportion of the area than footslopes (Venter 1990) and sodic patches are but elements embedded in footslopes (i.e.

in terms of biomass production, sodic sites are probably only important at a smaller scale).

Hypothesis 1: Grass biomass production (at a $1m^2$ scale) is higher on sodic patches than on crest patches of the Skukuza land system in a semi-arid granitic savanna, in both the presence and absence of herbivory, in both wet and dry years at a monthly and seasonal temporal scale. **Two key questions** were included under hypothesis 1: 1) how much higher is grass biomass production ($1m^2$) on the sodic patches than on the crest? 2) do cumulative multiple clippings of the same plot result in similar or lower estimates of productivity when compared with previously unclipped standing biomass?

Many parameters are used to define forage quality including, palatability (influenced strongly by carbon (C):nitrogen (N) ratios), digestibility and crude protein content and the content of nutrients and minerals which are limiting to herbivores. In this study, the following indices will be used to determine relative forage quality: C:N ratios, N content, sodium (Na) content, phosphorus (P) content and N:P ratios. Sodium and P content are important minerals determining forage selection while N concentrations relate more to palatability and digestibility (Naiman *et al*. 2003). Phosphorus and N are important to both plants and animals for growth (Scholes and Walker 1993). In herbivores, P is present in a number of structural components and is part of many biochemical reactions (Ternouth 1990). Plants are often N or P limited. Foliar N:P ratios have been used to directly determine whether plant communities are either N or P limited, though these thresholds vary greatly between ecosystems (Tessier and Raynal 2003; Koerselman and Meuleman 1996). Sodium is important as a macronutrient, and is a critical ion in the process of osmoregulation (Michell 1985). Large grazing ruminants (including cattle) show marked preference for forage with high Na levels (McNaughton 1988; Grant and Scholes 2006; Morris 1980). Sodium is not an essential nutrient to grasses, but it is to mammals, which are frequently Na limited (Scholes and Walker 1993). If freely available, ruminants will consume Na in quantities greatly exceeding their requirements (Michell 1985). It is hypothesised that sodic forage is of higher quality relative to crest

forage, and even though sodic patches occupy a relatively small landscape proportion, higher forage quality make sodic patches important at the landscape scale.

Hypothesis 2: Forage quality is higher in sodic patches than on crests, which leads to higher utilisation by herbivores. **Four key questions** were included under hypothesis 2: 1) how much higher are levels of total N, C, Na and P in the foliar material of sodic patch grasses than crest grasses? 2) what is the relationship between forage quality in the crest and sodic patches and soil N-availability? 3) what is the extent of utilisation on the sodic patches ($1m^2$) when compared with the crest patches during a dry and wet year? 4) what is the relationship between forage quality, production and utilisation?

Soil N-availability is an important index to use in order to compare areas with different production potentials or strategies. Co-occurring soil and foliar stable $\delta^{15}N$ isotope values help to determine broad differences in soil N-availability between sodic and crest soils. It is important to determine differences between sodic and crest patches in order to make broad inferences about biomass production and quality differentials between sites (Garten and Van Miegroet 1994; Dawson *et al*. 2002). Furthermore, foliar $\delta^{15}N$ values are used to indicate differential attributes of N-cycling in crest and sodic patches. These isotopic values have been used as indicators of differential uptake, loss or different N-sources (Martinelli *et al*. 1999; Amundson *et al*. 2003). Anticipated differences in these values may elucidate possible production strategies relating to N-limitation or mechanisms for heavy defoliation (Dawson *et al*. 2002).

Water Use Efficiency (WUE), is defined as the C gain per unit of water lost, and thus relates directly to production strategies. The WUE attributes of a plant are largely determined by genetics through evolution, and environmental conditions (Chapin *et al*. 2002). Water limitation is the environmental condition which would differentiate between sodic and crest patches, which would imply different WUE levels in the different patches. Foliar $\delta^{13}C$ levels have been often used as an index for assessing WUE (Dawson *et al*. 2002) and will be used in this study to make inferences about anticipated differences in biomass production levels as a function of water availability. The

assumption of this study is that precipitation is the same across both sites (sites are in close proximity to each other; <50m apart), but that water availability to the plants will differ due to landscape position, soil texture, chemistry and surface condition, though inter-annual precipitation variability must also be taken into account.

Hypothesis 3: Grasses growing on the relatively water and nutrient limited crest have higher $\delta^{13}C$ values and lower $\delta^{15}N$ values than grasses on sodic patches. **One key question** was included under hypothesis 3: what is the range of $\delta^{13}C$ and $\delta^{15}N$ values of *Sporobolus nitens* (a dominant grass species from the sodic patch), *Digitaria eriantha* (a dominant grass species from the crest), and *Urochloa mossambicencis* (a grass species found in both the crest and sodic patches)?

CHAPTER 2: LITERATURE REVIEW

2.1 Savannas

Savannas are second in terms of global terrestrial primary production after tropical forests and occupy almost half of Africa (Scholes and Walker 1993). In Africa, savannas support most of the human population and livestock agriculture. Savannas occur in the drier tropical areas of the earth and are characterized by the coexistence of trees and grasses where there is a continuous grass canopy and discontinuous tree canopy. The interactions between the trees and grasses are unique and complex and both components have a strong effect on ecological processes such as hydrology, nutrient cycling and primary production (Scholes and Walker 1993). The composition of the tree-grass communities in semi-arid savannas is controlled among others by light, temperature, climate seasonality, water, nutrients, herbivory and fire (Van Wilgen *et al.* 2003; Scholes and Walker 1993). None of these factors can be considered in isolation as the amount of water and nutrients available in the soil affects the amount of biomass (fuel load) that is present. Herbivory reduces the biomass which may reduce fire occurrence and the climatic conditions determine the conditions which allow or prevent fires (Van Wilgen *et al.* 2003).

Globally, savannas and grasslands differ with respect to geology, rainfall and temperature. The KNP is similar to semi-arid parts of the Serengeti National Park (SNP) in rainfall, but is much warmer on average than Yellowstone National Park (YNP), while Lamto savannas are among the most warm and moist in the world (Figure 2.1).

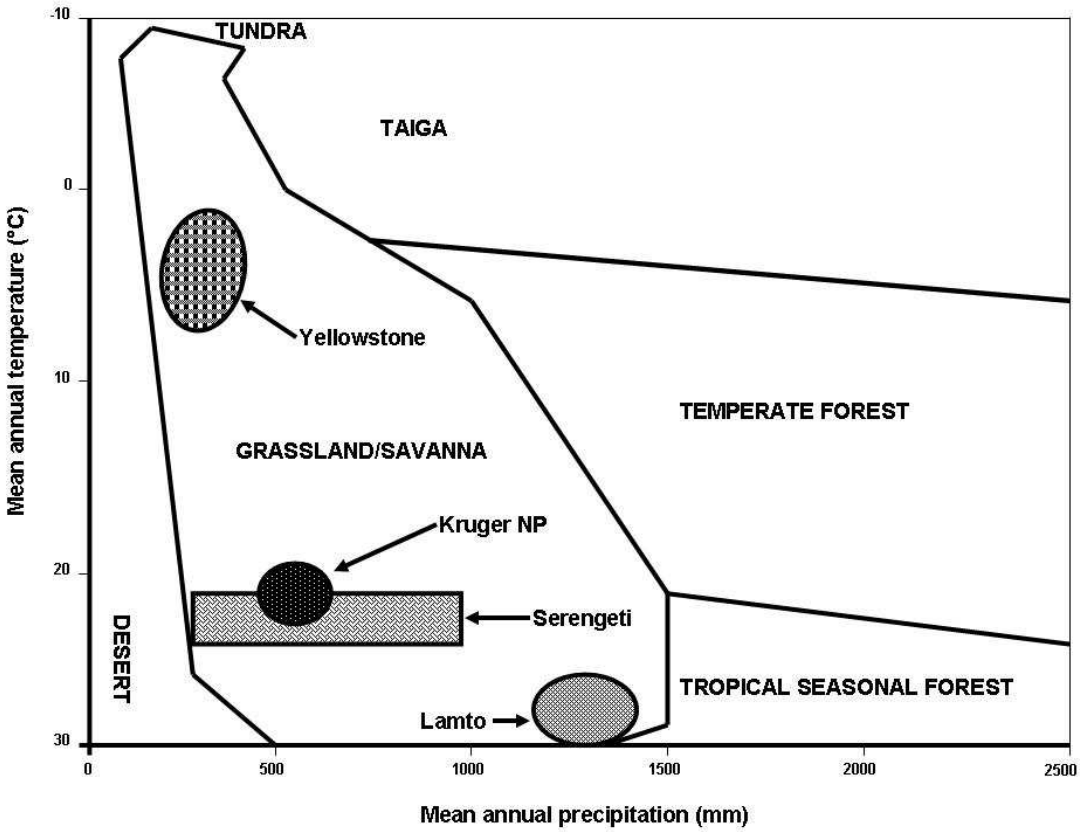


Figure 2.1: The approximate placement of the Kruger National Park savanna relative to the savanna of Serengeti National Park, East Africa; the tropical grassland of the Lamto Reserve, West Africa and the temperate grassland of Yellowstone National Park, North America in Whittaker's (1975) climate diagram (adapted from Leriche et al. 2003 and Frank et al. 1998)

2.2 The Skukuza land system

The KNP is roughly bisected geologically and climatically: granite underlies the western half and basalt the eastern half, with rainfall decreasing from south to north. Although the Lowveld savanna region is semi-arid, the southern KNP receives an annual mean rainfall between 500 and 700 mm. This wetter region of the KNP is known as the Skukuza land system, dominated by *Combretum zeyheri* and *Combretum apiculatum* savanna (Venter *et al*. 2003) and this study was conducted within this landscape type (Figure 2.2).

The thin sandy mantle of the western KNP has been formed in semi-arid conditions from the weathering of underlying Na-rich, acidic granites, resulting in the undulating landscape of the Skukuza land system (Venter 1990). This undulating landscape is characterised by broad, rounded, convex crests, generally straight midslopes, and well defined, concave footslopes. These sequences of crests, midslopes and footslopes give rise to the catena phenomenon. Catenas are common and in this context refer to associations of soil forms and vegetation communities occurring in a predictable sequence along a hillslope (Chappel 1992). This study selects and compares two patch types which are embedded in this catena – crest patches and sodic patches.

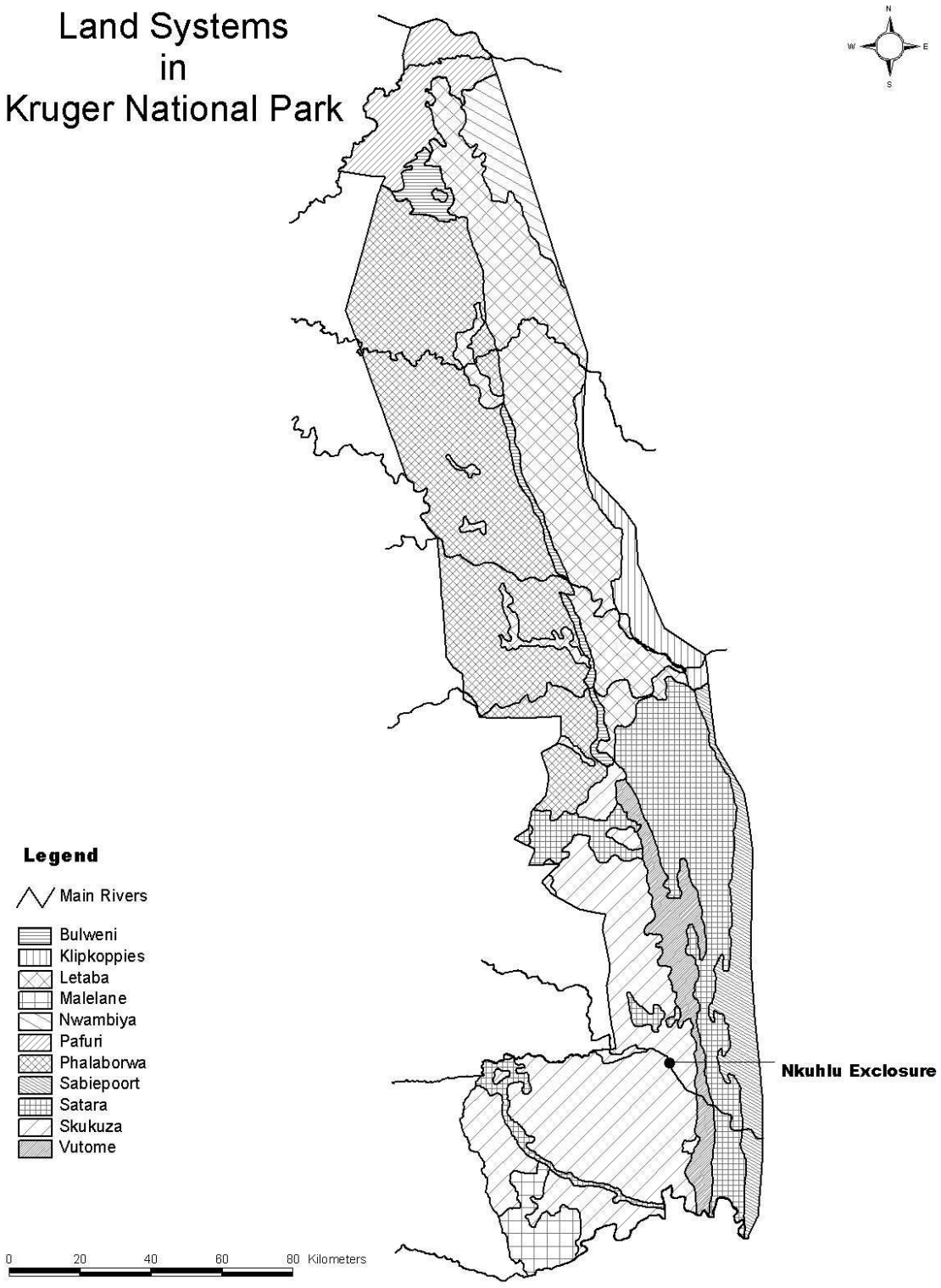


Figure 2.2: Land systems of the Kruger National Park (Venter 1990), indicating the position of the study area (the Nkuhlu Research Exclosure)

2.3 Catenas – crest and sodic patches

The topography of the landform has a marked influence on soil profile and catenary development, since this development is dependant on slope for flux of water, particulate matter and solutes both downward through the profile, and in a downslope direction (Chappel 1992). Ion movement and clay illuviation are dominant soil-forming processes, with distinct soil horizons and catenary sequences being the result (Scholes and Walker 1993). Mobile clays are weathered from the parent rock at the crest. Transport takes place down the hillslope through the process of illuviation (seasonal pulses of soil water moving laterally through the soil). The clays are deposited in the footslope, resulting in bands of clay-rich and clay-poor soil profiles along the hillslope, parallel to the slope contours. These weathered granites also release sufficient Na to promote clay dispersion, or deflocculation, especially in sodic patches (Chappel 1992; Dye and Walker 1980; Khomo and Rogers 2005). Soil profiles occur in a specific sequence down the hillslope; sandy, hydromorphic, duplex and alluvial (Venter 1986), and are observed to be associated with specific vegetation assemblages (Venter *et al*. 2003). These predictable soil profile sequences along the slope and plant-soil associations are termed a catena.

In the various studies on catenas in the region (Chappel 1992; Khomo and Rogers 2005; Venter 1990), the terms crest, midslope, footslope and valley-bottom or channel have been used, mostly referring to landform and spatial position along the slope. Studies relating to soil-vegetation associations or ecosystem function have used the terms broad-leafed savanna, crest or uplands, seepline, sodic patch, fine-leafed savanna, ephemeral wetland and riparian. These terms are not interchangeable, and are heavily context dependent. In the context of this study, the terms crest patch, seepline, sodic patch, ephemeral wetland and riparian zone will be used. The riparian zone will not be discussed. The seepline will be viewed as a boundary element between crest and sodic patches, and the ephemeral wetland will be viewed as a boundary element between the sodic patch and the riparian zone.

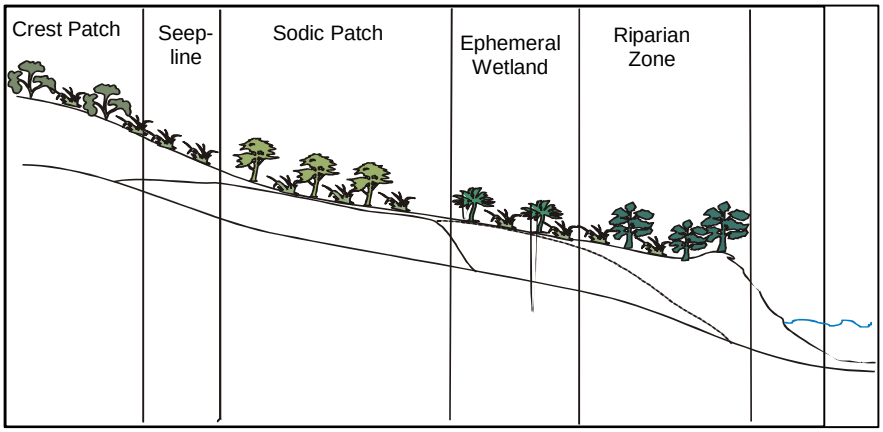


Figure 2.3: Schematic diagram of the Lowveld granitic catena indicating the five landscape positions

Crests situated at the top of the catena (Figure 2.3) in the Skukuza land system are characterised by moderately deep, red, apedal, sandy soils on bedrock. A nutrient-poor broadleaf savanna, relative to the lower slope, characterised by *Combretum zeyheri* and *Combretum apiculatum* with a scattering of *Sclerocarya birrea* subsp. *caffra* is found. An ample sward of grass is generally to be found on crests throughout the year; the species *Digitaria eriantha*, *Panicum maximum*, *Pogonarthria squarrosa* and *Aristida congesta* being commonly found (Chappell 1992; Venter *et al*. 2003; Scholes *et al*. 2003; Scholes and Walker 1993).

Sodic patches are open areas with low standing herbaceous biomass and are usually associated with lower footslopes and valley bottoms of especially granitic catenas (Venter 2003). These patches consistently occupy footslope positions (Figure 2.3), and as such are associated with hydrological drainage lines. These patches form discontinuous, patchy boundaries between the riparian and upland zones. They are particularly prevalent in river bends and have the general appearance of an open savanna, with a sparse scattering of medium-sized shrubs and a very short grass layer (Khomo and Rogers 2005). Sodic patches occur where the soils are affected by the accumulation of mono-valent Na ions and the electrolyte concentration determines the Na concentration at which the soil structure is modified (Sumner 1993). Sodium modifies the soil by dispersion; the

mono-valent Na ions cause mutual repulsion of soil particles resulting in a loss of soil structure (Chappell 1992). These areas experience illuvial clay deposition within the catena. The soil has a distinct duplex structure. A coarsely textured A-horizon of variable depth supports most plant life, and overlays a B-horizon of deflocculated, heavy clay. This almost impenetrable B-horizon may be the limiting factor for the rooting of woody species, accounting for the sparse and short woody layer. Woody vegetation is dominated by thickets of *Euclea divinorum,* and *Acacia grandicornuta*. Commonly found grass species include *Sporobolus nitens* and *Cynodon dactylon* (Chappell 1992).

2.4 Determinants of grass biomass production

2.4.1 Water and Carbon

NPP is the net C gain by plants through the process of photosynthesis using soil water and atmospheric C; also described as the difference between C gained by gross primary production (GPP) and C released by plant mitochondrial respiration (Ovington 1957; Gates 1962; Woodwell and Whittaker 1968; Odum 1968; Leith and Whittaker 1975). Aboveground NPP (ANPP) of tropical savannas and grasslands has been estimated as 540 g DM m^{-2} yr^{-1}; over four times higher than the ANPP of the least productive biomes (desert: 150 g DM m^{-2} yr^{-1} and tundra: 80 g DM m^{-2} yr^{-1}) and just under half the ANPP of the most productive biome (tropical forest: 1400 g DM m^{-2} yr^{-1}) (Chapin *et al.* 2002). Total NPP for the Skukuza land system has been estimated as 419 g DM m^{-2} yr^{-1}, of which 155 g DM m^{-2} yr^{-1} (37%) is grass production (approximately 50% of which is underground: ≈ 77 g DM m^{-2} yr^{-1}) (Scholes *et al*. 2003). This compares well with 60 g DM m^{-2} yr^{-1}, estimated for the aboveground grass layer at the Nylsvley Nature Reserve (NNR), a savanna often compared with KNP (Grunow 1980). Both NNR and KNP estimates are much lower than those reported for Sussex chalk grassland (691 g DM m^{-2} yr^{-1}), ten grasslands in western North America (212 - 236 g DM m^{-2} yr^{-1}) (Grunow 1980), Lamto Reserve savanna in West Africa (non-grazed grass only: 440 g DM m^{-2}) (Leriche 2003) and the SNP savanna in East Africa (664 g DM m^{-2} yr^{-1}) (McNaughton 1985),

where both precipitation (Figure 2.1) and soil fertility are greater than in the study area. NPP is strongly correlated to precipitation and temperature, being highest in warm moist environments, and lowest in cold and/or dry environments (Chapin *et al.* 2002).

Photosynthesis converts light energy into chemical energy (sugars and starches) that is available to support plant growth and maintenance. Photosynthesis takes place in chloroplasts of the mesophyll cells of the green leaf, and is controlled by availability of light energy and water (to produce ATP and NADPH), CO_2 (to produce carbohydrates and release O_2), N (to produce photosynthetic enzymes such as RUBISCO) and temperature (which controls the rate of reactions). Plants regulate CO_2 delivery to the chloroplasts by changing the size of stomatal openings in the leaf. This aims to minimise water-loss through transpiration, and maximise photosynthesis. Atmospheric CO_2 diffuses into the intercellular air spaces of the leaf across a gradient of high to low concentration. The CO_2 then dissolves in water on the mesophyll cell surfaces and diffuses further into the chloroplast. There are two main photosynthetic pathways. C_3 photosynthesis initially fixes CO_2 (carboxylation) using RUBISCO, producing three-carbon sugars, in which 20 – 40% of C is lost through photorespiration. In the C_4 photosynthetic pathway, CO_2 is initially fixed by phospho-enolpyruvate (PEP) in the mesophyll cells during the day, producing four-carbon organic acids which are transported to bundle sheath cells for decarboxylation. The CO_2 released from the decarboxylation then enters the C_3 cycle of photosynthesis. The major advantages of C_4 photosynthesis are that less water is lost and less N is required to maintain a given rate of photosynthesis compared to C_3 plants. Species using the C_4 photosynthetic pathway dominate many warm high-light environments such as savannas. All grass species in this study follow the C_4 pathway, which enables an increase in photosynthetic water use efficiency (WUE) relative to C_3 plants in dry environments (Chapin *et al*. 2002, Hobbie and Werner 2004, Lambers *et al*. 1998).

Naturally occurring stable C isotopes (^{12}C and ^{13}C) differ in the number of neutrons but have the same number of protons. ^{13}C has a concentration of -8‰ in atmospheric CO_2 and is expressed as an isotope ratio ($\delta^{13}C$). ^{13}C is the heavier isotope, and reacts more slowly in some reactions, particularly carboxylation of CO_2 by RUBISCO. In C_3 plants

^{12}C (the lighter isotope) is preferentially fixed and assimilated (Lambers *et al*. 1998). This is called fractionation or, discrimination against the heavier isotope. Fractionation – discrimination/partitioning of heavy (^{13}C) and light (^{12}C) isotopes between a source substrate ($C_{atmosphere}$) and the product (C_{foliar}) of stable C isotope ratios between the atmosphere and the intercellular environment varies in response to many factors. These include soil moisture, low humidity, irradiance, temperature, N-availability, salinity and morphological features such as leaf boundary layer resistance, hydraulic conductivity and leaf internal resistance to CO_2 and H_2O (Dawson *et al*. 2002). C_4 plants have a distinct and relatively small isotopic signature range, closer to the atmospheric ^{13}C concentration (-11 to -15‰ using $\delta^{13}C$ notation), as they incorporate much more ^{13}C than C_3 plants during photosynthesis. PEP carboxylase has a very high affinity for CO_2, reacting with most of the CO_2 entering the leaf. Therefore, there is little discrimination against the heavier $^{13}CO_2$ in C_4 photosynthesis (Chapin *et al*. 2002). C_3 plants typically have $\delta^{13}C$ ranges of between -25 to -29‰ (Lambers *et al*. 1998).

$\delta^{13}C$ data have often been used as an index for assessing WUE. Generally, the closer the range of values of foliar $\delta^{13}C$ are to that of the atmospheric standard value (-8‰) the higher the WUE of the plant (Chapin *et al*. 2002; Dawson *et al*. 2002, Lambers *et al*. 1998). However, $\delta^{13}C$ – and WUE – levels are known to be species dependent, although these levels have been shown to vary intraspecifically from site to site (Garten and Van Miegroet 1994; Dawson *et al*. 2002). Much published work linking $\delta^{13}C$ to water use efficiency comprise the use of C_3 plants, while C_4 plants in southern Africa display no relationship between precipitation and $\delta^{13}C$ (Swap *et al.* 2004). Plants sampled in this study are all C_4 plants, but significant statistical findings in the pilot study justify the exploration of the use of $\delta^{13}C$ in investigating water limitation between crest and sodic sites, and possibly WUE differences in C_4 plants in the study site.

Aboveground grass NPP in semi-arid savannas areas has a positive linear relationship with precipitation received in the growing season (Knapp *et al.* 2006, Scholes *et al*. 2003). Soil moisture however, is often a better correlate as the soil provides a storage component, reflecting previous years' excesses or deficits in water availability (Knapp *et al*. 1998). As explained earlier, sodic and crest patches receive the same precipitation but

have very different soil characteristics. Not only does this result in different soil moisture between sites, but plant available water (PAW) will also differ. PAW in this context, is a more useful index than soil moisture and was measured in this study.

PAW is the water that can be stored in soil and be available for plant uptake, and is defined as the difference between the soil's water content at field capacity (i.e. water retained after gravitational water has drained) and permanent wilting point (i.e. the point at which water is no longer available to the plant and the plants wilt) (Kramer 1949; Slayter 1967; Larcher 1975). In this study soil moisture was measured using a combination of tensiometers to measure water matric potential (the tension with which the soil retains water) and time-domain reflectometry (TDR) to measure volumetric water content (the volume of water per the volume of soil) (these methodologies described in section 3.1.6). Sodic soil in the study site retained water at a significantly greater mean pressure of 3291.4 mm than crest soils which retain water at a mean of 2223.9 mm. The wetter sodic soils yielded a mean of 0.31 m^3m^{-3}, compared to crest soils which yielded a mean of 0.13 m^3m^{-3}.

In each soil type, there is a unique relationship between the volume of retained water, and the tension at which it is held in the pore spaces. This relationship is called the water retention characteristic and is governed by the distribution of pore sizes in the porous medium (Carsel and Parish 1988). A relationship curve is described for each medium or soil type (sand, clay, loam, etc). This relationship can be plotted by testing soil samples directly, or by estimation according to soil texture (Carsel and Parish 1988; Zeleke and Si 2005). Soil textural classes in the study area are sandy loam for crest soils, and sodic soils are sandy clay loam (Fisher 2006). In the same study by Fisher (2006), gravimetrically measured soil moisture and water retention was always higher in sodic than in crest soils. Dye and Walker (1980) report much slower infiltration rates for the B horizon than for the A horizon in sodic soils of Zimbabwe. Saturated hydraulic conductivity (K_{sat}) tests for both sodic and crest surface soils were conducted in 2002 by UKZN staff when tensiometers and TDR instrumentation were installed in the study site. For sodic soils, a K_{sat} of 0.66mm.h^{-1} fell within the conductivity range of sandy clay, and crest soils

resulted in a K_{sat} of 45.07mm.h^{-1} which fell in the conductivity range of sandy loam. Results from saturated conductivity tests performed in the study area compares well with Fisher's (2006) textural classes, as sodic soils have higher clay contents than crest soils (Table 2.1). Typical water retention characteristic variables for sandy loams and sandy clays have been estimated from Carsel and Parish, (1998) and Lorentz *et al*. (2000) and the resultant water retention characteristics are presented in Figure 2.4. These water retention characteristic curves were used to estimate PAW for each soil type.

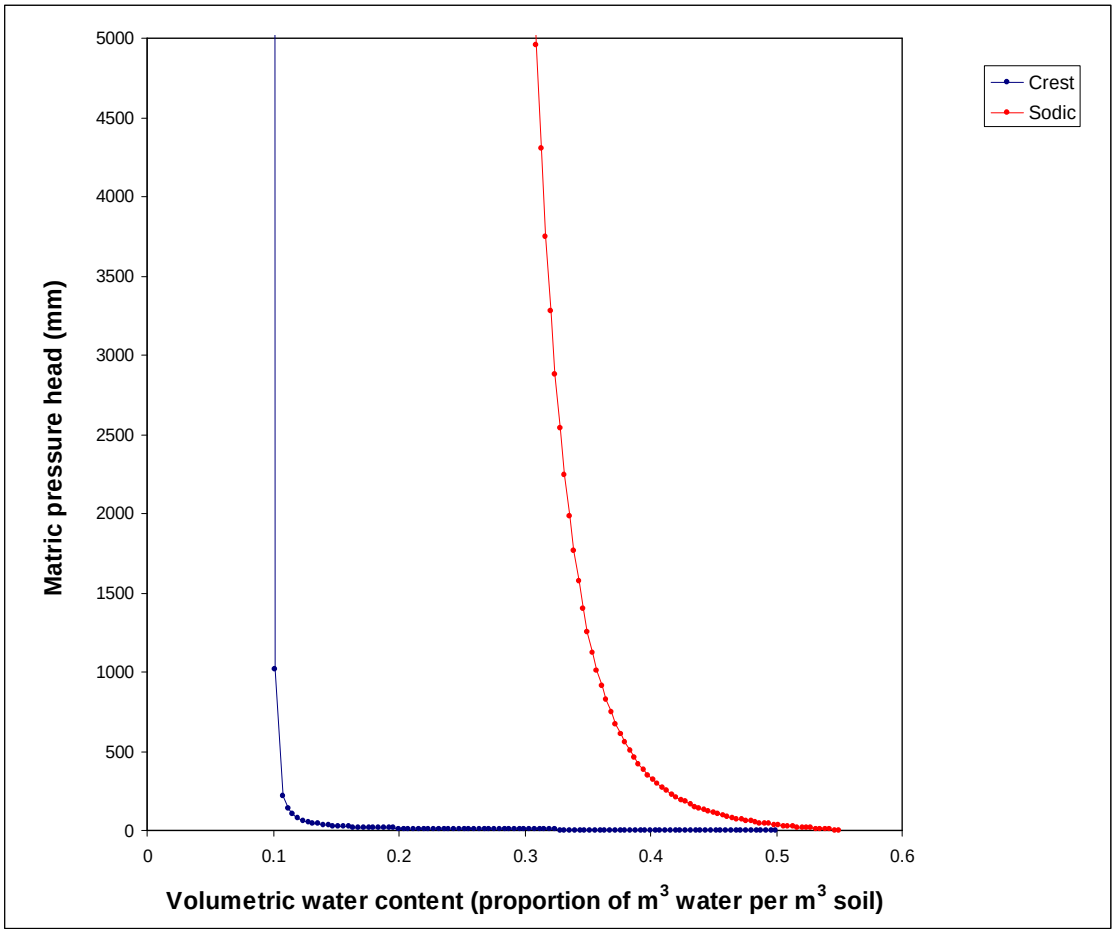


Figure 2.4: Estimated water retention characteristics for the surface (10 cm) soils at the crest and sodic patches, transect 7, Nkuhlu exclosure (drawn by the author using data from Lorentz et al. 2000)

At soil moisture levels of above 20%, clay soils generally have higher PAW than sandy soils under the same precipitation levels (Chapin *et al*. 2002). It was therefore expected that during the growing season sodic soils would have higher PAW than crest soils. The higher PAW will enable the sodic soils to support higher grass biomass production. A more sandy soil, with relatively large pores will hold water under lower tensions than a more clay soil (Chapin *et al*. 2002). As soon as the soil water tension is increased (by drainage, drying through evaporation or transpiration), most of the water is drained, decreasing the water content considerably. The remaining water (hygroscopic water) is held in the pore space and by surface tension. It requires significant increases in soil water tension to remove this hygroscopic water from the soil. Clay (particle size < 0.002mm) has a large distribution of pore sizes, with pores much smaller than sand (particle size 0.05 to 2mm) and a larger porosity (Chapin *et al*. 2002). Sandy loam (as found in the crest) has an average porosity of 43%, and sandy clay (as found in the sodic patch) has an average porosity of 51%. This means that clayey materials retain water within the pore space over a large range of soil water tensions. However, relative wetness and retention does not reveal where plant available water availability is higher.

According to the water retention characteristic curves (Figure 2.4) for the sandy clays (sodic) and sandy loams (crest), at a mean tension of 3291 mm (matric pressure head) sodic soil (sandy clay) should yield a water content of 0.32 (m^3 water per m^3 soil) and at a tension of 2223 mm crest soil (sandy loam) should yield a water content of 0.10. These values relate accurately to the observed water content (TDR) presented in section 3.1.6, where sodic soils yield a mean of 0.32 and crest soils yield a mean of 0.13. These monitored differences can therefore be ascribed to the differences in hydraulic characteristics of the soils due to the difference in textures.

The plant available water (PAW) is normally defined by taking the difference between the volumetric water content at a tension of 0.1bar (1000 mm) (Ward & Trimble 2004) - and the residual water content (determined by the saturated hydraulic conductivity tests at each site) (Lorentz et al. 2001) of the water retention characteristic. The residual water content of sodic soils is 0.18 and 0.1 for crest soils (Table 2.1). In this case the PAW

would be 0.002 for the crest soils and 0.18 for sodic soils (Table 2.1). Sodic soils therefore have a much higher PAW than crest soils and the vegetation at the crest patch obviously would have to make use of water uptake during the drainage period and of water deep in the profile or at the soil/bedrock interface.

Table 2.1: Water retention characteristics derived for the Crest and Sodic site (courtesy of Lorentz, unpublished 2008)

Site	Ksat (mm/h)	Texture		Saturated water content	Residual water content	Plant available water
		From Ksat	From Fisher 2006			
Crest	45.07	SaLm	SaLm	0.50	0.10	0.002
Sodic	0.66	SaCl	SaClLm	0.55	0.18	0.180

Since sodic soils are less water limited than crest soils, it is further expected that grasses sampled from the crest need to be more WUE. In other words, crest soils, which have a higher hydraulic conductivity, will absorb relatively more precipitation, but will retain water for a relatively shorter period than sodic soil. Sodic soils will not only retain much precipitation, but will also be recharged by water from crest soils through the lateral movement of soil water. It is expected that crest patch grasses are more water-limited and therefore will be more enriched with ^{13}C than sodic patch grasses. Wheat cultivars grown under dry conditions had a higher WUE and lower $\delta^{13}C$ than cultivars well supplied with water (Farquhar and Richards 1984). Even though genetic controls over WUE and $\delta^{13}C$ have been established, and $\delta^{13}C$ ranges for C_4 and C_3 plants are discrete, WUE was negatively correlated to lower $\delta^{13}C$ (≈-25; were the total range did not differ by more than 1‰) values in *Eucalyptus* clones (Le Roux et al. 1996) in South Africa. In Australia, a wide variety of C_3 species were sampled for $\delta^{13}C$ along a rainfall gradient. Higher (-20 to -26‰) $\delta^{13}C$ community mean values were revealed in plants from arid areas, than those from high rainfall areas (-27 to -34‰) (Stewart *et al*. 1995). Stewart (1995) suggests that $\delta^{13}C$ is a better indicator of environmental water availability over time, than WUE *per se*, which is difficult to measure in the field.

2.4.2 Nutrients

The availability of N and P is seen as the main limiting factor for grassland productivity in savannas (Augustine and McNaughton 2004; Augustine et al. 2003; Scholes et al. 2003; Scholes and Walker 1993). In the KNP, on the catenal scale, footslopes – and indeed sodic patches – typify nutrient-rich fine-leafed savannas, relative to crests which typify nutrient-poor broad-leaf savannas (Scholes *et al*. 2003). The P cycle is almost entirely restricted to cycling in the soil-plant system, with a large organic pool of P which is converted to plant available forms through a variety of physical, chemical and biological processes. The nitrogen cycle is a fairly open cycle with a large atmospheric component and many processes where nitrogen can be lost to the atmosphere. Denitrification and volatilisation are just two avenues of gaseous N loss from systems (Scholes *et al*. 2003, Chapin *et al*. 2002).

Soil N availability in the Lowveld region seems to be highly variable spatially and temporally, at wide-ranging scales, and is strongly linked to rainfall events and soil moisture which is determined by soil texture (Fisher 2006; Scholes *et al*. 2003). Studies in the park have not been able to establish clear relationships between soil and foliar N, nor were the highest soil N levels correlated to favoured grazing patches at multiple scales in the region, in both sodic and crest patches (Grant and Scholes 2006).

In the Skukuza land type (embedded in the Skukuza land system, and including the study area), Bray soil phosphorus (P) increases from the crest (±5 mg $P.kg^{-1}$ soil) to (±15 mg $P.kg^{-1}$ soil) the A horizon of the footslope (Venter 1990). Fisher (2006) reports double the amount of total P in the crest (10 mg $P.kg^{-1}$ soil) when compared with Venter's Bray P (1990) but similar amounts for the sodic soils of the Nkuhlu exclosure.

Fisher (2006) reports higher total soil nitrogen (N) means in sodic soils (0.11 %N) than in crests (0.09 %N). Available N (ammonium (NH_4^+) plus nitrate (NO_3^-)) ranges are also higher in sodic soils (5.1 – 13.5 μg $N.g^{-1}$ soil) than in crest soils (1.1 – 4.8 μg $N.g^{-1}$ soil).

Stable isotopes provide insights into biogeochemical interactions between plants, soils and the atmosphere (Evans 2001; Handley and Raven 1992). Plants mediate the flux of energy and materials through ecosystems through gas exchange and water and nutrient uptake by roots. These affect metabolism and resource status of the soil, and eventually feeds back to influence plant function via dynamics of soil nutrients and water availability (Dawson *et al*. 2002). The $\delta^{15}N$ of vegetation and soil is a function of the rate and isotopic composition of inputs and outputs, and the internal N transformations that occur in a plant-soil system. Means of foliar and soil $\delta^{15}N$ in a savanna (Tanzania) were reported as 2.1 to 3.26‰ and -1.5 to -2.1‰, respectively (Amundsen *et al*. 2003).

Plant $\delta^{15}N$ is not only affected by N availability. The following factors can all affect foliar $\delta^{15}N$: multiple N-sources which have isotopically distinct values; mycorrhizal associations, changes in plant demand and temporal and spatial variation in N availability (Dawson *et al*. 2002). Different ^{15}N abundance of coexisting plants may provide information about differences in N_2 fixation, rooting depth, or levels of mycorrhizal colonisation among species (Frank *et al*. 2004). Discrimination is positive in most biological systems and reactions; therefore, the product should have a lower $\delta^{15}N$ value than the substrate (Evans 2001). $\delta^{15}N$ can also give insights into N cycling rates. Mycorrhizae increase the volume of soil exploited by plants, and increase the efficiency of the plant to take up water and nutrients (Chapin *et al*. 2002; Lambers *et al*. 1998), and grass species, *Urochloa mossambicensis* were found to be more frequent in the drier, nutrient poor crest than in the sodic patch (Reid 2005). In east Africa, trees, shrubs and forbs were sampled for both $\delta^{15}N$ and $\delta^{13}C$. High foliar $\delta^{15}N$ were correlated to low foliar $\delta^{13}C$ values, indicating water and N use from a soil which is water-limited but has a rich N-source (Handley *et al*. 1994).

A study of the relationships between soil N dynamics and natural $\delta^{15}N$ abundance found that plants of the same life form group and species became more enriched with ^{15}N as N availability increased. Also, the difference between $\delta^{15}N$ abundance in leaves and soil became smaller along a gradient from N-poor to N-rich forest. Therefore, foliar $\delta^{15}N$ values and enrichment factors ($\delta^{15}N_{foliar}$ - $\delta^{15}N_{soil}$) are correlated to soil N availability,

increased rates of N-cycling and increased loss of N (Garten and Van Miegroet 1994; Dawson *et al*. 2002).

Natural $\delta^{15}N$ abundance data shed light not only on the longer-term N richness, but also on the relative openness of a system with regard to N cycling. The openness of the cycle refers to lesser or greater inputs and outputs of N, relative to lesser or greater internal cycling of N (Dawson *et al*. 2002). Globally, $\delta^{15}N_{foliar}$ values are depleted when compared to $\delta^{15}N_{soil}$ as a result of fractionation (Amundson *et al*. 2003). In a study comparing tropical and temperate forests it was found that $\delta^{15}N_{foliar}$ values from tropical forests were significantly enriched when compared to those from temperate forests (Martinelli 1999). Tropical forests were both more open (increased loss from the system causes further fractionation) and had higher soil N availability. This trend continued when N-rich tropical forests were compared with N-poor tropical forests: more open and less N-limited tropical forests had more enriched $\delta^{15}N_{foliar}$ values than N-poor tropical forests (Martinelli 1999).

^{15}N is discriminated against during volatilisation in open, laboratory systems (Handley and Raven 1992). In YNP, it was found that NH_3 volatilization from urine patches enriched grassland soil with ^{15}N. Soil enrichment was due to the volatilization of isotopically light NH_3. NH_3 $\delta^{15}N$ increased from −28‰ to −0.3‰ and was lighter than the original urea-N added (1.2‰) 10 days earlier (Frank *et al*. 2004). Volatilization increases with soil-pH, which is higher in sodic sites than crests (Fisher 2006). Fisher (2006) also found that the potential denitrification rate is significantly higher in sodic patches than on crests. Denitrification also enriches soil $\delta^{15}N$ (Dawson et al. 2002), preferentially losing the lighter ^{14}N. It is expected that soil and foliar $\delta^{15}N$ values from the sodic patch will be enriched compared to those from the crest. This may indicate that sodic patches experience relatively more open N-cycling (increased denitrification and volatilisation, and increased inputs), and soil-N is more available in sodic patches.

As previously mentioned, productivity can be co-limited by more than one nutrient, in many cases, N and/or P. The most strongly limiting element determines the cycling rates

of elements through the plant (Chapin *et al*. 2002). Foliar N:P ratios have been used to determine whether a system or community is N, P or co-limited (Augustine et al. 2003; Tessier and Raynal 2003; Koerselman and Meuleman 1996). Much early investigation into the use of this elemental ratio was done in a marine environment on algae (Redfield 1958). The "Redfield ratio" (N:P) of 14:1 was tabled, above which algal production responded to P fertilization (P-limited) and below which algae were N limited. In the absence of fertilization trials, the use of this ratio could be a convenient tool to assess nutrient limitation within systems. These elemental ratios are more variable in terrestrial plants, since they have a far greater capacity for nutrient storage (Chapin et al. 2002). It has been suggested that a community averaged N:P ratio is more useful to explore system limitation (Koerselman and Meuleman 1996), as individual species may vary considerably with regard to special P uptake adaptations. In European wetland systems and in the Catskill system, the Redfield ratio was shown to be applicable, while upland systems seem to be both N and P limited at lower N:P ratios than those of wetland vegetation (Koerselman and Meuleman 1996; Tessier and Raynal 2003). Several grassland studies (Kenya, SNP, Sahel) suggest N is limiting <7 and P at >25, though the ratio of sole P limitation was only encountered in the Sahelian study (Augustine et al. 2003). Foliar N:P ratios between 12 and 16 suggest co-limitation. In the study area however, upland grassed seem to be co-limited by N and P, and N:P ratios are not reliable indicators of limitation without conducting interactive fertilization experiments (Craine 2008). The ratios reported for these grassland studies will be used in this study as an assessment of relative limitation. It is expected, since soil P is higher in the sodic patch, that co-limitation would be prevalent in crest foliage.

2.4.3 Herbivory

Migratory herds of ungulates in temperate grassland (e.g. YNP) and tropical savanna ecosystems (e.g. SNP) graze as much as 45% and 65% of the ANPP, respectively (Frank et al. 1998). Grazing pressure in central Kenyan rangeland is consistently high (>60% of ANPP) in dry years, and is greater in nutrient-rich sites (73% of ANPP) than in nutrient-

poor sites (43% of ANPP) in wet years (Augustine *et al*. 2003). Various studies in semi-arid savannas have indicated that areas intensely utilised by herbivores often have higher biomass production (McNaughton 1989, Turner *et al*. 1993). Augustine *et al*. (2003) found that variation in ANPP in central Kenya was correlated to consumption rates of large ungulates. In some ways, grazing by large mammals may mimic the effects of fire. For instance, altering the canopy structure which increases light relative to ungrazed sites. Holdo et al. (2007) suggests that the only strong effect of herbivores on both productivity and soil N occurs via the indirect reduction of pyrodenitrification through consumption of above ground plant parts vulnerable to fire. Grazing is heterogenous spatially and temporally, at multiple scales. Species responses and shifts, and aboveground NPP in response to grazing are mediated by below-ground storage status, soil nutrient availability and soil moisture. In North American tallgrass prairie, compensatory growth occurs in sites not grazed the previous year, while sites subjected to two years of grazing do not display compensatory growth (Knapp *et al*. 1998). A similar trend was revealed in Lamto savannas of West Africa, where unclipped grassland plots produced more than regularly clipped plots (Leriche *et al*. 2003). Within one growing season in another tallgrass prairie study, higher mowing frequencies resulted in highest biomass productivity, and higher foliar N and P levels (Turner *et al*. 1993), although the accumulation of belowground N and P reserves was limited. Although Lamto productivity decreased with clipping, N and P foliar levels also increased with clipping (Leriche *et al*. 2003). In YNP, herbivores elevated N:P ratios in vegetation as a result of enhancing foliar N concentration (Frank 2008). The photosynthate that would have been stored as reserves, or used for root, flower and seed production, is instead used to replace lost leaf area. In the short term, previously ungrazed sward may respond positively to utilisation, but in the long term, production and quality may be limited by insufficient root biomass or stored nutrients (Turner *et al*. 1993, Frank 2008). Milchunas and Lauenroth (1993) summarized a large number of empirical studies in a meta-analysis, and found that although grazing does at times appear to increase productivity, in most cases it had a negative or neutral effect on plant growth.

Grazing lawns in east Africa as described by McNaughton (1989) indicated that a strong herbivory feedback maintains the structure and function, and not the edaphic variability. It is thought that in most southern African savannas, edaphic variability, such as is found in the catena, gives rise to and supports specific vegetation assemblages, and that these patches attract herbivores according to the differential nutrient status of the vegetation (Grant and Scholes 2006; Naiman *et al*.2003; Scholes and Walker 1993). How intense herbivory influences the biomass production in the study area is poorly understood, as most studies focus on peak-season clippings exposed to herbivory or where herbivory is excluded. This study will use a combination of methods in order to gain a greater understanding of how herbivory influences production.

In YNP grasslands, grazers simultaneously increased soil N availability (stimulated net N mineralization and nitrification per unit area) and N conservation (reduced N loss from the soil per unit net N mineralization) (Frank *et al*. 2000). In the same study, grazed grassland with high rates of N cycling had substantially lower soil $\delta^{15}N$ relative to values expected for ungrazed grassland with comparable net N mineralization and nitrification rates. These soil ^{15}N results suggest that ungulates inhibited N loss at those sites. Therefore, large herbivores regulate grassland processes by partly controlling N availability to plants, microbial productivity, and N retention.

Using a grazing tolerant grass (*Poa pratensis*), another YNP study revealed that grazing promoted root exudation of C, which was quickly assimilated by the microbial population in the rhizosphere of clipped plants (Hamilton and Frank 2001). The effects of the C exudates was positively correlated to larger soil inorganic N pools, increased plant N uptake, higher leaf N content, and increased photosynthesis. Therefore, there is a general positive feedback mechanism by which herbivory promotes plant regrowth as well as energy and nutrient flows in grazed landscapes. Abandoned cattle kraals or bomas, have been found to be more fertile than the surrounding landscape many decades after abandonment in the semi-arid savannas of eastern and southern Africa (Augustine 2003; Augustine *et al*. 2003; Scholes and Walker 1993). In fact, both livestock and grazing

wildlife are key in redistributing N and P from the landscape into these patches through preferential utilisation of these nutrient hotspots.

Grant and Scholes 2006 showed in their study which involved comparing forage utilisation between crest and sodic patches among others, that crests were the least utilised zones, while sodic patches were found to have significantly higher utilisation scores. Using dung occurrence and game counts as an index of presence, it was also found that large mammalian herbivores spend much more time on sodic patches than on crests (Figure 2.5) throughout the year, except at the end of the dry season (unpublished data Grant 2003). On investigation of foliar nutrient contents, significantly higher levels of Na was the only mineral which separated sodic patches from crests (Grant and Scholes 2006). In east Africa, patches with higher levels of foliar Na supported higher concentrations of large mammalian herbivores than patches with significantly less foliar Na, though these patches did not differ edaphically (McNaughton 1988), whereas crest and sodic patches in the study area do differ edaphically (Grant and Scholes 2006, Venter 1990). These studies highlight the role of nutrients in determining herbivore distribution and possibly, biomass production. The role of Na is especially important to mammals in semi-arid ecosystems (McNaughton 1988; Scholes and Walker 1993). Investigating Na foliar content in sodic patches and crests is expected to be important in explaining reported preferential grazing on sodic patches. Sodium is sought after by ruminants, even though their nutritional requirements are satisfied (Michell 1985).

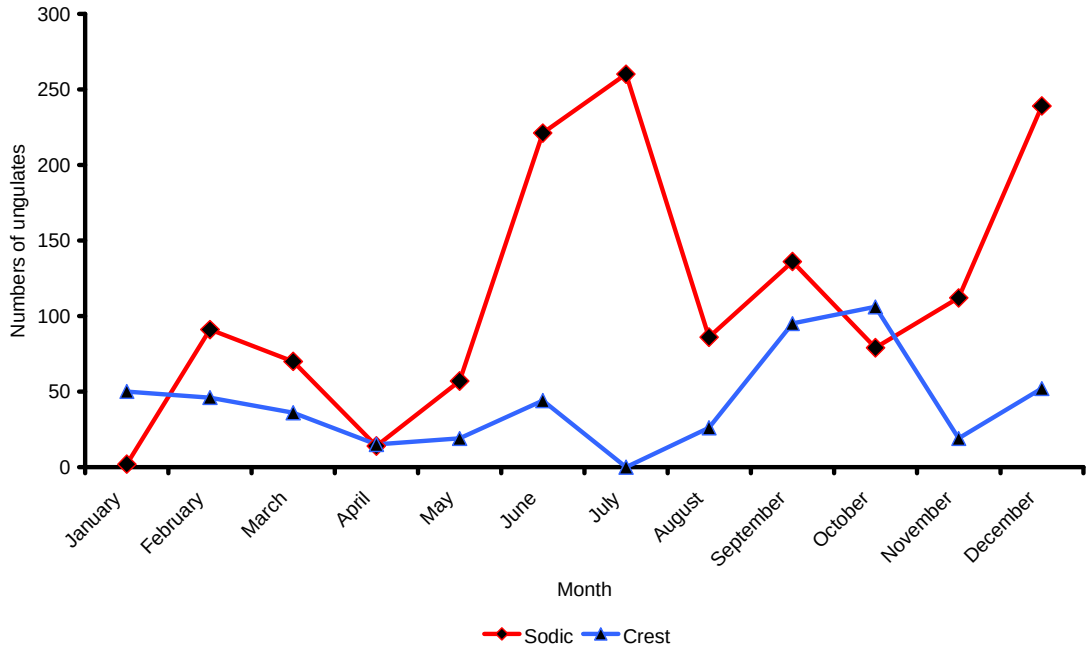


Figure 2.5: Unpublished data collected by Grant (2003) in the Skukuza land system, indicating number of grazing animals per month in sodic and crest patches

Sodic patches in the KNP and Nysvley Nature Reserve are always highly utilised and mammalian herbivores show great preference for these areas, despite a very low standing crop throughout the year (Scholes and Walker 1993; Grant and Scholes 2006). This study suggests that sodic patches produce more grass biomass than crest zones at the $1m^2$ scale, but since defoliation occurs at a rate which prohibits significant biomass accumulation, the standing crop assessment method would always grossly underestimate the production potential of these patches. This has implications for increasing understanding of herbivore distribution spatially and temporally, as well as heightened awareness of the importance of these forage patches and their contribution to the greater landscape as a possible source of relatively high quality and high quantity forage, and a sink for nutrients in the larger landscape. Large grazing mammals respond to heterogeneity in soil and plant nutrients across the landscape, and may play an important role in maintaining the nutrient enriched status of highly productive and intensively grazed sites (Augustine *et al.* 2003).

2.4.4 Topography

In mesic and semi-arid areas, footslopes have been shown to be more productive than relatively nutrient-poor uplands in terms of grass biomass production. At the catena scale, whether burned or unburned, footslopes have consistently higher grass production levels compared to the crests in tall-grass prairies of the central US (Briggs and Knapp 1995). This same trend was reported for the semi-arid savanna of the northern KwaZulu-Natal savanna Lowveld, under various agricultural grazing treatments in commercial rangeland (Fynn and O'Connor 2000). It is expected that this study will reveal the same trend that sodic patch grass biomass production is greater than that of the crest. Within the study area, the land type (smaller scale than land system) with the greatest area of footslope: crest was found to support the highest herbivore density in the KNP, at the land type scale (Grant and Scholes 2006).

2.4.5 Fire

Fires, which are an intrinsic feature of southern African ecosystems, cause pyrogenic losses of N from plants and soils (Aranibar *et al*. 2003) and affect both woody and herbaceous vegetation structure, function and composition. Fire intensity, frequency and seasonality are affected by many factors, among which fuel load, chemistry and moisture are important (Trollope 1982; Trollope 1984; Trollope and Tainton 1986; Van Wilgen *et al*. 2003). Fire and its interactive effects with herbivory determine to a large extent the ratio of trees and grasses in savannas (Van Langevelde *et al*. 2003). Due to perpetual low herbaceous standing crop it is unknown to what extent fire affects sodic patches, and indeed how fire affects different landscape positions within a catena. Since the establishment of the exclosure, different fundamental drivers (e.g. fire and herbivores) have been excluded from the study site. Not enough data are available for the study site to factor in fire as a specific co-determinant of grass biomass production. Therefore, fire cannot be included in the analyses of this study, though it is recognised that fire is an

important factor in the short and long term dynamics of forage production and quality dynamics (Mentis and Tainton 1984).

CHAPTER 3: METHODS AND MATERIALS

3.1 Site Description

3.1.1 Location

Sampling was conducted in and around the 185 ha Nkuhlu Research Exclosure along the eastern bank of the Sabie River, about 27 km from Skukuza, Kruger National Park (KNP) (24° 59' 37"S and 31° 46' 27"E). The site comprises a 70 ha southern camp which is completely fenced off so that no animals can enter ("full exclosure"), as well as a 40 ha northern camp which is fenced off to prevent elephant and giraffe from entering, but allows all other animals access ("partial exclosure") (Figure 3.1). The two camps are separated by an unfenced zone, which serves as a control area. Fences were erected in October 2001, but large grazing herbivores were effectively excluded from the area only since August 2002. This site is representative of the Skukuza land system (Venter *et al*. 2003) and its characteristic catenas (Figure 2.2).

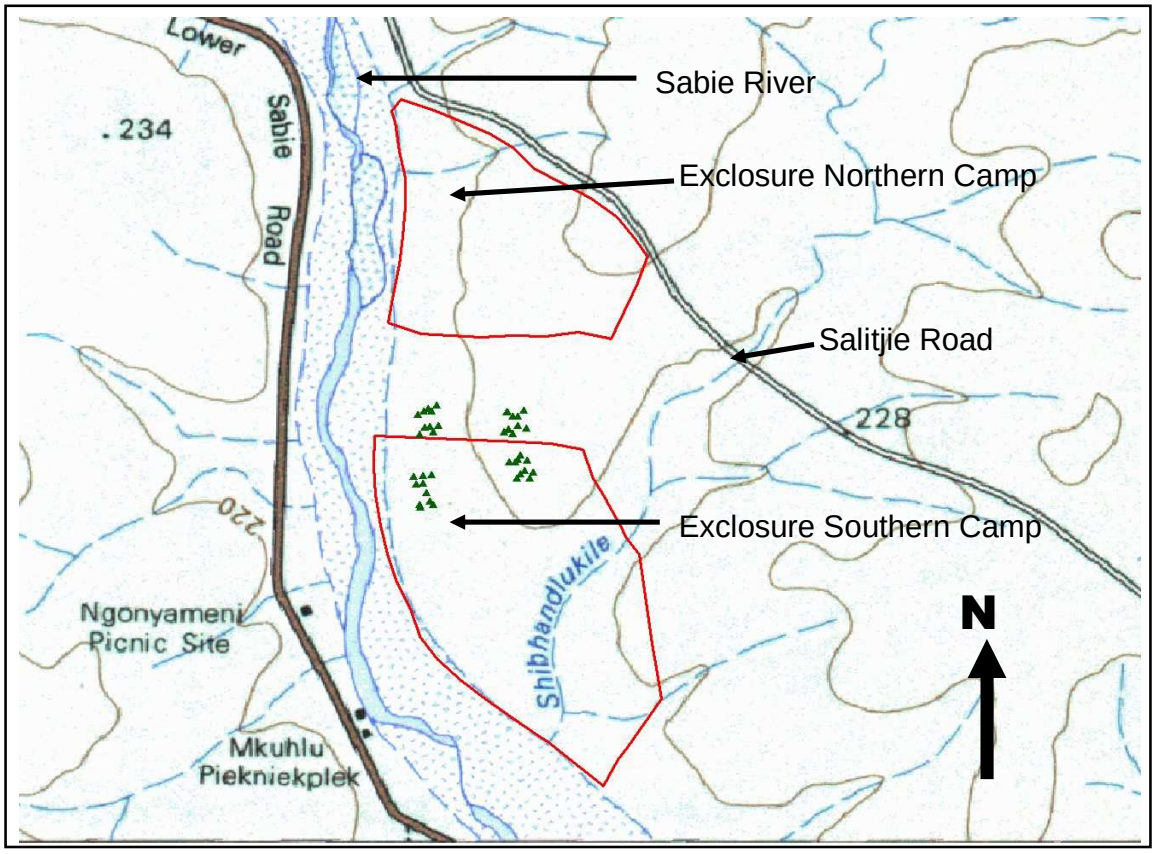


Figure 3.1: The Nkuhlu Research Exclosure site along the Sabie River in the southern Kruger National Park. Sampling points are indicated by green triangles, straddling the northern fence of the southern 70ha full exclosure, which excludes all herbivore larger than a hare, since October 2001.

3.1.2 Terrain

The Nkuhlu exclosure area consists of sloping topography, with average slopes of between 3% and 5%, sloping from the crest on the eastern fences, westward to the Sabie River. Close to the river, the slopes are gentler, usually less than 1%, and there are some areas where the river bank forms a small levee, so that the terrain slopes slightly up to the river bank (Paterson and Steenkamp 2003). A large sodic patch is located behind the riparian levee in the gently sloping area. The site is drained by two seasonal streams, one in each camp. A small stream flows through the northern camp, with the larger

Shibandlukile stream, with a side tributary, flowing through the southern camp. The altitude is between 210 m and 250 m above sea level.

3.1.3 Geology

The geology of the area consists of gneissic granite and grey migmatite of the Nelspruit Suite, Swazian Erathem. Gneiss is a coarse-grained metamorphic rock which covers a large area of the KNP and typically gives rise to shallow, usually gravelly, greyish-brown to reddish-brown soils (Paterson and Steenkamp 2003, Venter 1990).

3.1.4 Soils

The distribution of the various soil map units is shown on the soil map and accompanying soil profile descriptions (Appendix III). The crest soils of the Nkuhlu exclosure site are shallow, greyish-brown and have coarse sandy textures. The soils are classified as eutric leptosols where the profile is less than 25 cm deep to rock, and as eutric regosols where it is greater than 25 cm deep to rock, according to the World Resource Base for Soil Resources (FAO 1998). They are slightly acidic, mainly due to the parent material and cover most of the upper portion of the exclosure site (Paterson and Steenkamp 2003).

Sodic soils are deeper, more structured (duplex) brown calcareous soils with sparser vegetation (due to dispersed clays), and occur at the foot of the slope. Soil patches covered with herbaceous vegetation are interspersed by extensive bare patches with a hard upper crust. They are classified as gleyic calcisols where gleying occurs deeper than 50 cm and as calcic gleysols where gleying occurs at depths less than 50 cm deep (FAO 1998). These soils show a clay increase to the subsoil, are moderately to strongly alkaline, and have a high sodium (Na) content in the subsoil (Paterson and Steenkamp 2003). Fisher (2006) reports soil Na values of 103.3 $mg.kg^{-1}$ in sodic soils, and 22.4 $mg.kg^{-1}$ in crest soils. The electric conductivity (EC) values of sodic sub-soils are also very high (>300 $S.m^{-1}$), meaning that the soils will be classified mostly as *saline-sodic*

soils. The strip of deeper, brown alluvial soils along the Sabie River is siltier, and becomes narrower towards the north of the partial exclosure. These soils generally increase in depth moving down the slope (Paterson and Steenkamp 2003).

3.1.5 Climate

The nearest weather station to the exclosure is the Skukuza Meteorological Station (≈27 km), which supplied the weather data for this study. Data were made available by the South African Weather Bureau. Monthly rainfall (mm) totals were collated for the three years (2002/2003, 2003/2004 and 2004/2005) which run from July to June. The actual cumulative rainfall data for the sampling period are plotted together with long term cumulative rainfall data from 1940 – 2005 (Figure 3.2). Annual rainfall data (mm) were used to characterize the sampled years as either “wet” (>Average Cumulative Total) or “dry” (<Average Cumulative Total). These classes are assigned arbitrarily for the purposes of classifying the sampled years only. The Average Cumulative Total (ACT) for the station is 581.8 mm per annum, calculated from January to December (1940 – 2005; South African Weather Bureau).

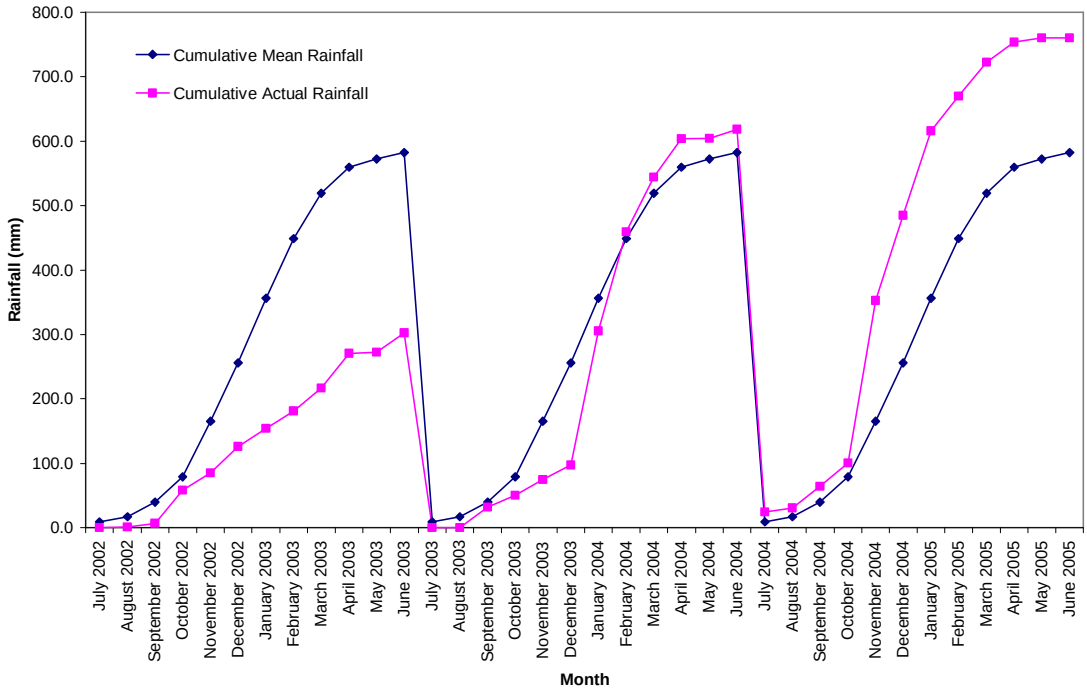


Figure 3.2: Mean cumulative and actual cumulative rainfall (mm) from July 2002 to June 2005 for the Skukuza Meteorological Station

The first sampling year, hereafter referred to as Season 1 (2002/2003) received 302.5 mm (51.9% ACT) and was classified as a dry year. Monthly rainfall totals from November to March each fell below 50% of the long-term average per respective month, as well as respective monthly ACT. Season 2 (2003/2004) received 618.1 mm (106.2% ACT) and was classified as a wet year. The early wet season (November and December) was relatively dry, receiving less than 50% of the long term monthly mean. The middle of the wet season was the wettest, as January 2004 received 208.2 mm, over double the long-term mean for that month, and a third of the total rainfall for Season 2. Season 3 (2004/2005) received 760 mm (130.6% ACT) and was classified as a wet year. The early wet season received most rainfall, peaking in November which received 252.4 mm, almost three times higher than the long term average for that month, and more than double ACT. Monthly maximum and minimum temperature (˚C) means were collated for

the years 2002 to 2005, running from July to June, and are plotted along with long term temperature data (1940 – 2005) (Figure 3.3).

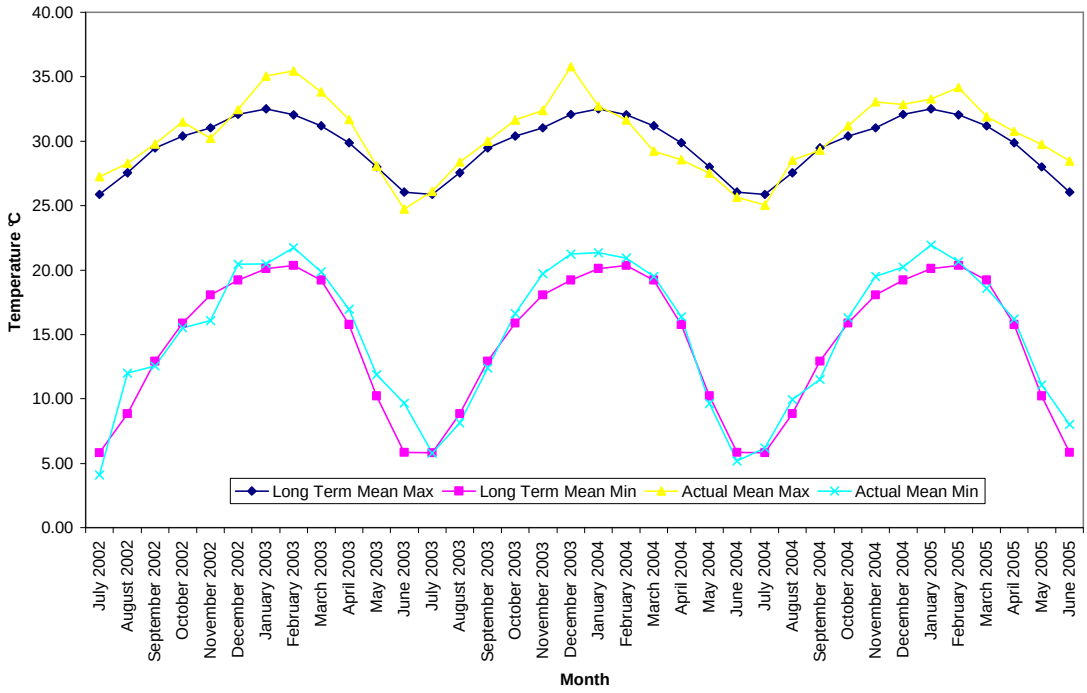


Figure 3.3: Long term mean and actual mean monthly temperature maxima and minima (˚C) from July 2002 to June 2005 for Skukuza Meteorological Station

Both mean monthly maxima and minima for Seasons 1 to 3 reveal above long term average (1940 – 2005; South African Weather Bureau) temperatures during the wet season (November to March) by ≈ 1 – 2 ˚C. Maximum temperatures in Season 1 were higher than the long-term by ≈ 2 ˚C during the mid- to late wet season (31 – 35˚C December to April), while Season 2 maxima of comparable range were higher than long term mean values in the early wet season. Maximum temperature values in Season 3 were higher than the long term by ≈ 1 ˚C throughout the wet season. The temporal trends of minimum temperatures during the wet seasons through Seasons 1 to 3 corresponded to the trends of maximum temperatures for the same period.

3.1.6 Soil Moisture

Soil moisture is measured either gravimetrically or volumetrically. In this study, it is measured volumetrically using automatic field instrumentation. The soil-hydrology instrumentation, installed in the Nkuhlu exclosure by Prof. Simon Lorentz of the University of KwaZulu-Natal (UKZN), which supplied the study with soil moisture data, enables a more accurate assessment of water available to the plant than rainfall data alone.

3.1.6.1 Volumetric Water Content

Volumetric Water Content (VWC) data were collected by UKZN staff using Time Domain Reflectometry (TDR) instrumentation, permanently placed in the sodic patch and crest within the sampling area inside the exclosure. The instrumentation was only operational from late 2005; hence the data reflect real time readings from January to June 2006 at probe depths of 200 - 1000mm. Data are expressed as m^3 water per m^3 soil (range: 0.00 to 1.00). Estimates of VWC are reported as means. Data from all probe depths were combined. Data were available from January to June 2006 and are used to report relative differences between the crest and sodic patch soil moisture estimates. The wetter sodic soils yielded a mean of 0.31 m^3m^{-3}, compared to crest soils which yielded a mean of 0.13 m^3m^{-3}.

3.1.6.2 Matric Pressure Head

The matric pressure head (mm) expresses capillary pressure or the tension at which soil retains water. These data were collected from permanently placed tensiometers placed throughout the exclosure site in both sodic patches and crest areas. Data were collected for the sampling period of November to May for the years 2002/2003, 2003/2004 and 2004/2005, at probe depths of 200 – 1000mm. Data from all tensiometer nests were combined. Estimates of matric pressure head are reported as means. Sodic soil retains

water at a significantly greater mean pressure of 3291.4 mm than crest soils which retain water at a mean of 2223.9 mm. These soil moisture estimates have been made available by UKZN to estimate PAW, described in the Literature Review in section 2.4.1. Data were not as comprehensive as hoped, due to large gaps in the data due to instrumentation malfunction. This limited me to aggregating data from across sodic sites and across crest sites. Therefore, all interpretation, extrapolation and analysis of these data should be done with caution.

3.1.7 Patch delineation and classification

Two crest patches and two sodic patches were identified in the 70ha exclosure (Figure 3.4). Each patch is referred to as a sub-unit. The border of each sub-unit was delineated subjectively and mapped on foot using a hand-held Garmin GPS unit. The waypoints were downloaded and sub-unit size (ha) calculated with ArcMap software. Within the exclosure, the total area defined as crest was 22.23 ha and was larger than the total area defined as sodic which was 13.68 ha (Table 3.1). In August 2004 imagery of the exclosure site was collected during a LIDAR flight survey. Features of the imagery included: a geo-rectified digital format, 3-colour RGB (Red, Green and Blue) bands, digital elevation and was of high resolution (25 cm^2 = 1 pixel). This imagery has been made available by the Post-Flood Research Programme of the University of the Witwatersrand. The delineated borders of sub-units of crest and sodic areas within the exclosure were superimposed on this imagery (Figure 3.4). Sodic 2 is the smallest sub-unit and is displayed separately in Figure 3.5 for clarity.

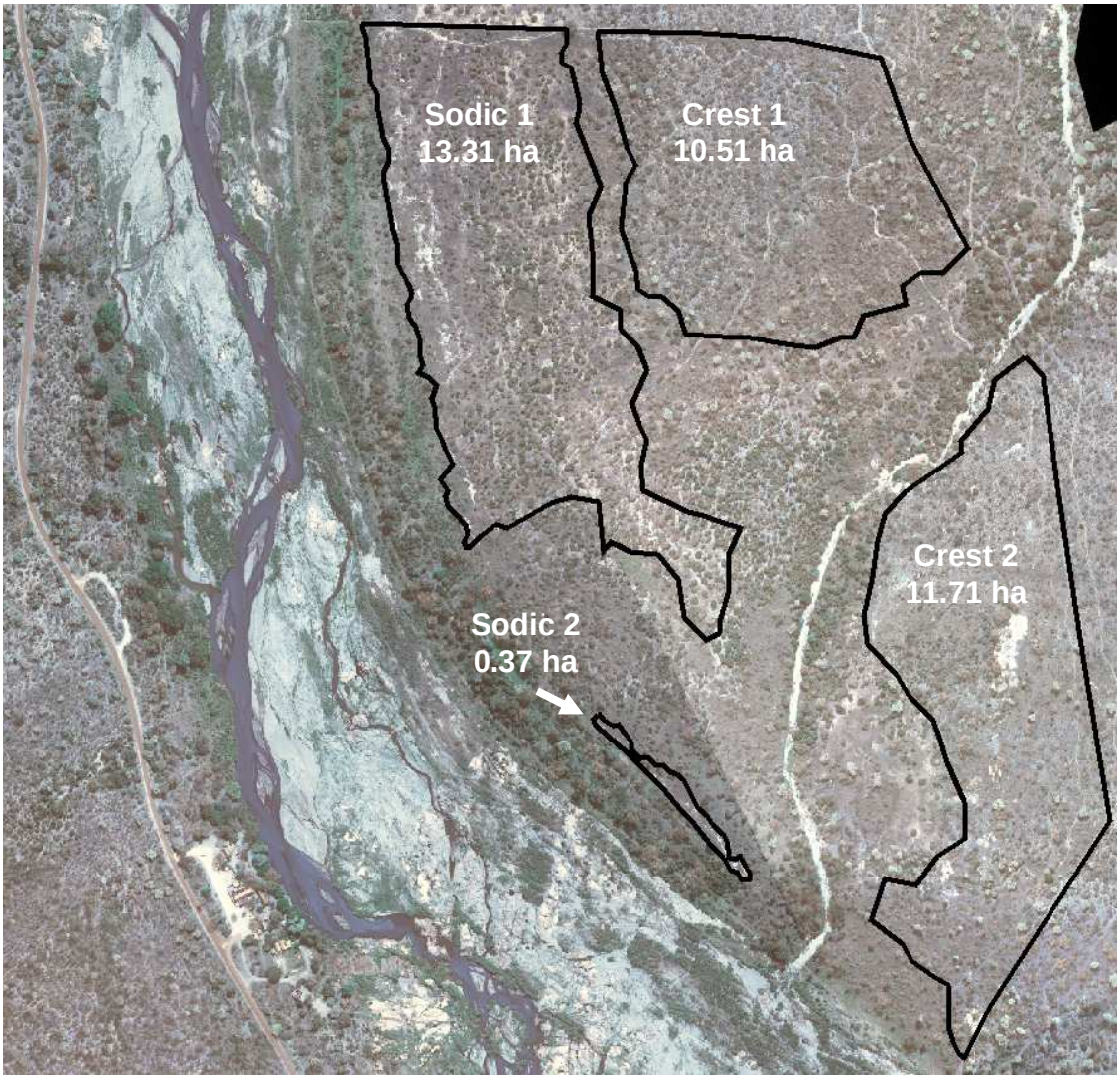


Figure 3.4: Study area (24° 59' 37"S and 31° 46' 27"E) showing delineated Sodic and Crest patch sub-units and area (ha) inside the Nkuhlu Research Exclosure

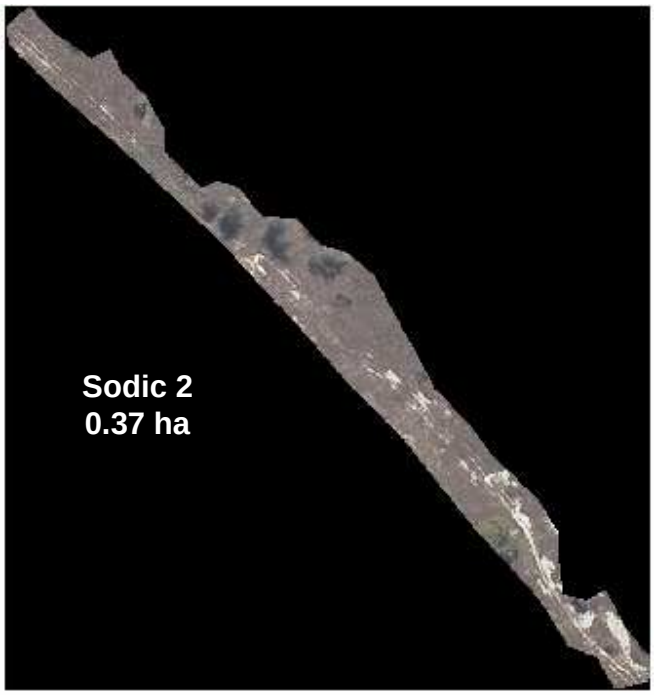


Figure 3.5: Image of area within the exclosure delineated as Sodic 2, 0.37 ha

Table 3.1: The area of Crest and Sodic terrain and sub-units within the exclosure

Terrain Sub-unit	Area (ha)	Terrain Total Area (ha)
Crest 1 Crest 2	10.51 11.71	**22.23**
Sodic 1 Sodic 2	13.31 0.37	**13.68**

Classified digital images of each sub-unit were generated by the manual selection of class points (over 100 points per class per sub-unit) from the RGB images. Subjective visual analysis of the RGB images advised the selection of five classes:

- Bare soil
- Grass
- Green tree
- Brown tree
- Yellow tree

This method aimed to identify all area per sub-unit covered by trees, and to isolate this area from the grass and bare ground. Trees were visually identified from the images. Since not all trees conformed to distinct spectral ranges, green, brown and yellow tree categories were applied based on appearance. These colour categories reflect pragmatic and subjective classes, that have no ecological relevance in this study. All image classification and data extrapolation were conducted with ERDAS Imagine software, which was then trained to classify the entire area of each sub-unit.

As a verification analysis, confusion matrices (Appendix I) were calculated using ArcMap software. One hundred points, per class, per sub-unit were randomly picked on RGB images, and the classification of each point recorded. These points were plotted against those observed (i.e. if a selected “grass” point was indeed classified as such or other). It was arbitrarily decided that every class within each sub-unit should equal or exceed a 70 percent accuracy threshold, confirming the viability of classification data. This point selection method and analysis technique is a per pixel analysis and is biased towards increased classification accuracy. Every class within each sub-unit exceeded the 70 point accuracy threshold, confirming the viability of classification data (Appendix II and Table 3.2).

In each classified image (Figures 3.6 to 3.9), brown represents area covered by brown tree, light green represents grass, dark green represents green tree, yellow represents yellow tree and white represents bare soil. Figures 3.6 to 3.9 are not to scale relative to each other.

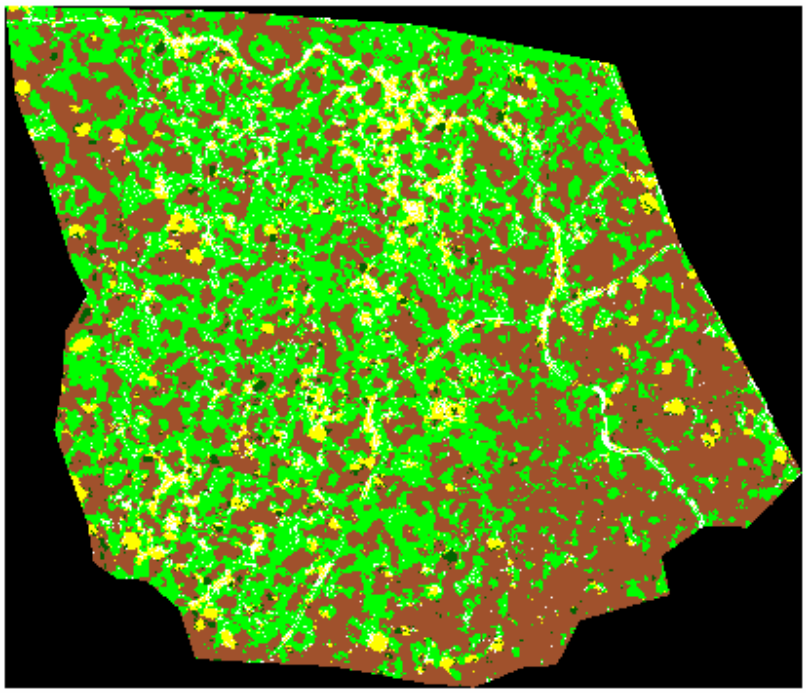


Figure 3.6: Classified image of Crest 1

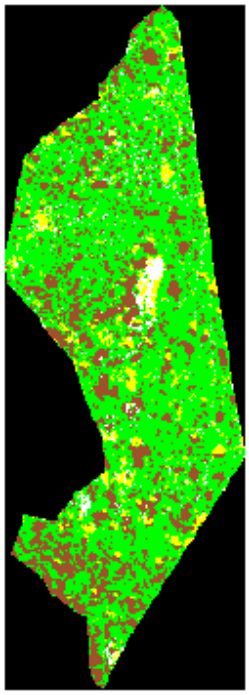


Figure 3.7: Classified image of Crest 2

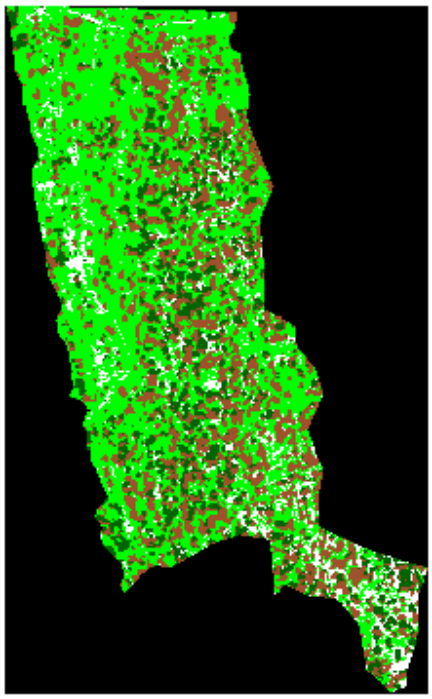


Figure 3.8: Classified image of Sodic 1

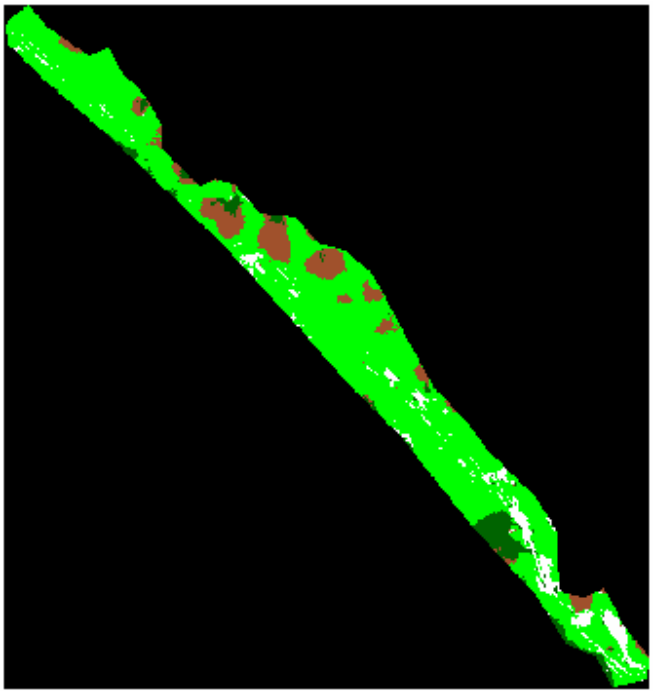


Figure 3.9: Classified image of Sodic 2

Table 3.2: Class proportions per terrain sub-unit within the exclosure

Terrain	Classes	Proportion
Crest 1	Bare	0.06
	Grass	0.4
	Tree	0.55
Crest 2	Bare	0.04
	Grass	0.65
	Tree	0.31
Sodic 1	Bare	0.09
	Grass	0.52
	Tree	0.39
Sodic 2	Bare	0.07
	Grass	0.77
	Tree	0.16

Sub-unit proportions within terrain types were not significantly different ($p>0.05$) (data not shown) when equivalent proportions per terrain type sub-unit were paired, and compared with a student's t test (STATISTICA 6.0). Classified proportions were determined per terrain type and extrapolated to calculate the area (ha) covered by grass, bare soil and trees within the area defined as crest and sodic, within the exclosure. The total grass producing areas within the crest and sodic areas within the exclosure were 11.46 ha and 8.85 ha respectively and were calculated by multiplying the respective "grass" class proportion mean by the area of the terrain type. The imagery I have used is the only one available for the inside of the exclosure. I decided to use it, since it was high quality imagery, and would add value to the spatial aspect of the overall study. Park-wide data on sodic patch location and size relative to other patch types do not exist. It must be kept in mind that the imagery is a once off snapshot, hence only descriptive statistics can be reported. Inferential statistics such as variance cannot be calculated for the area.

3.2 Grass biomass sampling design

Permanently placed transects of 10m x 20m plots traverse the exclosure site running from the macrochannel floor to the crest (Figure 3.10). Of the twelve transects across the exclosure site, sampling for this study was conducted in the sodic and crest areas of transect 7 – inside the exclosure experiencing no large mammalian herbivory – and transect 6 – outside the exclosure experiencing full herbivory. Four sampling sites were delineated:

- 2 within exclosure (crest and sodic patch)
- 2 outside exclosure (crest and sodic patch)

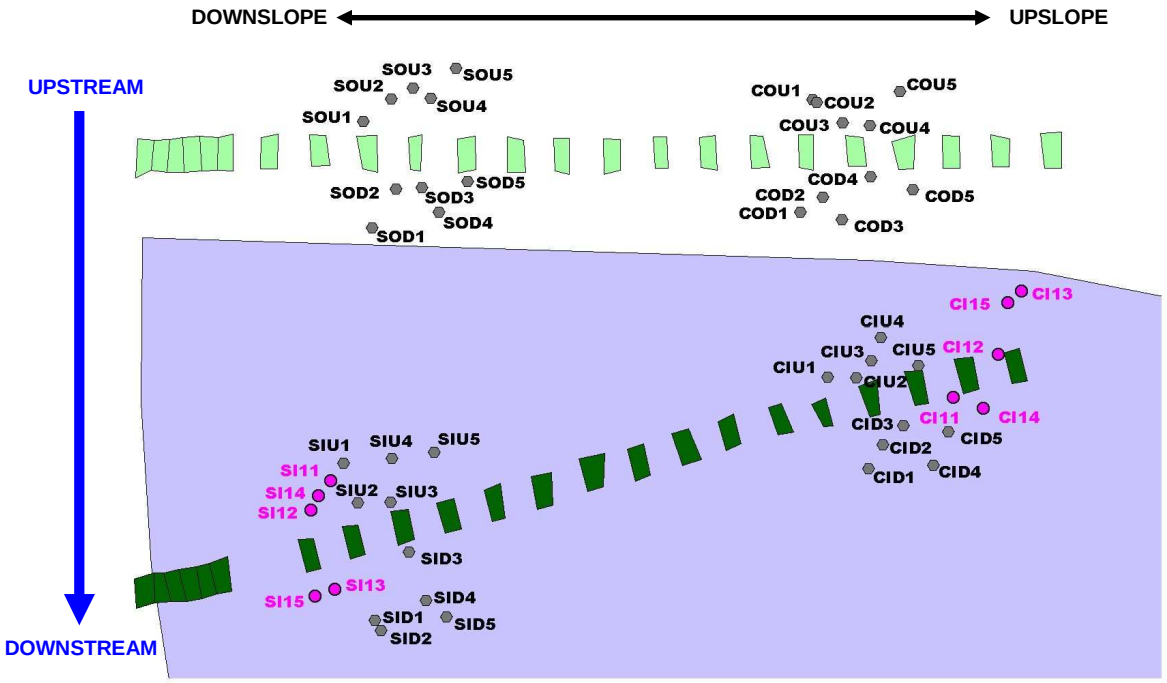


Figure 3.10: Diagram of the sampling area indicating the position of transect 6 (light green) outside the exclosure (white background), transect 7 (dark green) inside the exclosure (light blue background) and the location of biomass plots with plot reference names (CIU for instance, is an abbreviation for "Crest Inside Upstream"; SOD = "Sodic Outside Downstream"). Plots in pink added in Feb 2004. Crest plots occupy an upslope position relative to sodic plots. The schematised blue arrow on the left of the diagram indicates the position and flow direction of the Sabie River

The terrain units were qualitatively delineated based on a combination of the following:

- Presence/absence of typical woody and herbaceous vegetation
- Soil colour and texture
- Position on the slope
- Relative openness of the site

All 4 sites were situated in the non-burnt area of the exclosure site, straddling the fence in order for differences in slope, rainfall and soil type to be minimalised. These four sampling sites are henceforth referred to as treatments:

- Crest Inside (CI)
- Sodic Inside (SI)
- Crest Outside (CO)
- Sodic Outside (SO)

3.3 Grass biomass sampling methodology

Two grass biomass clipping regimes were applied:

- Monthly clipping of permanently placed plots in the four abovementioned treatments to obtain productivity data
- Monthly clipping of previously unclipped areas (standing biomass) inside the exclosure to obtain production data. This treatment is hereafter referred to as standing biomass.

3.3.1 Productivity

In November 2002, within treatments CI and SI, $1m^2$ (n=10) circular plots/sub-samples were permanently positioned (using metal pegs) at a distance (≥10m) apart so that each sub-site was statistically independent. Within treatments CO and SO, ten plots per sub-

site were permanently positioned similarly. In each treatment, plots were placed both upstream (U) and downstream (D) of the aforementioned exclosure transects 6 and 7 (Figure 3.10), which run perpendicular to the Sabie river.

To standardise the sub-samples, positioning was limited to areas not under trees within relatively homogenous stands of grass. It was observed that productivity variability was much greater inside the exclosure than outside. Therefore, five additional plots were added to CI and SI from February 2004 to the end of the study:

- CI plots (n=15),
- SI plots (n=15),
- CO plots (n=10), and
- SO plots (n=10).

Each plot was assigned an individual reference name as follows (Figure 3.10):

- CI
    - CIU (Crest Inside Upstream) 1 to 5
    - CID (Crest Inside Downstream) 1 to 5
    - CI (Crest Inside) 11 to 15 – added February 2004

- SI
    - SIU (Sodic Inside Upstream) 1 to 5
    - SID (Sodic Inside Downstream) 1 to 5
    - SI (Sodic Inside) 11 to 15 – added February 2004

- CO
    - COU (Crest Outside Upstream) 1 to 5
    - COD (Crest Outside Downstream) 1 to 5

- SO
    - SOU (Sodic Outside Upstream) 1 to 5
    - SOD (Sodic Outside Downstream) 1 to 5

Circular plots were used to minimise possible boundary problems which could be encountered during sampling, because with a circle and square of the same surface area, the circumference of the circle is smaller than the perimeter of the square. Plots were arranged randomly, but were stratified in order to correspond to permanently marked exclosure transects 6 and 7 (Figure 3.10), because of the close proximity to hydrological instrumentation thereby enabling the use of spatially cross-referenced data.

The sampling method included clipping the grass in each plot with shears every month at a height of 3 cm, oven-drying the foliar samples in paper bags at 60^{O}C for 7 days, and recording dry matter (DM). As a baseline, all plots were clipped to a height of 3 cm in November, before the onset of the wet season. This was done at the beginning of each sampled year, but was seldom necessary as very little biomass carryover was evident. The sampling period was December to May (growing/wet season) for the years 2002/2003, 2003/2004 and 2004/2005, which are henceforth referred to as Seasons 1 to 3, respectively. Productivity data are expressed as grams of dry matter produced per square metre per month (g DM m^{-2} $month^{-1}$). Data from inside the exclosure reflect productivity, while data from outside are an index of utilisation in the same area during the sampling period to quantify defoliation due to grazing under natural conditions. Data obtained are used to investigate productivity at the $1m^2$ sub-sample scale, between sodic patch and crest.

3.3.1.1 Data analysis

Even though productivity data did not conform to the normal distribution pattern ($p<0.05$), repeated measures ANOVA and the Fisher LSD post-hoc test (STATISTICA 8.0) were used to test for differences between treatments (CI, CO, SI and SO) and

seasons (1 to 3). In this study, the sub-sample/plot is repeatedly sampled (monthly) and is therefore the smallest/basic experimental unit. Means of repeated productivity measures per plot are used to test for differences between seasons and treatments. In cases where seasons did not differ significantly ($p>0.05$), only differences between treatments are discussed. No non-parametric equivalent test was available to test for repeated measures, and so parametric statistics are used, keeping in mind that the data do not fulfil parametric assumptions. Data are displayed as point graphs.

3.3.1.2 Spatial extrapolation of grass biomass productivity

Grass biomass productivity means (g DM m^{-2} $month^{-1}$) are calculated by aggregating seasons 1 to 3 for both crest and sodic treatments inside the exclosure (CI and SI) were extrapolated to each respective terrain type within the exclosure, and then converted from m^2 to hectares by multiplying by 10 000 to calculate the mean productivity of crest and sodic areas in the exclosure in the growing season. This index is a monthly estimate of production in the growing season (i.e. g DM m^{-2} $month^{-1}$).

3.3.2 Standing Biomass

Once monthly, throughout the sampling periods of Seasons 2 and 3, 10 x $1m^2$ previously unclipped plots were clipped in both sodic and crest patches within the herbivory exclosure (n = 10 in sodic patch; n = 10 in crest per month) in an area not further than 50 m from permanent monthly clipped plots. These locations were chosen randomly. Data derived from this series reflect the accumulated standing biomass production. Standing biomass in this case therefore refers to how much grass biomass is produced over a specified spatial scale, without any previous defoliation (except for invertebrate herbivory) and is referred to as $production_{SB}$. These plots are referred to as $plots_{SB}$.

The sampling method for the $plots_{SB}$ included clipping the grass with shears in each circular plot at a height of 3cm above ground, oven-drying the foliar samples in paper

bags at 60^{O}C for 7 days, and recording dry matter (DM). The sampling period was January to June (growing/wet season) for the years 2003/2004 (Season 2) and 2004/2005 (Season 3). Standing biomass data are expressed as grams of dry matter produced per square metre (g DM m^{-2}). Differences in DM between months were tested for statistical differences using a factorial ANOVA (STATISTICA 8.0). In cases where production did not differ significantly ($p>0.05$) between seasons, only differences between treatments are discussed. Means and the corresponding 95% confidence limits are displayed. As a result of incomplete data the months of March and May were omitted from the abovementioned analyses.

3.3.3 The effect of defoliation history on production

To determine whether the estimates of productivity differed between regularly clipped sward (monthly clipped plots from inside the exclosure) and a sward which was unclipped for three years ($plots_{SB}$ inside the exclosure), it was necessary to create a paired data set, listing estimates of one month's growth in both swards. Monthly productivity (g DM m^{-2} $month^{-1}$) was estimated in $plots_{SB}$ as follows:

To obtain an estimate of change in monthly standing biomass for unclipped plots, the mean (n=10 per terrain type) $production_{SB}$ for one month per terrain type was subtracted from individual $production_{SB}$ values (n=10 per terrain type) of the following month (e.g. the mean of sodic $production_{SB}$ for January 2004 is subtracted from each February 2004 $production_{SB}$ value). These values (n=10 per terrain type) then provide estimates of monthly productivity (g DM m^{-2} $month^{-1}$) in $plots_{SB}$ for a specific month (e.g. February 2004). Negative values were assumed to be zero production. These data were then compared with productivity data from monthly clipped plots (n=15 per terrain type) for the same month and terrain. The data were not normally distributed. Therefore, nested ANOVA (using generalized linear models with an identity link function) was used to test for statistical differences between treatments and terrain types. The data were adjusted in the analysis to fit a Poisson distribution. In this experimental design, treatment (monthly

clipped vs. standing biomass) is nested in terrain (sodic vs. crest). This procedure was used to test the months of February 2004 and February 2005 separately, as the only months with complete set of comparable data. Data are presented as point graphs, and inferential statistic listed in tabular form.

3.4 Forage Quality

Each DM productivity foliar sample from Seasons 2 and 3 was milled and analysed for total content of N, C, P and Na. These analyses were outsourced to the Agricultural Research Council analytical laboratories in Nelspruit (Na and P) and Pretoria (N and C).

3.4.1 Method for C and N determination

The milled samples were used directly for C and N determinations on a Carlo Erba NA 1500 C/N/S Analyser, using approximately 10 to 15mg sample weighed into a tin foil container for each determination (Bellomonte 1987). The sample and tin container are ignited at high temperature (1020 °C) in oxygen (on a chrome oxide catalyst) to produce carbon dioxide (CO_2), nitrogen gas (N_2) and oxides of N (plus other oxides etc.). The gases produced pass through silvered cobalt oxide (to remove oxides of S and halogens etc) and a column of copper (540 °C), which reduces the oxides of nitrogen to nitrogen gas (and removes excess free O_2). After removal of water vapour by a trap of anhydrous magnesium perchlorate, the N_2 gas and CO_2 are finally separated by gas chromatography using a helium carrier gas and detected by a thermal conductivity detector. The instrument is calibrated against a pure organic compound of known composition. In this case the standard was the ethyl ester of 4-Aminobenzoic acid, which contains 8.48% N and 65.4% C.

3.4.2 Method for P and Na determination

The milled samples were subjected to wet digestion with a ratio 2:1 of 55% Nitric Acid and 70% Perchloric Acid. Sodium was then detected using flame atomic emission spectroscopy using air-acetylene. The determination of P was based on the colorimetric method in which a blue colour is formed by the reaction of ortho phosphate and the molybdate ion. The phosphol-molybdenum complex was read at 660nm.

3.4.3 Nutrient data analysis

All nutrient data conformed to the normal distribution pattern ($p>0.05$). Repeated measures ANOVA and the Fisher LSD post-hoc test (STATISTICA 8.0) were used to test for differences between treatments (CI, CO, SI and SO) and seasons (2 and 3). In this study, the sub-sample/plot is repeatedly sampled (monthly) and is therefore the smallest/basic experimental unit. Means of repeated foliar nutrient measures per plot are used to test for differences between seasons and treatments. In all cases, seasons did not differ significantly ($p>0.05$) and only differences between treatments are discussed. Data are displayed as point graphs.

C:N ratios and N:P ratios were calculated from the nutrient means per treatment (the mean of C in treatment CI is divided by the mean of N in treatment CI, etc.) and are reported without inferential statistics. It was inappropriate to statistically compare repeated measures data (nutrient data from monthly clippings) and point data (nutrient data from standing biomass) in the same analysis. Therefore, monthly nutrient means from both monthly clipped productivity plots and standing biomass plots are descriptively compared and displayed in line graphs. Data from both seasons 2 and 3 are aggregated. The purpose of these Figures is to discuss the change in foliar nutrient content through the growing season, and relative differences in the nutrient content between sodic and crest forage, in monthly clippings and standing biomass. It is inappropriate to calculate means of, and statistically analyse ratios (a ratio being a statistic *per se*), therefore C:N ratio and N:P ratios are only descriptively compared and displayed.

3.5 Utilisation

3.5.1 Relationships between grass biomass productivity and utilisation

Utilisation values were calculated by subtracting the monthly means of productivity ($gDM.m^{-2}.month^{-1}$) in the treatments "outside" from those "inside". The set of utilisation values were paired month-for-month with the set of productivity values for Seasons 1 to 3 for crest and sodic areas separately. Statistical correlations were tested using the Spearman test.

3.5.2 Relationships between quality and utilisation

The utilisation values used in the analyses described in 3.5.1 were converted to percentages. The set of monthly utilisation percentages were paired month-for-month with the mean monthly content of N, P, C, Na, C:N ratios and N:P ratios for Seasons 2 and 3. Statistical relationships between N, P, C and Na content and utilisation were tested using the Spearman test as utilisation data were not normal. C:N and N:P ratio data are displayed and discussed, but not statistically analysed.

3.6 Stable natural abundance isotopes

All stable isotope analysis of samples (collection described in 3.7.1 and 3.7.2) was outsourced to the Archeometry laboratory at the University of Cape Town. Plant and soil samples were oven-dried at $60^{O}C$ for 24 hours, then mill-ground. Ground samples were weighed individually in tin capsules. Samples were then combusted in an automated Elemental Analyzer (Carlo Erba device) and the resultant CO_2 and N_2 gas was introduced into a Finnigan 252 Mass Spectrometer using a continuous flow-through inlet system (Conflo device). $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were presented in standard delta (δ) notation relative to the PeeDee Belemnite (PDB) and atmospheric N_2 standards, respectively. This

method also provided the elemental composition (%C and %N) for each sample. Standard deviations for repeated measurements of laboratory standards are less than $0.1^{o}/_{oo}$ for $\delta^{13}C$ values and $0.3^{o}/_{oo}$ for $\delta^{15}N$ values.

3.6.1 Mixed species foliar samples

At the inception of this study, I aimed to investigate whether mixed grass species within the same terrain type shared similar WUE and N-cycling properties. Productivity foliar samples, which consisted of mixed species, from Season 1 were analysed for $\delta^{13}C$ values and $\delta^{15}N$ values, as described. Respective means from sodic values (SI and SO) and crest values (CI and CO) were aggregated due to low sample numbers and compared using a student's t test (STATISTICA 6.0). Data are presented as box-and-whisker diagrams.

3.6.2 Single species foliar samples and underlying soil samples

Significant differences ($p<0.05$) in ranges of $\delta^{13}C$ values and $\delta^{15}N$ values in the mixed species foliar samples of Season 1 prompted a more refined investigation of grass ecophysiological dynamics in the study. This involved taking into account the possible genetic/taxonomic controls on foliar $\delta^{13}C$ values, and the effect of plant-soil interactions and soil %N on foliar $\delta^{15}N$ values. At peak standing biomass (April) in Season 3, ten foliar samples (minimum 10g clippings per bag/individual sample) of the following species were collected from within the sampling area inside the exclosure, dried as described above and sent for analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios:

- *Sporobolus nitens* from sodic patch (n = 10)
- *Digitaria eriantha* from crest (n = 10)
- *Urochloa mossambicencis* from sodic patch (n = 10)
- *Urochloa mossambicencis* from crest (n = 10)

Species composition data from the productivity clippings revealed that the abovementioned species were common in their respective terrain types.

Four soil sub-samples from under each abovementioned sampled plant were collected by means of metal cores, hammered in 5cm deep. These four soil sub-samples per plant were then mixed to form a composite sample (minimum of 10 g per bag). The set of soil samples (n = 10) were paired to the set of co-occurring foliar samples (n=10). Composite soil samples were dried and analysed for $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios, as described above. Foliar and soil $\delta^{13}C$ and $\delta^{15}N$ values, per species, were compared using multi-factorial ANOVA (STATISTICA 6.0). Data are presented as box-and-whisker diagrams.

Soil %N data were available together with the isotopic analysis output. These data were grouped into sodic and crest soil types, and compared with a student's t test (STATISTICA 6.0).

CHAPTER 4: RESULTS

4.1 Grass biomass productivity

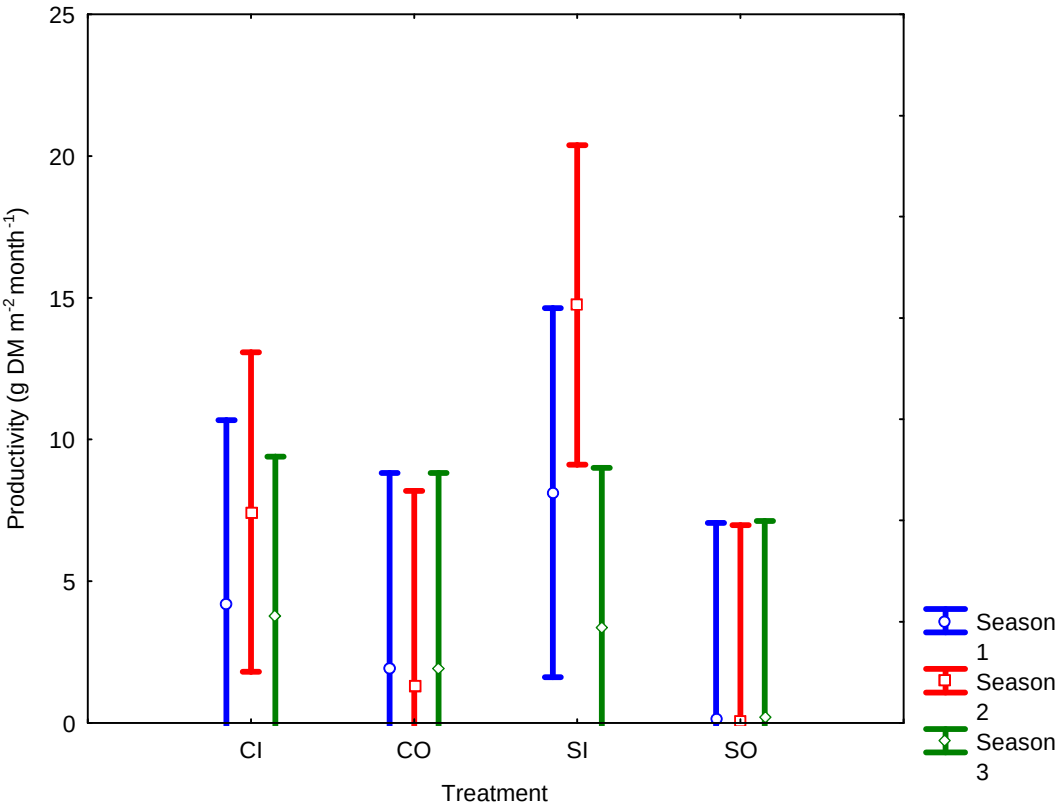


Figure 4.1: Grass biomass productivity (g DM m^{-2} $month^{-1}$) within each treatment per sampling season 1 (December 2002 – June 2003), season 2 (December 2003 – June 2004) and season 3 (December 2004 – June 2005). Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals

Means of productivity (monthly clipped plots) between treatments and seasons (Figure 4.1) were not significantly different (p=0.13; Repeated measures ANOVA), allowing the analysis between treatments without including season as a variable (Figure 4.2). Although not statistically significant overall, productivity of the inside sodic treatment

(SI) in season 2 (14.74 ± 2.83 g DM m^{-2} $month^{-1}$) was significantly higher ($p<0.05$, Fisher LSD test) than all other displayed productivity means in Figure 4.1, except that of inside crest treatment (CI) in season 2. Inter-seasonal variability of both outside crest and sodic treatments (CO and SO, respectively) are less than 1 g, possibly indicating an inter-annual control imposed by utilisation, while variability in CI (4 g) and SI (11 g) both reveal highest productivity in season 2. The low productivity in SI and CI in season 1(compared to season 2) could be attributed to low rainfall, while the converse is true for the productivity of season 2. Even though season 3 was the wettest year, productivity was lower ($p>0.05$) than the preceding years in both SI and CI, possibly the effect of clipping the same plots for three consecutive years. Productivity in SO and CO of season 2 was lower, although not significantly, than that of seasons 1 and 3 ($p>0.05$). This was not expected as Season 2 is classified as a wet year, and does not correspond with the inter-annual trend revealed by data from inside treatments. However, since data from treatments outside the exclosure reflect the post-utilisation sward, higher utilisation and not decreased productivity is revealed.

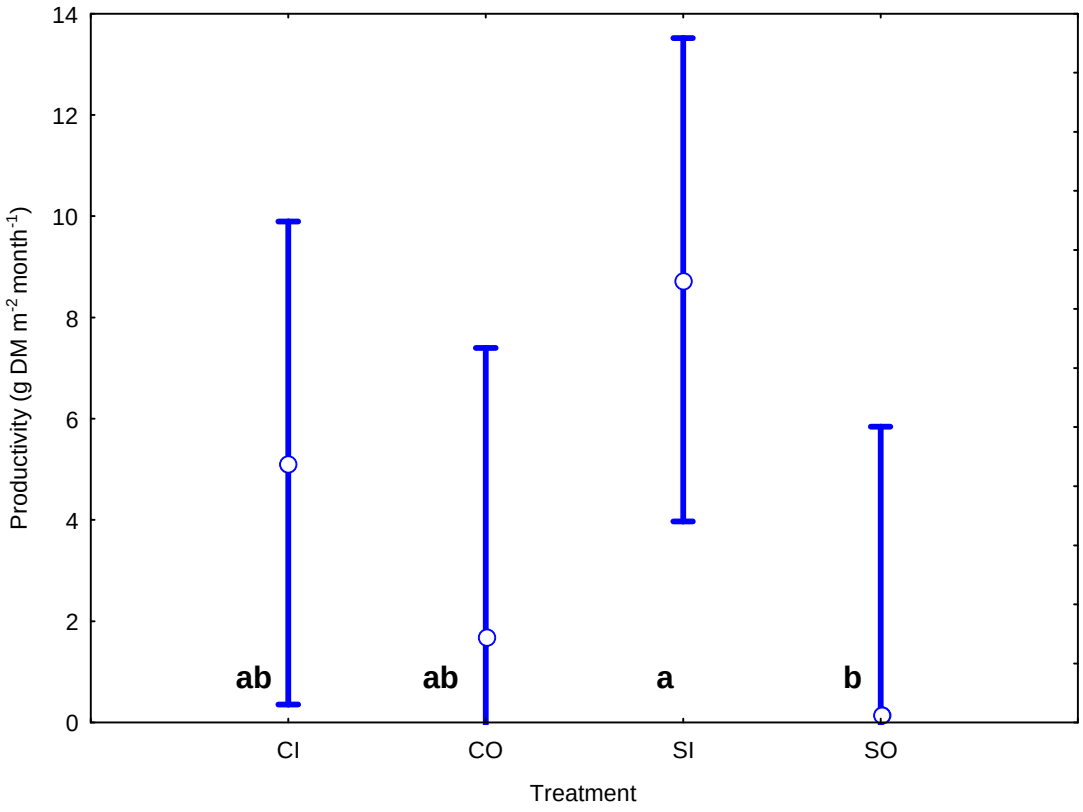


Figure 4.2: Grass biomass productivity (g DM m^{-2} $month^{-1}$) in each treatment for three growing seasons (2002 – 2005). Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

Across all seasons, there was no overall significant statistical difference (Figure 4.2) between treatments (p=0.1; Repeated measures ANOVA), although SI mean productivity (8.74 ± 2.37 g DM m^{-2} $month^{-1}$) was significantly higher (p=0.02; Fisher LSD test) than that of SO (0.15 ± 2.82 g DM m^{-2} $month^{-1}$). Productivity in CI (5.12 ± 2.37 g DM m^{-2} $month^{-1}$) is higher (p>0.05) than that of CO (1.71 ± 2.82 g DM m^{-2} $month^{-1}$). As mentioned earlier, data from treatments outside the exclosure (SO and CO) reflect the post-utilisation sward, while those from treatments inside the exclosure (SI and CI) reflect actual productivity. When comparing monthly growth (Figure 4.3) or season (Figure 4.1), productivity is consistently lower in outside treatments than inside

treatments of the corresponding terrain unit (crest or sodic patch). This finding will be explained as utilisation by grazers. Sodic patches therefore appear to be most utilised; SO productivity remains consistently close to zero in both Figures 4.1 to 4.3. SI productivity is higher, but not significantly so, than both crest treatments. Crests, with a smaller difference between CI and CO productivity (Figures 4.1 to 4.3), appear to be less utilised than sodic patches, though not significantly so.

Winter production, not part of the abovementioned analysis, in permanent plots inside the exclosure was measured once-off in November 2004 (SI = 6.02 ± 2.5 g DM m^{-2}; SO = 0.23 ± 0.1 g DM m^{-2}; CI = 6.06 ± 2.15 g DM m^{-2} and CO = 1.86 ± 0.6 g DM m^{-2}) in the sodic patch and 6.06 g DM m^{-2} in the crest) and represents growth for the dry months of July to October 2004.

Table 4.1: Area class proportions and class area per terrain unit within the exclosure

Class	Crest Proportions	Sodic Proportions	Crest Area (ha)	Sodic Area (ha)
Bare	0.05	0.08	1.04	1.09
Grass	0.52	0.65	11.64	8.85
Tree	0.43	0.27	9.55	3.75

Productivity means calculated over seasons 1 to 3 for both crest (5.12 ± 2.37 g DM m^{-2} $month^{-1}$) and sodic (8.74 ± 2.37 g DM m^{-2} $month^{-1}$) treatments inside the exclosure (Figure 4.2) were extrapolated to each respective terrain type within the exclosure, as described in the site description (Table 4.1). During the sampling period, the crest within the exclosure produced a mean of 596.0 kg DM per month and the sodic patch within the exclosure produced a mean of 773.5 kg DM per month.

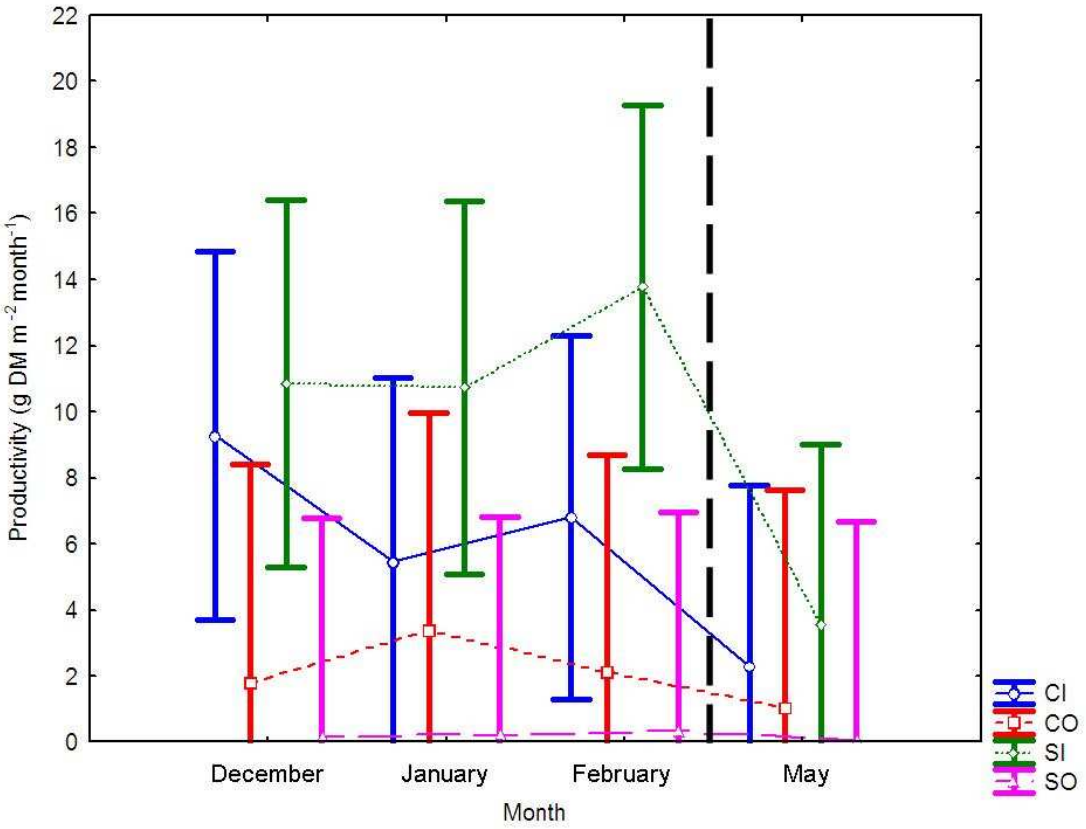


Figure 4.3: Grass biomass productivity (g DM m^{-2} $month^{-1}$) in each treatment over time (month's growth over three sampling seasons). Points denote means and vertical bars denote 0.95 confidence intervals. The bold dashed vertical line-break indicates missing values for the months of March and April

Trends of monthly clipped productivity differed significantly (Figure 4.3) between treatments ($p<0.05$), but in general an increase in productivity during months 2 and 3 of the season (January and February, respectively) was observed and lowest productivity observed at the end of the season in month 6 (May). The productivity curves follow the general rainfall pattern of the wet season (Figure 3.2).

4.2 The effect of defoliation history

4.2.1 Standing biomass

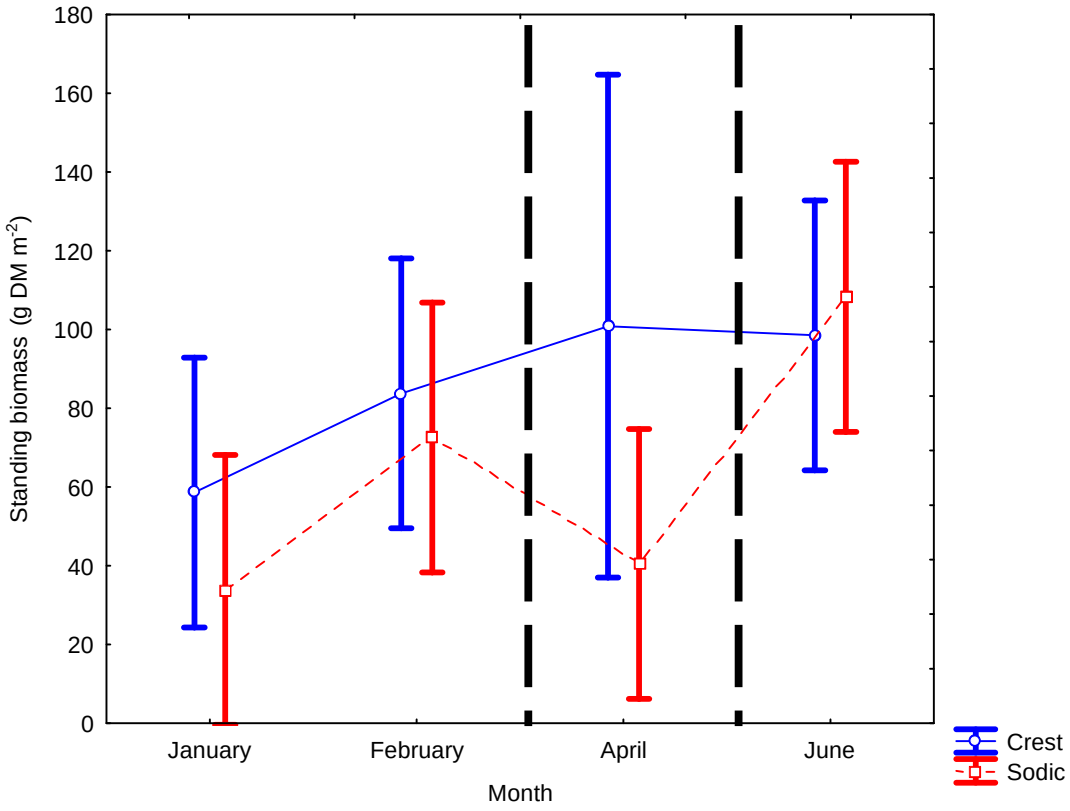


Figure 4.4: Standing biomass (g DM m^{-2}) accumulated in the crest (C) and sodic patch (S) inside the exclosure over time (months accumulated over sampling seasons 2 and 3). Points denote means and vertical bars denote 0.95 confidence intervals. The bold dashed vertical line-breaks indicate missing values for the months of March and May

In previously unclipped plots (where standing biomass was allowed to accumulate within the exclosure to that point in the season, and then clipped once-off) in the crest and sodic patch inside the exclosure, no overall statistical difference was found ($p>0.05$) between patch type and months of accumulation (Figure 4.4). It should be noted that data in April were collected by a different observer, and that observer bias in selecting sites may account for these comparatively low means in the sodic patch. In general, a trend of

increasing mass over time is observed in both patch types, with crest standing biomass being consistently higher than sodic standing biomass.

4.2.2 Comparison between monthly clipped and standing biomass production estimates

Table 4.2: Results of generalized linear nested ANOVA for the effect of terrain and treatment on productivity for February 2004 and February 2005

Month	Terrain		Treatment		DF	Scaled Deviance/DF
	Chi-squared	p-value	Chi-squared	p-value		
Feb-04	1.41	0.24	7.10	**0.03**	46	0.80
Feb-05	0.54	0.46	8.00	**0.02**	46	0.63

Monthly productivity estimates were significantly higher ($p<0.05$) in plots with a less intense defoliation history (i.e. $plots_{SB}$) than in monthly clipped plots, in both February 2004 and February 2005. Monthly productivity estimates did not differ significantly ($p>0.05$) between crest and sodic patches (terrain) within clipping treatments ($p>0.05$) (Table 4.2; Figures 4.5 – 4.6) although sodic productivity was consistently higher than crest productivity (Figures 4.5 – 4.6).

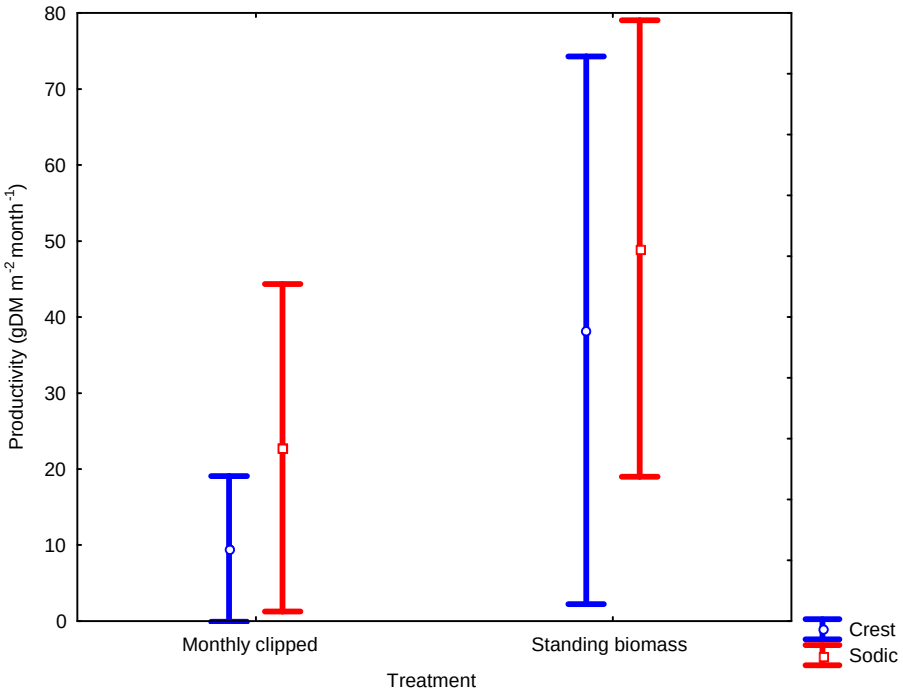


Figure 4.5: Grass biomass productivity estimates (g DM m^{-2} $month^{-1}$) for February 2004 in monthly clipped and standing biomass plots. Points denote means and vertical bars denote 0.95 confidence intervals

Monthly clipped productivity in the sodic patch (22.8 ± 10.44 g DM m^{-2} $month^{-1}$) was higher than that of monthly clipped crest (9.5 ± 4.46 g DM m^{-2} $month^{-1}$) in February 2004. Monthly productivity in standing biomass plots also revealed higher estimates in the sodic patch (49.02 ± 13.3 g DM m^{-2} $month^{-1}$) than in the crest (38.26 ± 16.0 g DM m^{-2} $month^{-1}$) (Figure 4.5). Monthly productivity is more than twice as high in sodic $plots_{SB}$ than in sodic monthly clipped plots and more than four times as high in crest $plots_{SB}$ than in crest monthly clipped plots in February 2004.

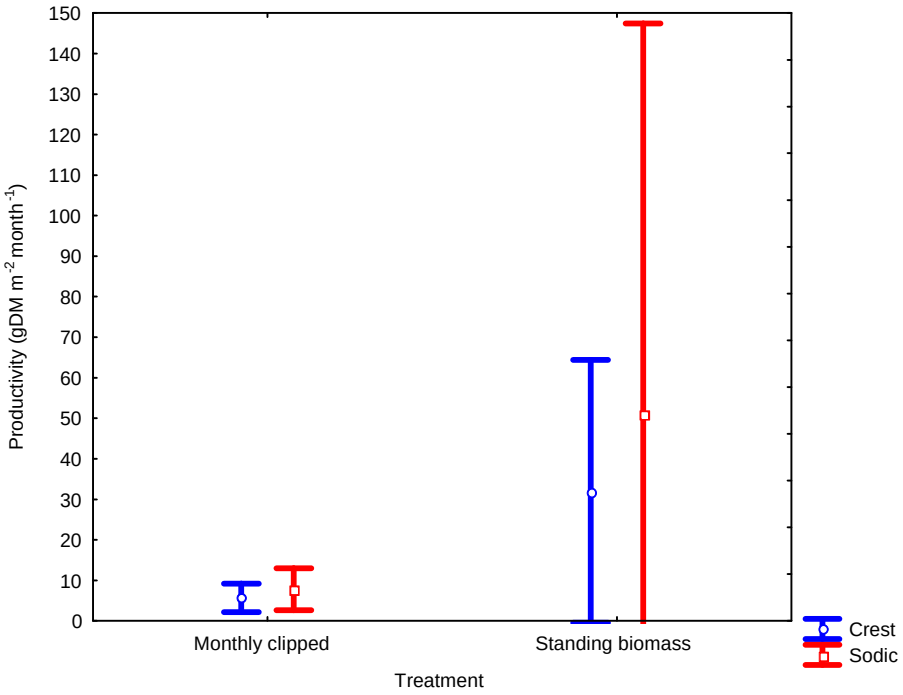


Figure 4.6: Grass biomass productivity estimates (g DM m-2 month-1) for February 2005 in monthly clipped and standing biomass plots. Points denote means and vertical bars denote 0.95 confidence intervals

Monthly clipped productivity in the sodic patch (7.8 ± 2.4 g DM m^{-2} $month^{-1}$) was higher than that of monthly clipped crest (5.7 ± 1.63 g DM m^{-2} $month^{-1}$) in February 2005. Monthly productivity in standing biomass plots also revealed higher estimates in the sodic patch (50.9 ± 42.67 g DM m^{-2} $month^{-1}$) than in the crest (32.0 ± 14.32 g DM m^{-2} $month^{-1}$) (Figure 4.6). Monthly productivity is more than six times as high in sodic $plots_{SB}$ than in sodic monthly clipped plots and more than five times as high in crest $plots_{SB}$ than in crest monthly clipped plots in February 2005.

4.3 Total foliar nutrient content

4.3.1 Nitrogen

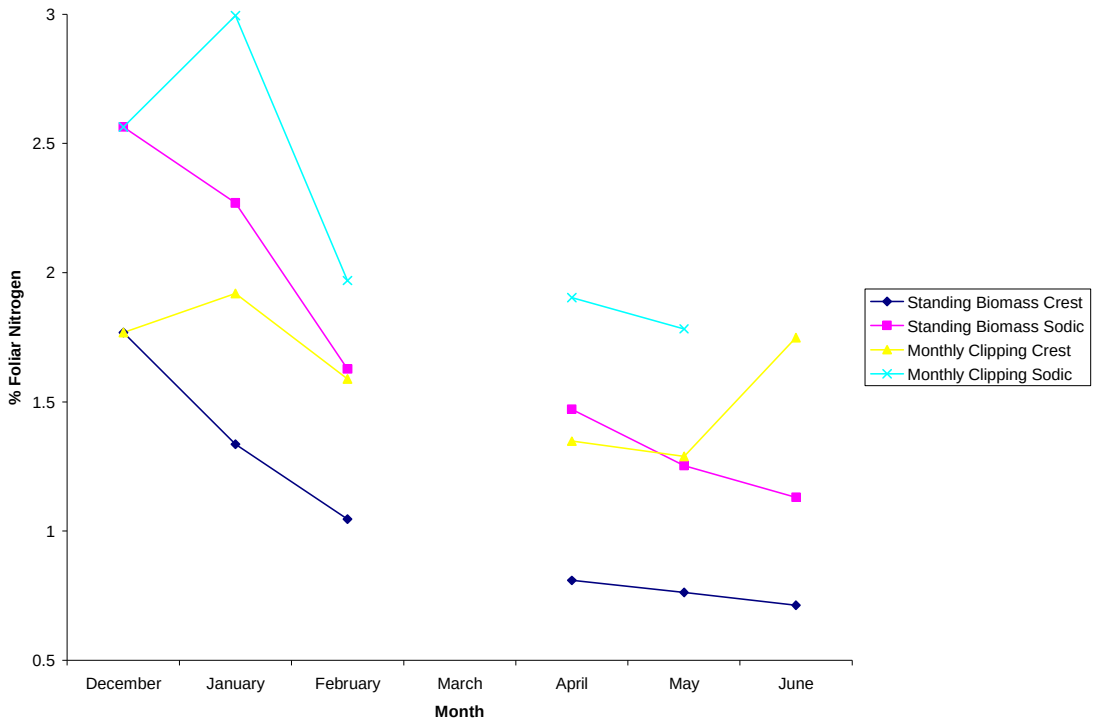


Figure 4.7: Change in percentage foliar nitrogen through the growing season in monthly clipped treatments inside the exclosure and standing biomass (seasons 2 and 3 combined)

Foliar nitrogen (N) decreases steadily as the growing season proceeds in regularly clipped and standing grass biomass (Figure 4.7). Nitrogen decreased from 2.5% N in January in sodic standing biomass to 1.1%N in June. Nitrogen peaked in January for both monthly clipped treatments (2.9 %N in sodic and 1.9 %N in crest foliage), which may be linked to rainfall which was just over double the 100.9mm long-term average for January in season 2 (208.2 mm) and 30% higher than the long-term average for January in season 3 (130.9 mm). Sodic patch N levels remain higher than those of the crest in corresponding treatments, and within both sodic and crest patches, monthly clipped plots maintained higher N levels than plots with standing biomass. Clipping of grass kept the grass in a

much greener, rejuvenating state and % N only decreased to 1.7% in monthly clipped sodic forage and 1.2% in monthly clipped crest forage in May. On the contrary, standing biomass had become moribund later in the season and %N decreased to under the palatability threshold of 1.5 %N for both sodic and crest forage.

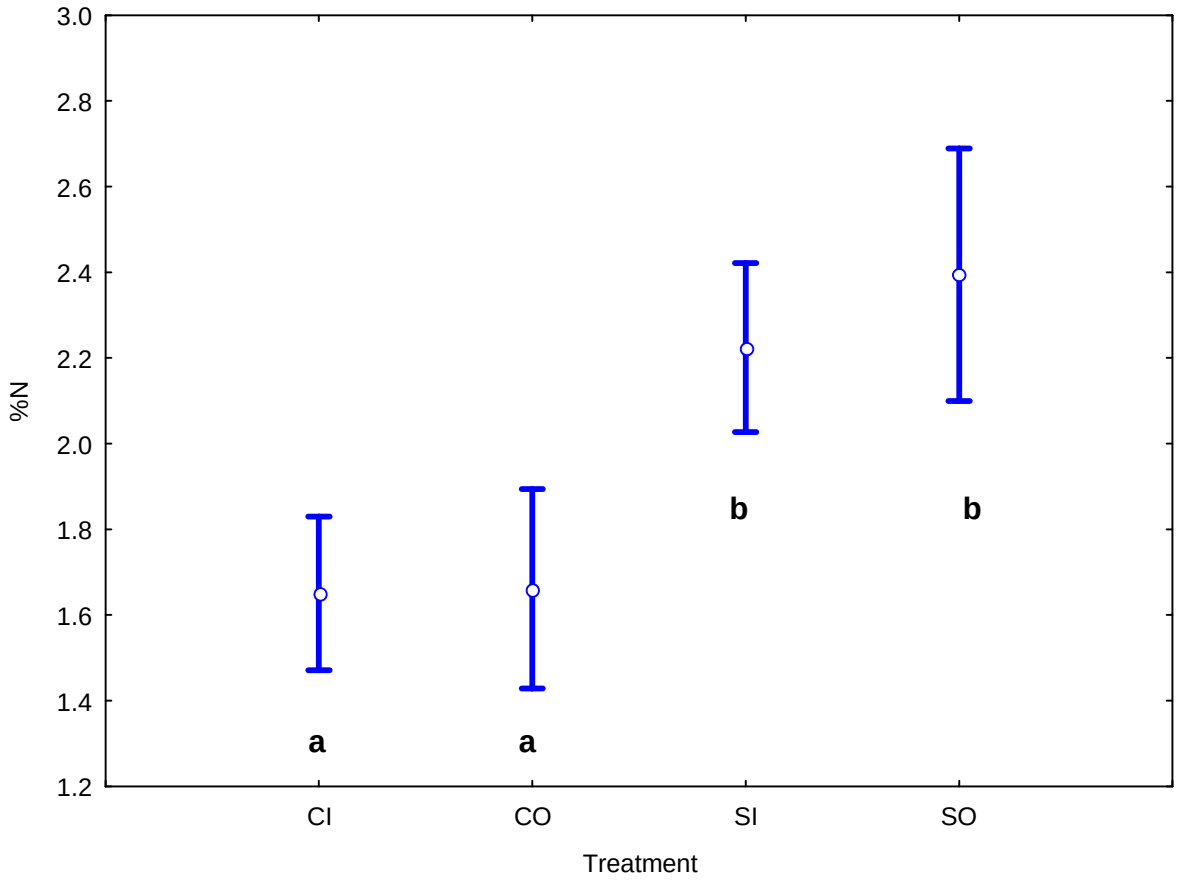


Figure 4.8: Percentage foliar nitrogen across all treatments over seasons 2 and 3. Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

Figure 4.8 reveals that an overall significant difference in foliar N means between treatments ($p<0.05$) was found with total N significantly higher ($p<0.05$) in sodic forage (SI = 2.2%N and SO = 2.3%N) than crest forage (CI and CO = 1.6%N). No significant

differences (p>0.05) were found between monthly clippings outside and inside the exclosure within terrain units. All treatment means remained above the palatability threshold of 1.5% N.

4.3.2 Phosphorus

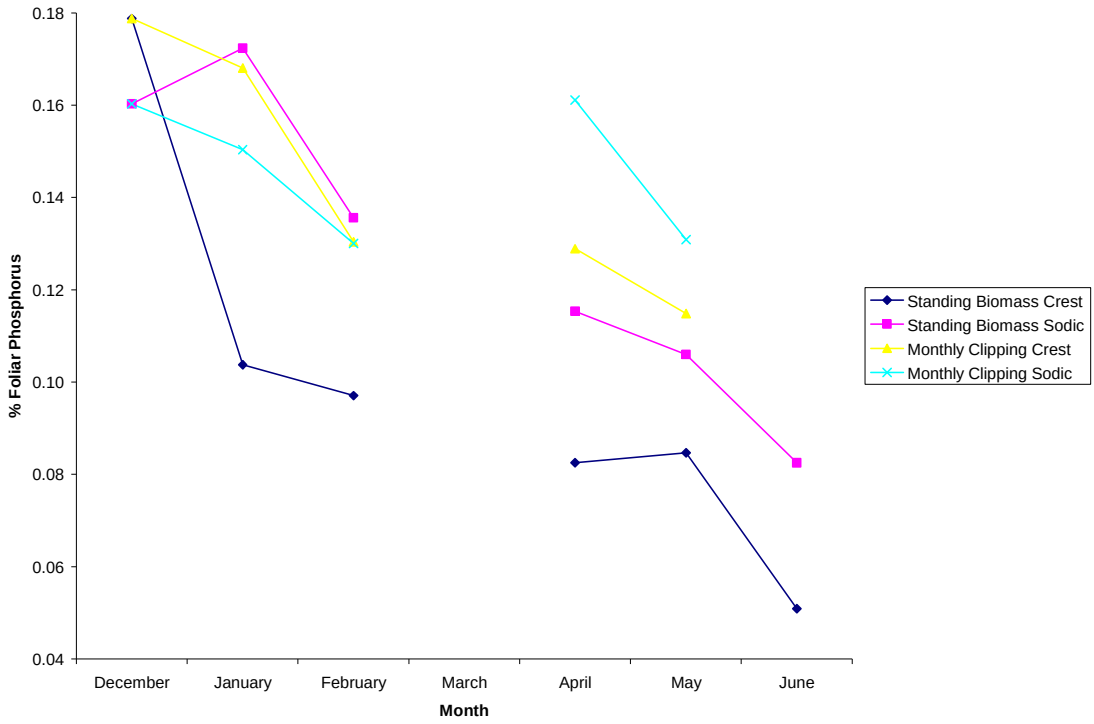


Figure 4.9: Change in percentage foliar phosphorus through the growing season in monthly clipped treatments inside the exclosure and standing biomass (seasons 2 and 3 combined)

Foliar phosphorus (P) decreased steadily in both clipped and standing forage in both crest and sodic patches as the growing season proceeded (Figure 4.9), with standing biomass decreasing the most; from 0.16 %P in December to 0.08%P in June in sodic forage and from 0.18% P in December to 0.05 %P in June in crest standing biomass. Monthly clipped crest forage dropped to 0.11 %P, while monthly clipped sodic forage remained higher than all other treatments in May with 0.13 %P. As with N levels, P levels are

consistently higher in monthly clipped foliage than in standing biomass, as clipping maintains the sward in a more active growing state, while standing crop becomes more moribund as the season progresses.

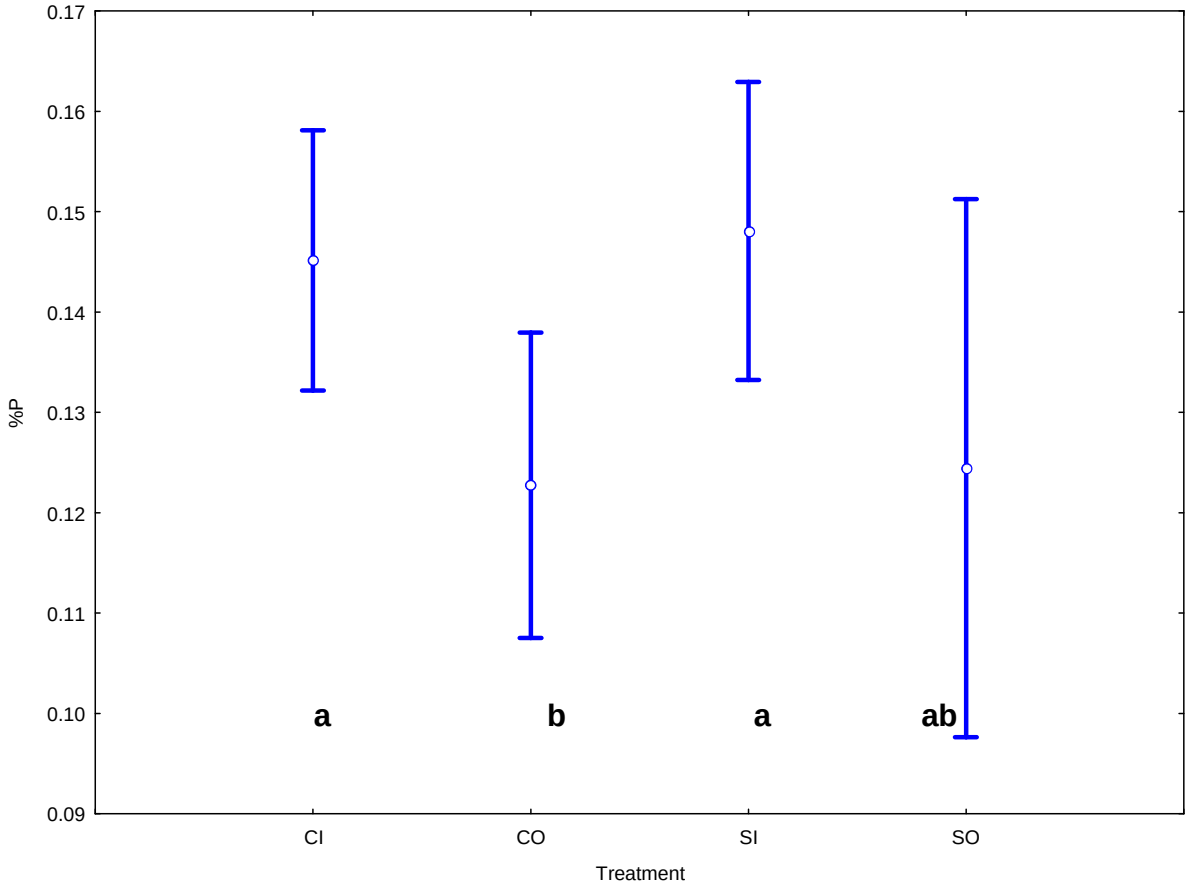


Figure 4.10: Percentage foliar phosphorus across all treatments over seasons 2 and 3. Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

No overall significant difference ($p>0.05$) in foliar P between treatments was found (Figure 4.10). However, means of 0.14%P in both CI and SI treatments were significantly higher than 0.12%P of CO (Fisher LSD test; $p<0.05$), and higher – but not significantly so – than 0.12%P of SO which had a wider range of values ($p>0.05$). It is doubtful whether defoliation *per se* underpins the apparent trend of low foliar P from outside the

exclosure, since both sets of plots were subject to the same experimental clipping intensity.

4.3.3 Carbon

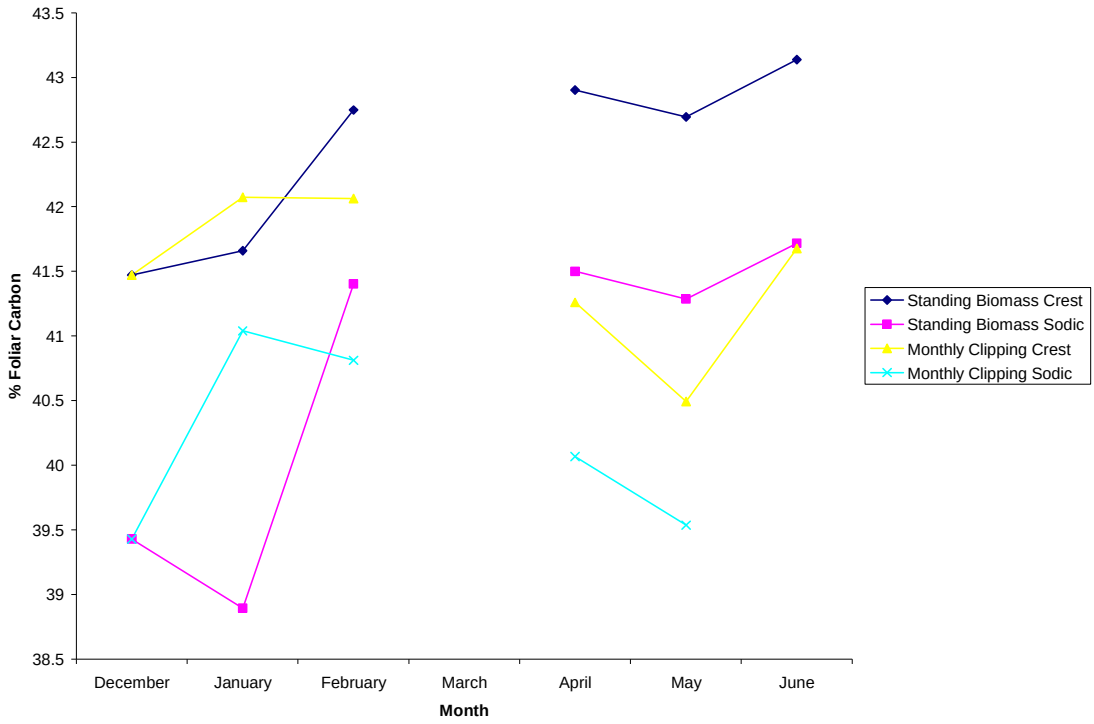


Figure 4.11: Change in percentage foliar carbon through the growing season in monthly clipped treatments inside the exclosure and standing biomass (seasons 2 and 3 combined)

Foliar carbon (C) increased steadily in both sodic and crest standing biomass as the growing season proceeded, and both ended the growing season (June; sodic = 41.7%C and crest = 43.1%C) on average 2% higher than December %C levels (Figure 4.11). Both sodic and crest monthly clipped treatments showed a similar increase in the early growing season followed by a decrease in the late growing season, but never fluctuated by more than 2% from December %C levels throughout the season. The accumulated growth within the terrains (crest and sodic patches) consistently displayed higher levels

of foliar C than the monthly clipped plots. Crest treatments displayed consistently higher C levels than sodic treatments.

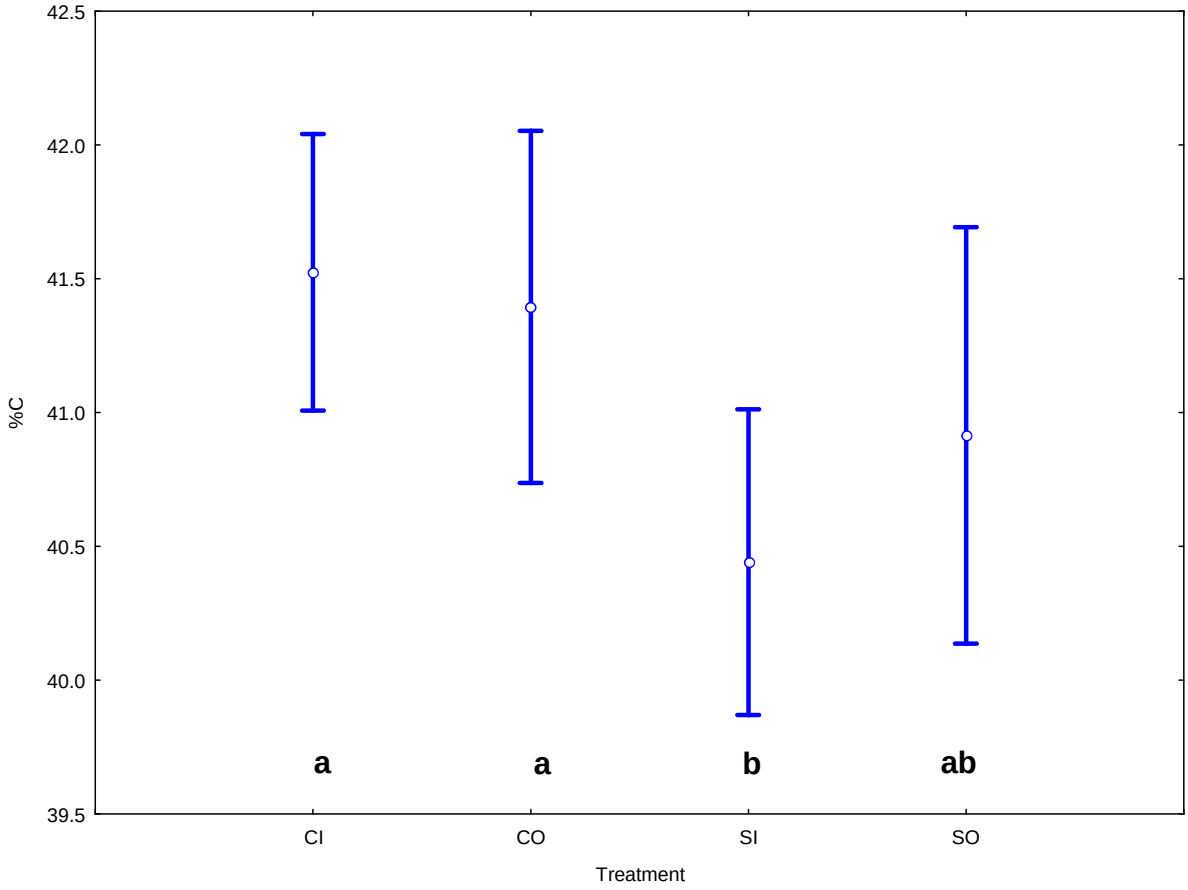


Figure 4.12: Percentage foliar carbon across all treatments over seasons 2 and 3. Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

An overall significant difference ($p<0.05$) in foliar C between treatments was found with crest foliar C on average (41.5%C inside the exclosure and 41.3%C outside the exclosure) significantly higher (Fisher LSD test; $p<0.05$) than SI (40.4%C) foliage, but not significantly higher than SO (40.9%C) foliage (Figure 4.12). Sodic foliage, although lower than crest in total C, did not differ significantly between SI and SO. Treatment means remained in a tight 1.5% range.

4.3.4 Sodium

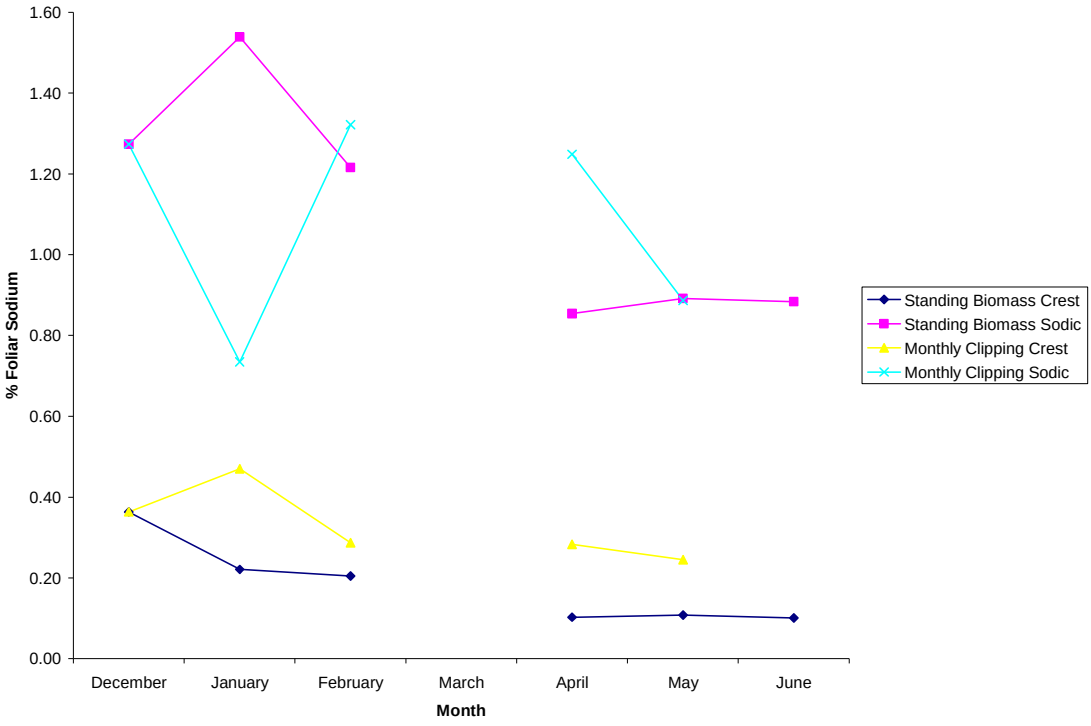


Figure 4.13: Change in percentage foliar sodium through the growing season in monthly clipped treatments inside the exclosure and standing biomass (seasons 2 and 3 combined)

As was expected, foliar sodium (Na) percentage consistently remained over two times higher in sodic forage than in crest forage – whether monthly clipped or in standing biomass (Figure 4.13), due to the higher level of soil sodium. Standing crest biomass displayed the lowest Na levels of all treatments (≤0.22%Na after January), and Na decreased in both crest and sodic forage (monthly clipped and standing biomass) as the season progressed. Sodium peaked in sodic standing biomass in January at 1.5%Na, and decreased to 0.88%Na in June.

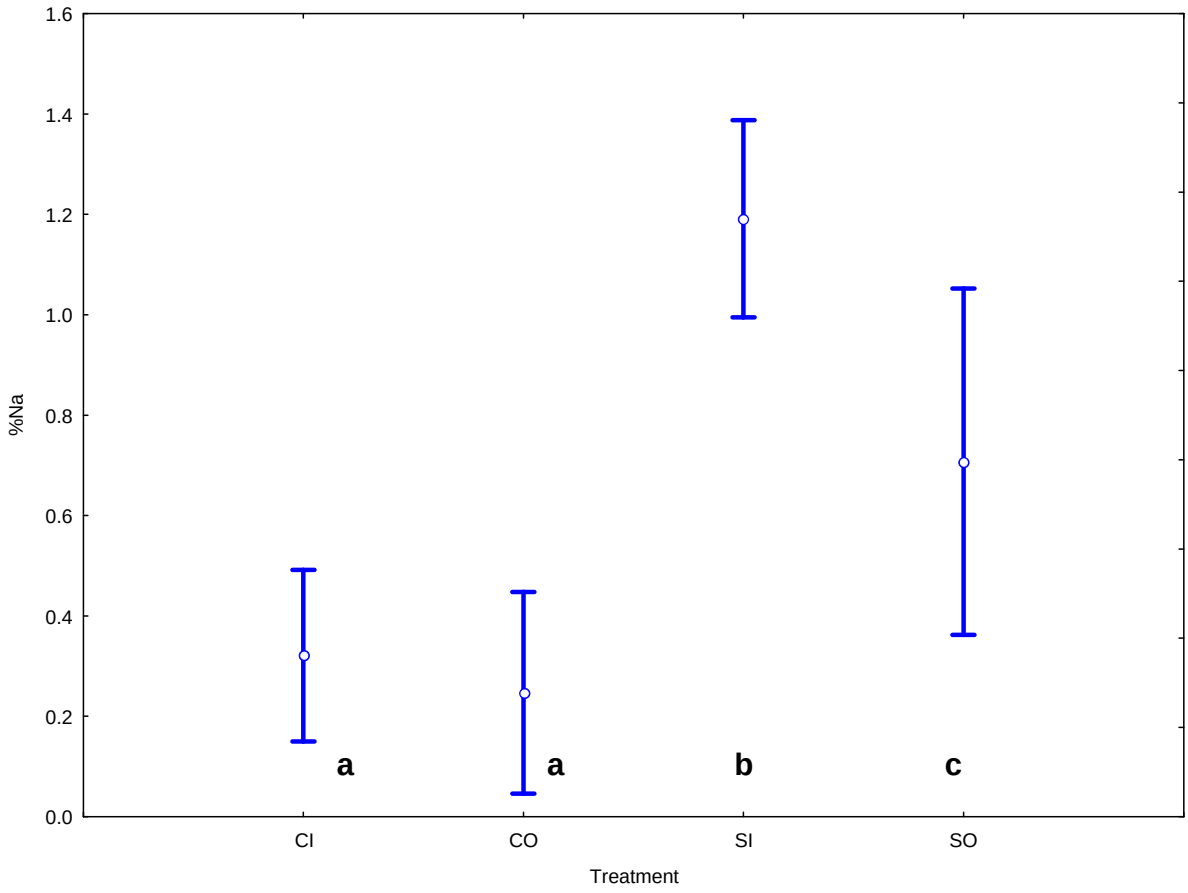


Figure 4.14: Percentage foliar sodium across all treatments over seasons 2 and 3. Treatment codes refer to the terrain – crest (C) and sodic patch (S) – and position relative to the exclosure – inside (I) and outside (O). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

An overall significant difference ($p<0.05$) in foliar Na between treatments was found with foliar Na significantly higher in all sodic treatments than that of the crest ($p<0.05$) and no significant differences within the crest (Figure 4.14). Foliage from SI (1.2%Na), however was on average significantly higher in Na than SO foliage (0.7%Na), and over three times higher than crest forage from inside the exclosure (0.3%Na) and outside the exclosure (0.2%Na).

4.3.5 C:N Ratios

Used as an index of palatability, lower C:N ratios inferred higher relative palatability in sodic forage. Both monthly clipped sodic treatments (SI = 18.2 C:N and SO = 17.1 C:N) were lower than both crest treatments (CI = 25.1 C:N and CO = 24.9 C:N), which was expected as sodic foliage is significantly higher in N and significantly lower in C than crest foliage (Figures 4.8 and 4.12).

4.3.6 N:P Ratios

N:P ratios were higher in sodic (SI = 15.9 N:P and SO = 19.9 N:P) than in crest foliage (CI = 11.8 N:P and CO = 13.8 N:P).

4.4 Utilisation

4.4.1 The relationship between grass biomass productivity and utilisation

Utilisation values were calculated by subtracting the monthly mean of productivity in the treatments outside the exclosure (CO and SO) from those inside the exclosure (CI and SI, respectively). In the context of the following 2 utilisation analyses, productivity (x-axis) data are monthly means from those inside the exclosure (CI and SI). Statistical correlations were tested using the Spearman test as data were not normally distributed.

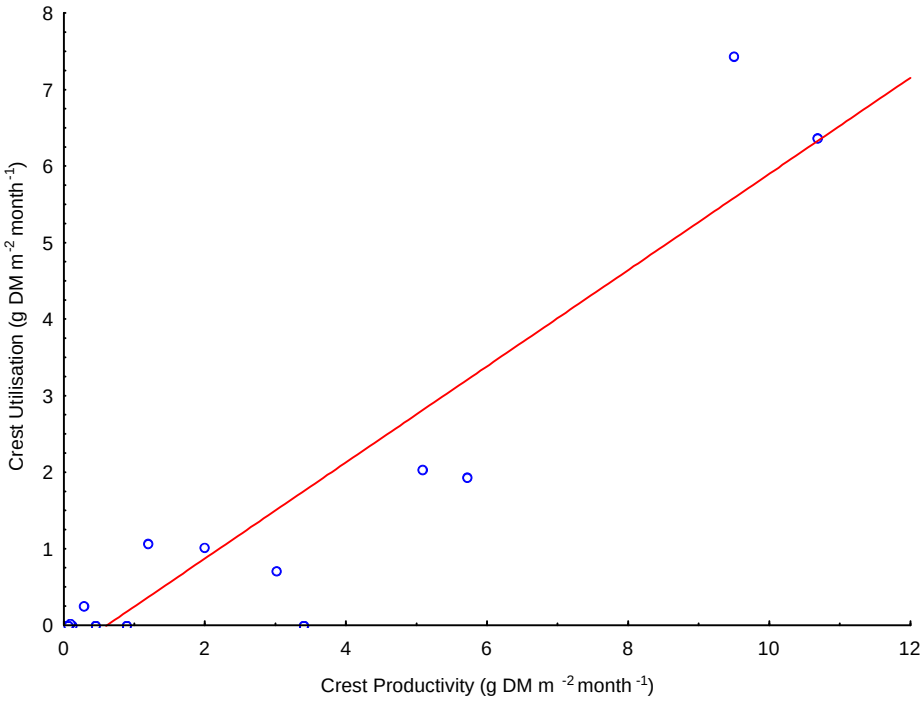


Figure 4.15: Relationship between the monthly means of crest productivity (g DM m^{-2} $month^{-1}$) and utilisation over three seasons (r=0.72, p<0.05)

Crest productivity was strongly correlated with crest utilisation during the three sampled seasons (r=0.72, p<0.05), as utilisation increased as productivity did (Figure 4.15).

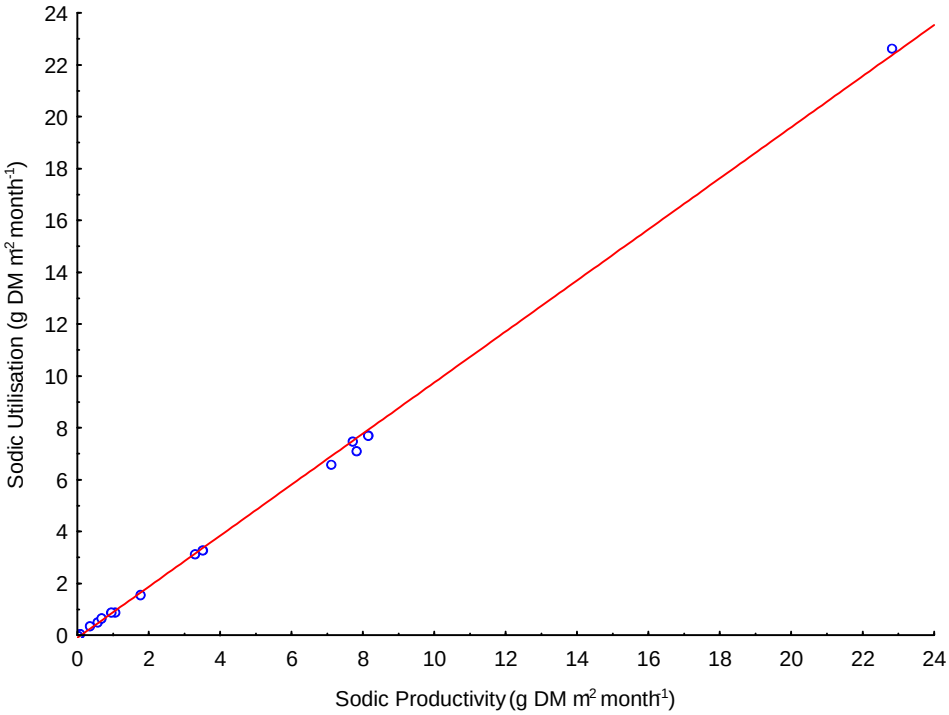


Figure 4.16: Relationship between the monthly means of sodic productivity (g DM m^{-2} $month^{-1}$) and utilisation over three seasons (r=0.99, p<0.05)

A very strong positive and significant relationship is apparent (Figure 4.16) between productivity and utilisation in the sodic areas. The significant tightness of fit indicates high utilisation of available forage on the sodic patch. The tightness of fit is attributed to productivity values from SO remaining close to zero throughout the sampling period (Figures 4.1 to 4.3). Both crest and sodic patches are utilised, but almost all sodic forage produced is utilised, whereas crests are utilised to a lesser degree.

4.4.2 The relationship between foliar nutrients and percentage utilisation

The monthly mean values for utilisation used in the analyses described in Figures 4.15 and 4.16 were converted to percentages, by dividing them by the paired amount produced inside the exclosures and multiplying them by 100. This set of monthly utilisation percentages were paired month-for-month with the total monthly foliar content of N, P,

C, Na, C:N ratios and N:P ratios for Seasons 2 and 3. Statistical relationships between N, P, C and Na content and utilisation were tested using the Spearman test as utilisation data were not normal. C:N and N:P ratio data are displayed and discussed, but not statistically analysed.

4.4.2.1 Nitrogen

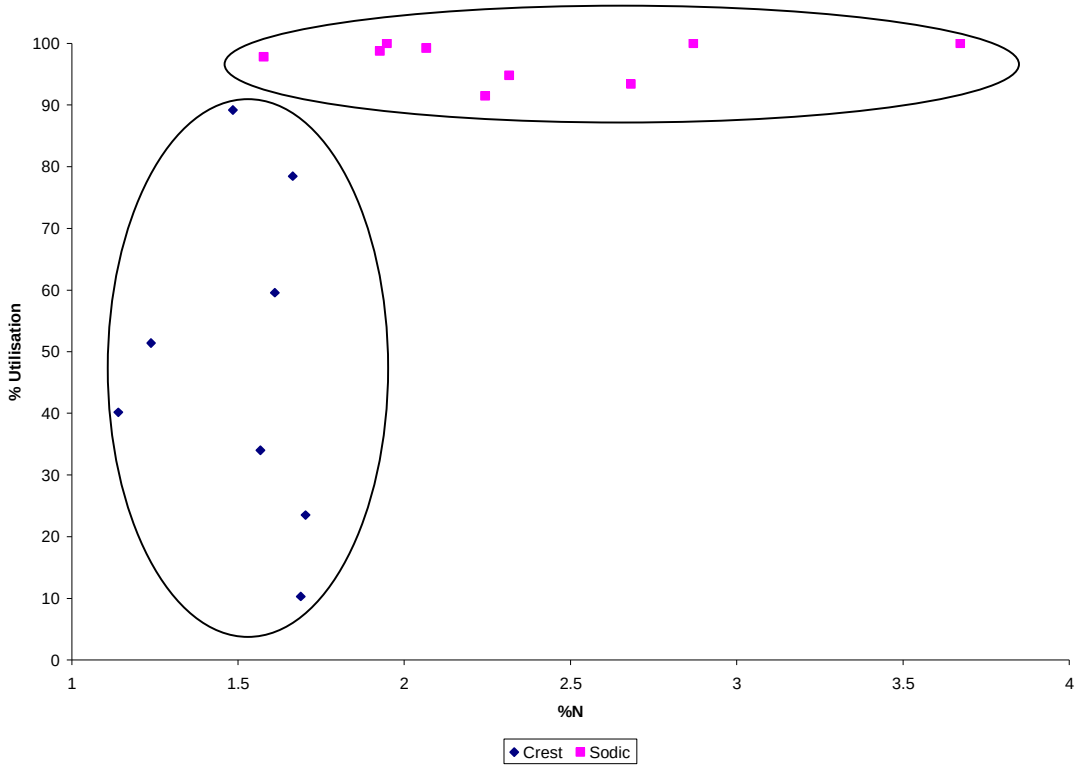


Figure 4.17: Relationship between percentage foliar nitrogen and percentage forage utilised in the sodic patch (r=0.16, p>0.05) and crest patch (r=0.016, p>0.05) over seasons 2 and 3

No relationships were apparent (Figure 4.17) between percentage N and percentage forage utilised for both the sodic and crest patch types. Relationships between percentage N and utilisation do not appear to be linear, and therefore linear fitting (especially in the crest) would be meaningless.

Figure 4.17 reveals that herbivores are possibly attracted to areas that support forage with higher N concentrations. Throughout the range of relatively higher sodic percentage foliar N (1.7-3.7% N), utilisation remains near 100%, while most crest forage sampled remained at a threshold of 1.7% N, and experienced a wider range of utilisation (8-90% utilisation). What is clear is that sodic forage is more preferred than crest, even at the lowest sampled point of 1.5%N.

4.4.2.2 Phosphorus

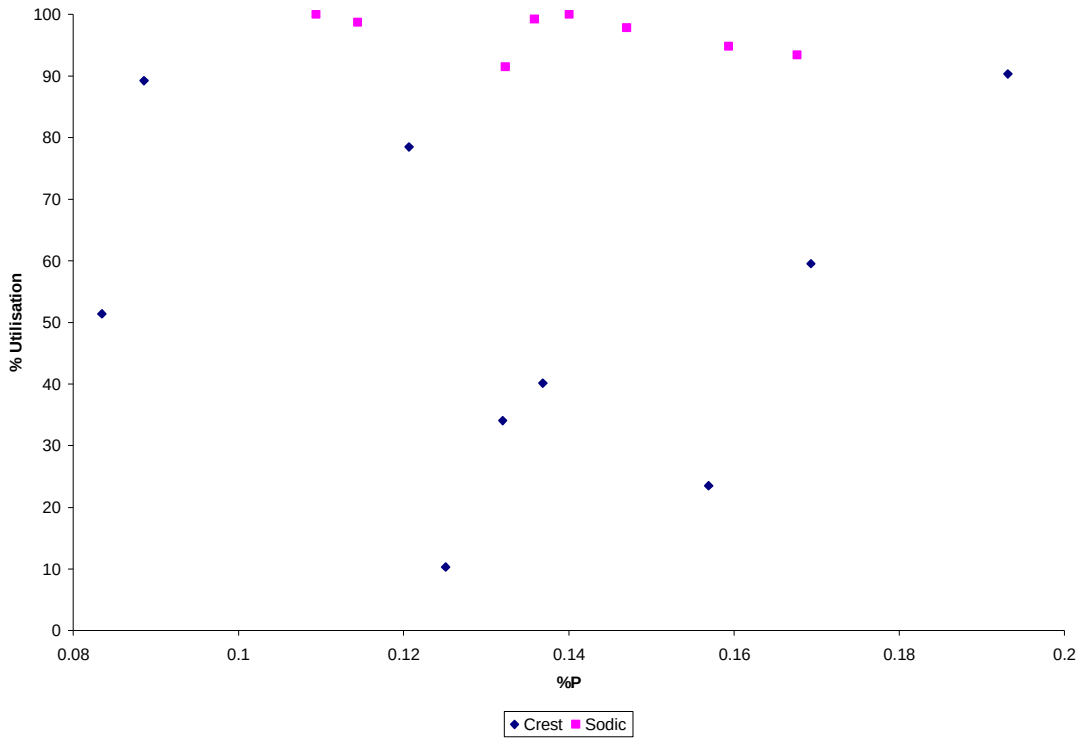


Figure 4.18: Relationship between percentage foliar phosphorus and percentage forage utilised in the sodic patch (r=-0.45, p>0.05) and crest patch (r=0.05, p>0.05) over seasons 2 and 3

No relationships were detected between percentage foliar P and percentage forage utilised for both the sodic and crest patch types (Figure 4.18). No correlations were

significant and linear fits would be meaningless, especially with regard to crest utilisation.

Figure 4.18, however, reveals that sodic and crest forage cover the same range of %P, and even though the range of crest %P (0.08 – 0.19%P) is wider, sodic forage (0.10 – 0.16%P) is still more utilised. It is suggested that P, although an important nutrient often limiting to secondary production, does not attract herbivores to the sodic patch, but may be important in combination with increased foliar-N and other nutrients in sodic forage.

4.4.2.3 Carbon

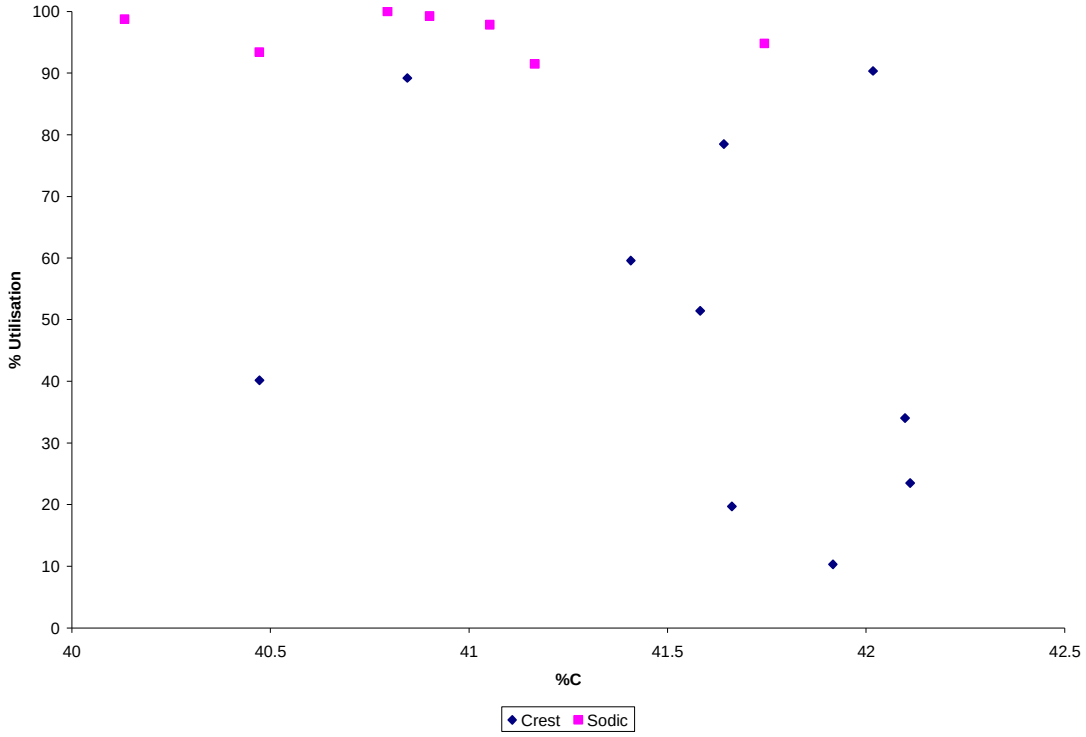


Figure 4.19: Relationship between percentage foliar carbon and percentage forage utilised in the sodic patch (r=-0.66, p>0.05) and crest patch (r=-0.35, p>0.05) over seasons 2 and 3

No relationships were detected between percentage foliar C and percentage forage utilised for both the sodic and crest patch types (Figure 4.19). Both correlations were not significant, and a linear fit – especially in the crest – would be meaningless. Grazers preferred sodic forage regardless of %C, which on average is lower in %C than crest forage.

4.4.2.4 Sodium

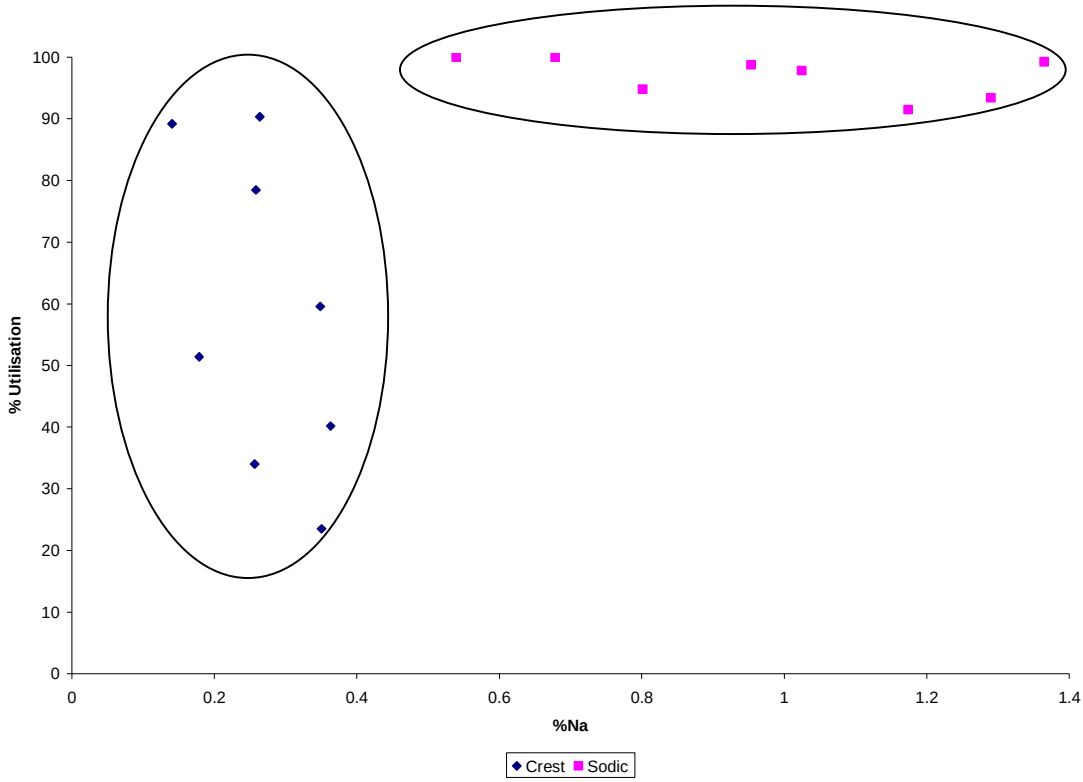


Figure 4.20: Relationship between percentage foliar sodium and percentage forage utilised in the sodic patch (r=-0.53, p>0.05) and crest patch (r=-0.38, p>0.05) over seasons 2 and 3

No relationships were apparent (Figure 4.20) between percentage foliar Na and percentage forage utilised for both the sodic and crest patch types. Relationships between percentage Na and utilisation do not appear to be linear, and therefore linear fitting – especially in the crest – would be meaningless.

Figure 4.20 reveals that herbivores are possibly attracted to areas that support forage with higher Na concentrations. Throughout the range of relatively higher sodic percentage foliar Na (0.5-1.3% Na), utilisation remains near 100%, while most crest forage sampled remained at an upper threshold of 0.3% N, and experienced a wider range of utilisation (23-90% utilisation). What is clear is that sodic forage is more preferred than crest, and the emergent point cluster pattern is very similar to that of N (Figure 4.17). This indicates that Na, like N in Figure 4.17, is possibly an important attracting nutrient for herbivores to concentrate their grazing in the sodic patch and may be important in combination with increased foliar-N and increased foliar-P in sodic forage.

4.4.2.5 C:N Ratios

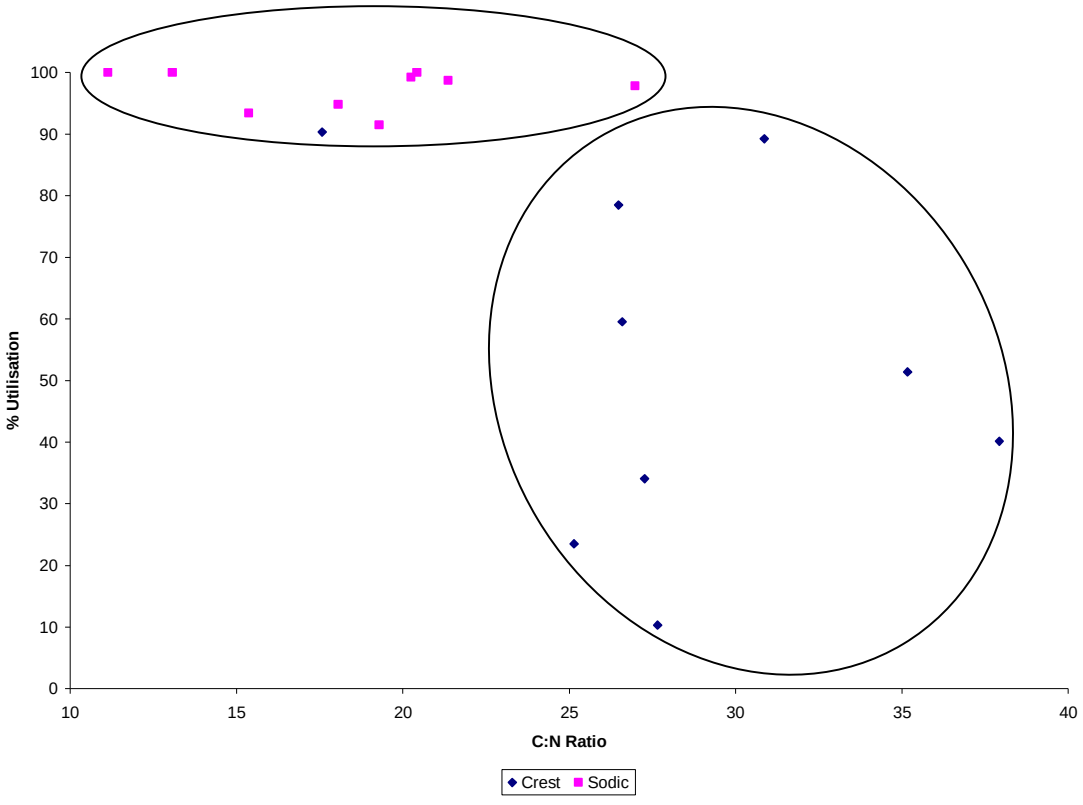


Figure 4.21: Relationship between foliar C:N ratios and percentage forage utilised in the sodic patch and crest patch over seasons 2 and 3

Sodic forage, with lower ranges of sodic foliar C:N ratios (11-27 C:N) experienced much higher (close to 100%) utilisation than crest forage, which mostly ranged from 25 to 37 C:N (Figure 4.21). It is interesting to note that the crest point with the lowest C:N ratios (17 C:N) was also the most utilised crest point at 90.3%. The importance of N as the main attracting nutrient has been discussed, but not relative to C:N ratios, which directly affect palatability. As sodic forage is more utilised, it will be kept at a relatively more immature state than crest forage keeping C:N ratios relatively low, while crest forage accumulates more standing crop as it matures under less utilisation, and would therefore have relatively higher C:N ratios.

4.4.2.6 N:P Ratios

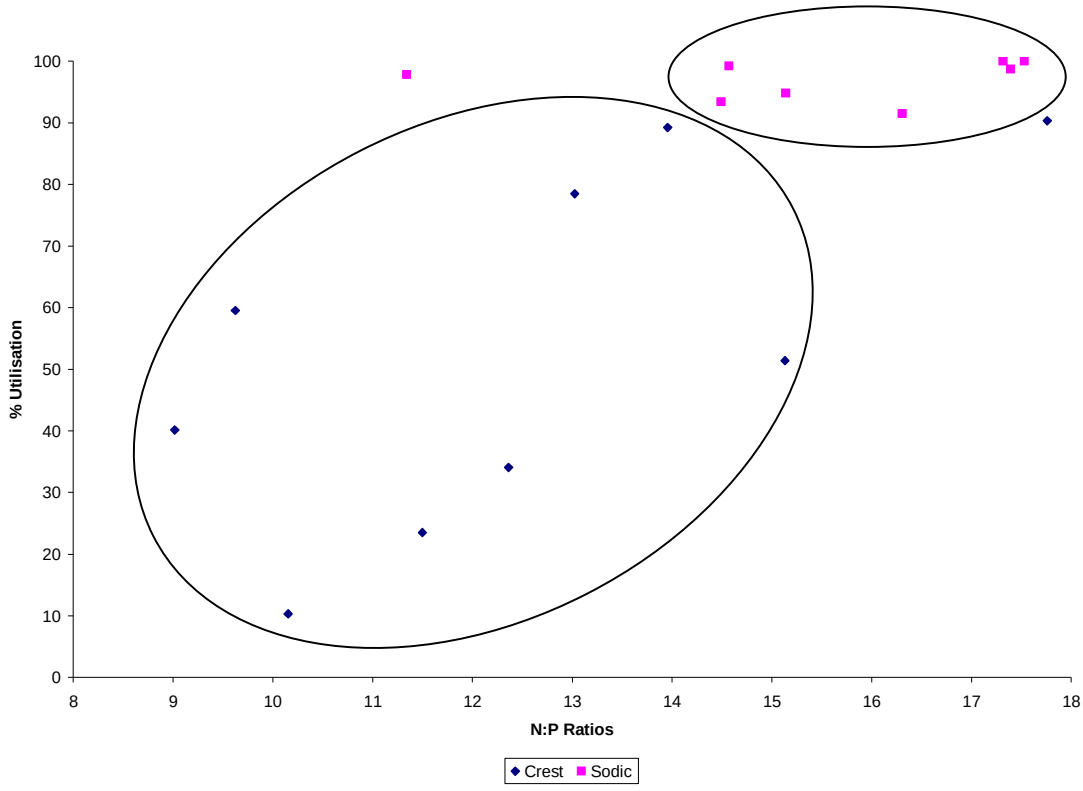


Figure 4.22: Relationship between foliar N:P ratios and percentage forage utilised in the sodic patch and crest patch over seasons 2 and 3

An overall correlation may be apparent (Figure 4.22) between N:P ratios and percentage forage utilised for both the sodic and crest patch types. Foliar N:P ranges overlap between crest (9-18 N:P) and sodic foliage (11-17 N:P). Sodic foliage remains more utilised (close to 100%) regardless of foliar N:P ratios.

4.5 Stable natural abundance isotopes

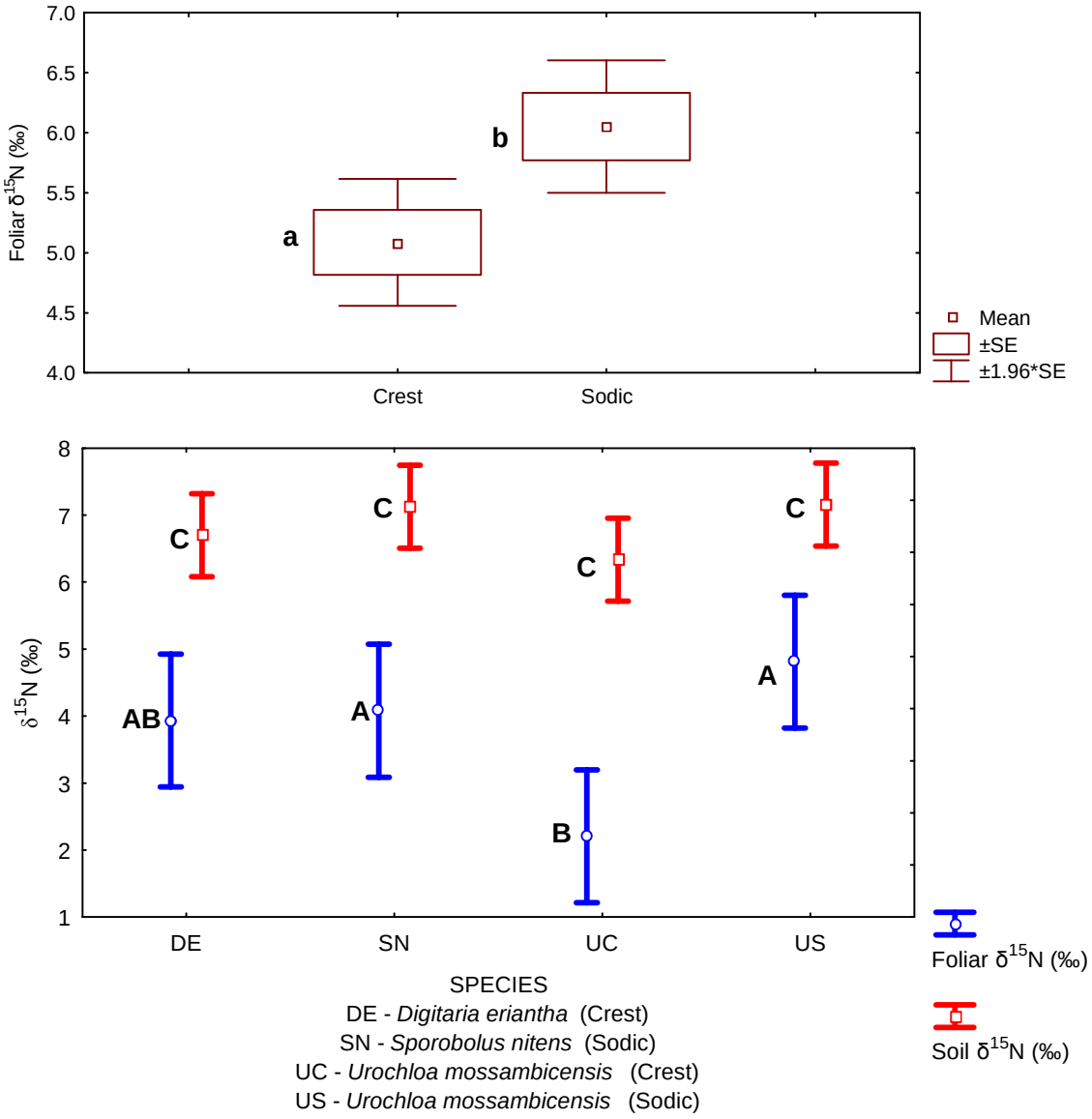


Figure 4.23: Foliar $\delta^{15}N$ values (‰) of mixed grass species samples from Season 1 in crest (n = 14) and sodic (n = 16) patches (above); and $\delta^{15}N$ values (‰) sampled during Season 3 from 4 grass species, foliar (n = 10) per species and underlying soil samples (n = 10) per species (below). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

$\delta^{15}N$ values from aggregated mixed species samples were significantly enriched ($p<0.05$) in sodic forage (6.05 ± 1.12‰) relative to crest forage (5.08 ± 1.01‰) (Figure 4.23 - above). Sodic foliar samples ranged from a minimum of 4.1‰ to a maximum of 9.15‰, while crest foliar samples ranged from a minimum of 3.18‰ to a maximum of 6.44‰.

Grass species had different foliar $\delta^{15}N$ values ($p<0.05$). No significant difference was found between values in the underlying soil sampling units (Figure 4.23). *Urochloa mossambicensis* (UC) that grew on the crest had foliar $\delta^{15}N$ values (mean 2.21 ± 0.78‰; range 0.93 – 3.61‰) significantly less enriched than those of *U. mossambicensis* (US) (mean 4.81 ± 1.9‰; range 3.04 – 9.71‰) and *Sporobolus nitens* (SN) (mean 4.08 ± 0.66‰; range 3.19 – 5.15‰) on sodic patches. UC was not significantly different from $\delta^{15}N$ values of *Digitaria eriantha* (DE) (mean 3.93 ± 2.22‰; range 1.9 – 8.99‰).

Soil $\delta^{15}N$ values did not differ between DE (mean 6.70 ± 0.5‰; range 5.89 – 7.5‰), SN (mean 7.13 ± 1.01‰; range 5.48 – 8.48‰) and US (mean 7.16 ± 1.45‰; range 5.12 – 10.21‰). No pattern or relationship between paired soil and foliar ranges were observed. Foliar $\delta^{15}N$ values were more enriched than soil $\delta^{15}N$.

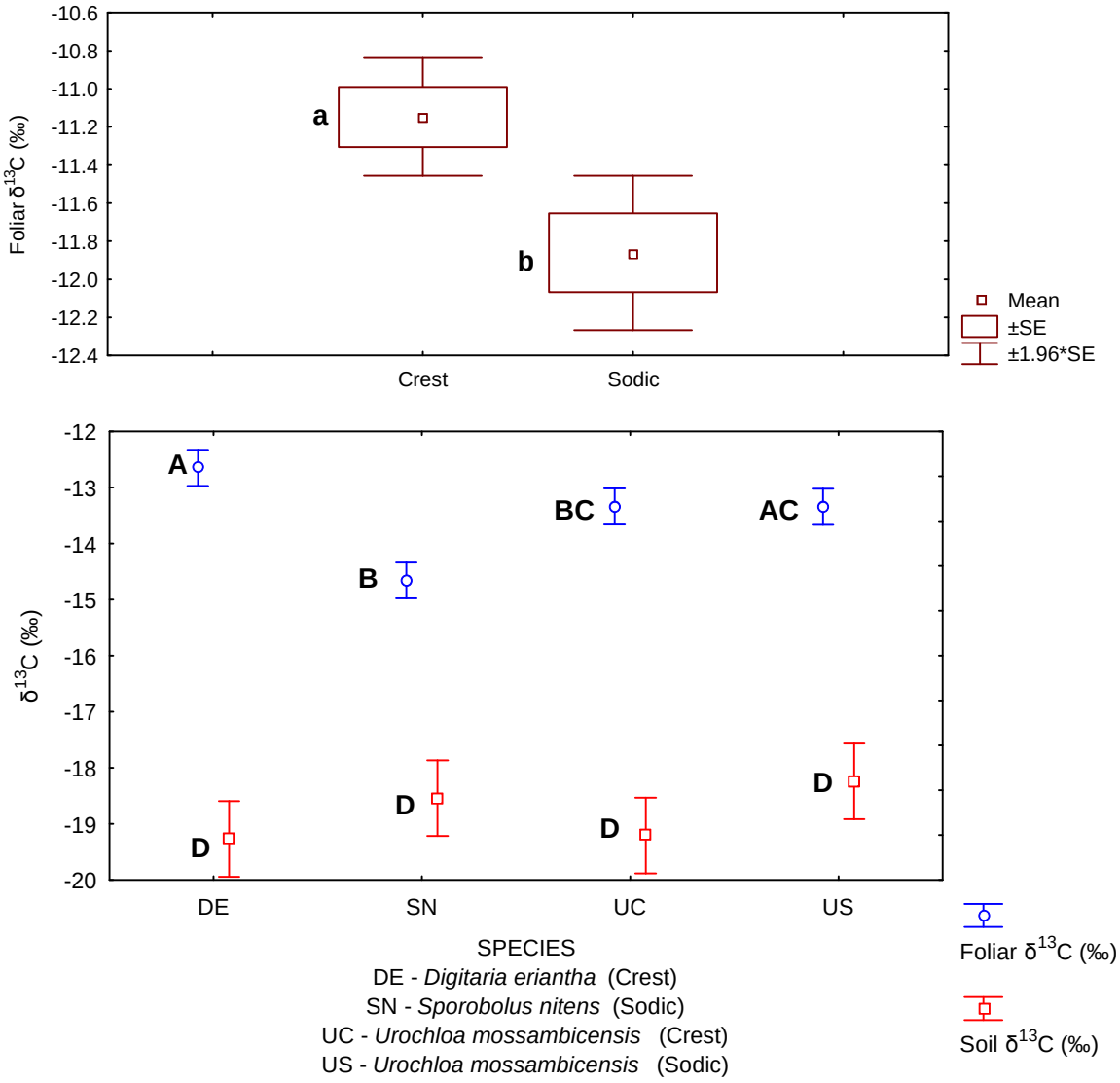


Figure 4.24: Foliar $\delta^{13}C$ isotope ranges (‰) of mixed grass species samples from Season 1 in crest (n = 14) and sodic (n = 16) patches (above); and $\delta^{13}C$ isotope ranges (‰) sampled during Season 3 from 4 grass species, foliar (n = 10) per species and underlying soil samples (n = 10) per species (below). Points denote means and vertical bars denote 0.95 confidence intervals. Data with similar letters are not significantly different

In mixed species foliar samples $\delta^{13}C$ isotope ranges in crest forage (-11.15‰ ± 0.59‰) were significantly enriched ($p<0.05$) relative to sodic forage (-11.86‰ ± 0.83‰) (Figure 4.24 - above). Mixed species crest foliar samples ranged from a minimum of -12.7‰ to a

maximum of -10.3‰, while sodic foliar samples ranged from a minimum of -14.01‰ to a maximum of -10.42‰.

An overall significant difference in foliar $\delta^{13}C$ was found between single species sampling units ($p<0.05$), though no significant difference was found between values in the soil sampling units (Figure 4.24 - below). Foliar SN ranges (mean -14.66 ± 0.4‰; range -15.22 – -14.01‰) were significantly less enriched than those of DE (mean -12.65 ± 0.33‰; range -13.38 – -12.32‰) and US (mean -13.35 ± 0.78‰; range -15.3 – -12.9‰), but not different to those of UC (mean -13.34 ± 0.36‰; range -14.2 – -12.98‰). Foliar ranges of UC did not differ significantly from US but were significantly less enriched than those of DE.

Soil ranges of DE (mean -19.27 ± 0.94‰; range -20.31 – -17.32‰), SN (mean -18.54 ± 1.0‰; range -20.16 – -16.91‰), UC (mean -19.21 ± 1.05‰; range -20.65 – -17.13‰) and US (mean -18.24 ± 1.2‰; range -19.96 – -16.43‰) did not differ significantly. No pattern or relationship between paired soil and foliar ranges were observed. Foliar $\delta^{13}C$ values were more enriched than soil $\delta^{13}C$.

4.6 Soil Nitrogen

Soil N data were collected in April 2005, together with data described in Figures 4.23 and 4.24 and are displayed in Figure 4.30.

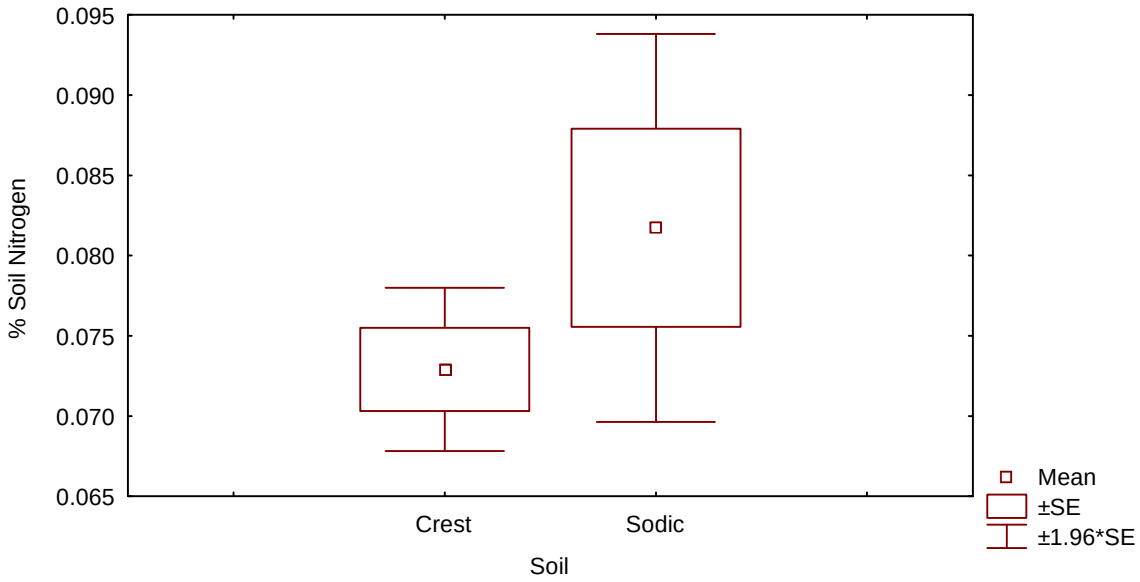


Figure 4.25: Percentage soil nitrogen in crest (n=20) and sodic (n=20) soils in Season 3

Crest (0.072±0.01 %N) and sodic (0.081±0.02%N) %N means were not statistically different (student's t test; $p>0.05$), but sodic soils were higher in %N than crest soils (Figure 4.25).

CHAPTER 5: DISCUSSION

The findings of this study can be incorporated into management practices, specifically to recommend that the scale, methodology and spatial arrangement for monitoring of forage production be conducted across the landscape, including patches of high herbivory eg sodic soils. The exclusion of other patch types along the catena, in this study, as producers of forage (e.g. riparian, seep line, etc.) does not downplay their ecological importance but allows for substantive information to be collected in just two of the catenal locations. The continued discussion of the catena concept facilitates an integrative systems view of these two patch types and provides a spatial context within which crest and sodic patches are embedded.

5.1 Ecophysiology

The ecophysiological aspects of this study deal with the availability of water and N to the plant, and are therefore discussed before productivity, quality and the utilisation of grass biomass. Water, nutrient availability and herbivory, among many other variables such as temperature, light, length of growing season, species diversity, fire and edaphic features and their interactions are key factors determining the composition, structure and functioning of savannas (Scholes and Walker 1993), and indeed grass biomass production (Haddad et al 2002; Briggs & Knapp 1995; McNaughton 1988). Data reported for this study relate to the former three variables water, nutrient availability and herbivory. Soil moisture data were not as comprehensive as hoped, due to large gaps in the data due to instrumentation malfunction. This limited me to aggregating data from across sodic sites and across crest sites. Therefore, all interpretation, extrapolation and analysis of these data should be done with caution.

Crests are more water limited than sodic patches. Species assemblages that are possibly more WUE would be expected to occur on crests. This then explains why $\delta^{13}C$ values of crest grass species, when aggregated, (Figure 4.29) or in the case of an individual species

such as (Figure 4.29) *Digitaria eriantha*, were significantly more enriched than those of both aggregated sodic grass species or an individual sodic grass species, *Sporobolus nitens*. The $\delta^{13}C$ values of a species which occurs over the entire catena, *Urochloa mossambicensis*, straddles the range of values between those of the crest and sodic ranges. This validates the hypothesis that crest environmental conditions are more water limited relative to sodic patches, and that species which are possibly more WUE would dominate the crest, while species which are adapted to a wider range of water limitation, is able to occur throughout the catena, but not dominate any landscape position (in the case of *U. mossambicensis*).

Soil $\delta^{15}N$ values (Figure 4.28) reveal that although sodic soils are slightly more enriched than crest soils (<1‰), the difference is not statistically significant. Figure 4.28 reveals that significantly more enriched values of natural abundance $\delta^{15}N$ were found in sodic patch foliage (aggregated multiple species) than in crest foliage indicating increased N-loss (possibly through denitrification, leaching and/or defoliation) or enrichment (possibly through urine and dung deposition by herbivores) in sodic patches relative to crests. Higher volumetric water in the sodic soil, as previously discussed, is an important factor in both mineralization and denitrification potential, of which the latter was found to be significantly higher in sodic soils (Fisher 2006). Denitrification is a fractionating process, releasing lighter nitrogen (^{14}N) atoms preferentially to the heavier atoms (^{15}N). Consequently, the remaining nitrogen available for plant uptake would be more enriched than before denitrification.

$\delta^{15}N$ values of *D. eriantha* do not differ significantly from those of two single species selected from the sodic patch (Figure 4.28). *Digitaria eriantha* (mean 3.93 ± 2.22‰; range 1.9 – 8.99‰) was expected to have a range of values comparable to *U. mossambicensis* sampled in the crest (mean 2.21 ± 0.78‰; range 0.93 – 3.61‰) because both were sampled from the crest. However, *D. eriantha* values remained closer to those sampled from species in the sodic patch. Since different species are being compared, it is difficult to determine why *D. eriantha* is more enriched than *U. mossambicensis* from the crest. The remaining single species (Figure 4.28) sampled revealed the same trend as the

aggregated species (Figure 4.26a); that foliar samples from the sodic patch are significantly more enriched in $\delta^{15}N$ than those from the crest, even within the single species of *Urochloa mossambicensis*.

In the case of the single species collected in both sodic and crest patches, *U. mossambicensis*, the difference between the soil and foliar values ($\delta^{15}N_{soil}$ - $\delta^{15}N_{foliar}$; per co-occurring pair) is smaller within the sodic patch than in the crest patch. Sodic soils therefore have relatively higher soil-N availability, inferring higher rates of N-cycling and experience greater N-loss than crest soils. A study of relationships in soil-N dynamics and natural $\delta^{15}N$ abundance found that plants of the same life form group (non N-fixers, as in this study) and species display an increase in foliar $\delta^{15}N$ values, and that the difference between $\delta^{15}N$ abundance in leaves and soil became smaller along a gradient from N-poor to N-rich forest. It was shown that foliar $\delta^{15}N$ values and enrichment factors ($\delta^{15}N_{foliar}$ - $\delta^{15}N_{soil}$) are correlated to soil N availability, increased rates of N-cycling and increased loss of N (Garten & Van Miegroet 1994). A global study by Martinelli *et al*. (1999) also revealed that tropical forests relatively richer in nitrogen and with more open N-cycles produced foliar samples significantly enriched in $\delta^{15}N$ than in N-poor tropical forests and temperate forests, and that this relative enrichment was correlated to relatively N-richer systems with more open N-cycles.

Therefore, significantly more enriched foliar $\delta^{15}N$ values from the sodic patch, significantly higher total foliar nitrogen from the sodic patch (Figure 4.10), higher productivity and significantly higher utilisation in the sodic patch (Figures 4.5-4.6), and significantly higher denitrification potential in sodic soils (Fisher 2006) reveal that sodic patches do indeed have relatively more soil-N availability and a more open cycling of nitrogen than do crests.

Furthermore, significantly higher mycorrhizal colonisation in crest *U. mossambicensis* as reported in Reid (2005) and relatively low $\delta^{13}C$ and $\delta^{15}N$ foliar values in grass sampled from the crest may suggest that the crest is a relatively drier and nutrient poor environment

5.2 Grass biomass productivity and utilisation

Studies by McNaughton (1989, 1985) in SNP show that more utilised patches produce more biomass than less utilised patches. However, drivers of productivity differ in their relative importance from ecosystem to ecosystem (Grant & Scholes 2006, Naiman et al. 2003). Nevertheless, naturally occurring sodic patches, widely but in some cases, incorrectly known as problem areas of production and erosion fit only for rehabilitation (Khomo & Rogers 2005, Chappell 1992) have monthly productivity which is higher, though not significantly so, than crests (Figures 4.5-4.6) in the study area. These are new findings, as little empirical data report on sodic productivity on a monthly or seasonal basis. It is believed that the paucity of quantitative data relating to productivity and utilisation is a direct consequence of the lack of herbivory exclosures in large, free-ranging grazing systems in the region.

The two main effects of these soils on plant growth are a high Na content, meaning that species which are tolerant of raised Na levels will thrive, and secondly, a tendency for the exposed soil surface to seal and form a crust, restricting infiltration and increasing erosion susceptibility (Paterson & Steenkamp 2003).

Most primary productivity data are reported annually, whether in areas including or excluding herbivory (McNaughton 1996). Therefore, for comparisons, mean accumulated growth data, detailed in Figure 4.8, are used. Data from the Nylsvley Savanna Biome Programme (Scholes & Walker 1993) have been often used for comparison with the studies in the KNP (Du Toit et al. 2003). Productivity of grasses in the Nylsvley Nature Reserve (mean of 600 mm precipitation p.a.) is 60 g DM m^{-2} $year^{-1}$ (Grunow et al. 1980), which compares favourably to the mean accumulated growth in crests of 66.7 ± 47.9 g DM m^{-2} but substantially higher that mean accumulated growth in sodic patches of 47.0 ± 44.4 g DM m^{-2}. The Nylsvley values were determined in the broadleaf nutrient-poor

savanna, which is more similar to the crest in the study area than the sodic patch (Scholes et al. 2003).

Soil moisture and PAW are inevitably linked to annual rainfall. Season 1 (2002/2003) received 302.5 mm (51.9% ACT) and was classified as a dry year (Figure 3.2). Monthly rainfall totals from November to March each fell below 50% of the long-term average per respective month, as well as respective monthly ACT. Season 2 (2003/2004) received 618.1 mm (106.2% ACT) and was classified as a wet year (Figure 3.2). The early wet season (November and December) was relatively dry, receiving less than 50% of the long term monthly mean. The middle of the wet season was the wettest, as January 2004 received 208.2 mm, over double the long-term mean for that month, and a third of the total rainfall for Season 2. Season 3 (2004/2005) received 760 mm (130.6% ACT) and was classified as a wet year (Figure 3.2). The early wet season received most rainfall, peaking in November which received 252.4 mm, almost three times higher than the long term average for that month, and more than double ACT. Productivity tracked rainfall for the first two years, then the clipping/defoliation effect led to a decline in year three

Multiple clippings or frequent/regular defoliation of grass in this study resulted in significantly lower production relative to if the plant is left to accumulate biomass (Figure 4.8) which concurs with other studies (Ferraro & Oesterheld 2002, Jaramillo & Detling 1988), but is contrary to what was found in the high-nutrient East African grazing system reported by McNaughton (1985). In a global meta-analysis covering 236 sites, Milchunas and Lauenroth (1993) found that although grazing does at times appear to increase productivity, in most cases it had a negative or neutral effect on plant growth. Reduction in productivity was positively related to grazing intensity and defoliation history (number of successive years of grazing) but this was less apparent in systems with comparatively longer evolutionary histories of grazing.

Considering that species life histories relate to WUE, and that PAW and soil-N are lower in crest soils, it can be deduced that crest species are especially sensitive to regular defoliation and may have adapted under a low frequency of defoliation, as the means of

accumulated crest production are higher than those of sodic growth ($p>0.05$) and the means of monthly clipped crest production are lower than those of sodic growth ($p>0.05$) (Figure 4.8). Conversely, even though an overall negative effect of defoliation is apparent, sodic grass species seem to be better adapted to regular defoliation than crest grasses. It has been suggested that crest production in the region accumulates more biomass than nutrient hot-spots due to its lower quality (and is therefore less utilised), and may act as a reserve forage source in the dry season, when sodic production ceases (Grant & Scholes 2006, Naiman et al. 2003).

Even though monthly defoliation had an overall negative effect on biomass production, both sodic and crest productivity were positively correlated to utilisation (Figures 4.19-4.20), indicating that biomass availability is an important variable when considering what influences foraging choices by large herbivores. In the KNP, biomass availability determines the large-scale distribution patterns and population size of herbivores (Naiman et al. 2003). McNaughton (1985) found that herbivore densities adjusted their densities to grass biomass productivity, that grazing stimulated production by maintaining the grass plant in an immature, fast-growing state, and that grazing was concentrated in patches that were intrinsically more productive in the landscape. Though not significantly so, sodic productivity was higher than that of the crest (Figures 4.5-4.6), and displays a much tighter linear correlation ($r=0.99$, $p<0.05$) to utilisation than crest productivity ($r=0.72$, $p<0.05$), indicating that herbivores consume almost all grazeable forage on sodic patches, while crest production is not utilised to the same extent. Future studies should include increased plot numbers in sodic sites of various sizes along different order streams. The use of movable, short term exclosures also needs to be included in any future sampling.

I suggest the mechanism which explains differential biomass productivity strategies for crest and sodic patches is that crest grasses accumulate biomass quickly and more efficiently (following rainfall pulses) than sodic grasses during the early rainy season due to their possibly higher WUE (Figure 4.27), while sodic grasses are being grazed preferentially after the dry season for their increased forage quality (Figures 4.9-4.18).

This coincides with the gestation periods of most large, herding grazer species in the region. While the sodic grasses are maintained at an immature stage through grazing, (inferring lower C/N ratios of recent growth) the crest grasses accumulate biomass, inferring a steady increase of C/N ratios of older growth, making them less preferable to grazers. A greater dependence on the low quality forage of the crests is experienced in the dry season than in the growing season, as sodic productivity drops to a minimum with the end of the rains, and as production has not been allowed to accumulate on the sodic patches during the growing season (Grant & Scholes 2006). This mechanism is further explained in that crest productivity from outside the exclosure did not differ from crest productivity inside the exclosure (Figure 4.5) during the growing season, when data were collected. Sodic productivity from outside the exclosure, however, remained significantly lower throughout the growing season. This may be a consequence of the fact that sodic sites represent only a small fraction of the total landscape (Venter 1990), relative to crests. Herbivores can therefore concentrate on and maintain the sodic sward in an immature growth stage during wet seasons, thereby encouraging continual grazing and high rates of consumption (Augustine *et al*. 2003).

5.3 Forage quality and utilisation

Percentage foliar nitrogen, phosphorus and sodium decreased steadily as the growing season progressed in both sodic and crest patches under all treatments (Figures 4.9, 4.11 and 4.15, respectively). This concurs with a study conducted in a semi-arid savanna in Botswana, where nitrogen and phosphorus also steadily decrease as the growing season progressed (Tolsma *et al*. 1987). This decreasing nutrient trend was also reported in Grant and Scholes (2006) for utilised sodic patches, but not for crest patches. In each case reported in this study, sodic forage remains higher in foliar nutrient content than crest forage, and monthly clippings remain higher in foliar nutrient content than accumulated growth. This is seen to be related to defoliation maintaining the sward in an active growing stage (McNaughton 1985, Grant & Scholes 2006).

Percentage nitrogen was significantly higher in sodic forage, within each treatment (Figures 4.10) and monthly clipped forage (inside and outside) compared favourably to 2.57% foliar N reported for sodic patches on granites during the growing season, while monthly clipped crest forage had much lower (1.6-1.7%) percentage foliar N than the 2.25% N reported for crests on granites during the growing season, in which case percentage-N was also significantly higher in sodic than in crest forage (Grant & Scholes 2006).

Percentage sodium was significantly higher in sodic forage across all treatments (Figure 4.16) and ranged from 0.7-1.1% foliar Na, slightly higher than the peak (0.69%) reported by Grant and Scholes (2006) for sodic patches on granite, which was also significantly higher than percentage-Na in crest forage. Crest forage percentage Na ranged from 0.2-0.3% which compares most favourably to the Na foliar content (0.31%) of crest forage at the end of the growing season (Grant & Scholes 2006).

Contrary to findings in Grant and Scholes (2006), within each treatment, percentage foliar-P was higher in sodic forage than in crest forage, though ranges overlapped. Foliar sodic percentage-P ranged from 0.12-0.14% P, which falls into the percentage-P range for in Grant and Scholes (2006), but does not range as high as 0.26% (growing season, granite sodic patches). Foliar crest percentage-P ranged from 0.10-0.14% P, which falls into the percentage-P range for in Grant and Scholes (2006), but does not range as high as 0.35% (end of dry season, granite crest patches). Higher foliar P from clippings inside than outside the exclosure is suggested to be linked to an indirect effect of herbivore exclusion, namely the absence of trampling. The absence of trampling is positively related to the occurrence of biological crusts in many arid and semi-arid surface soils. These crusts have been shown in some studies to significantly increase P uptake by plants (Harper and Belnap 2001). Biological crusts were noted to be more extensive inside the exclosure than out, and I suggest that a potentially significant role is played by their presence.

Considering the abovementioned quality indices from this study and its comparison (Grant & Scholes 2006), it can be determined that sodic forage is of higher relative quality when compared to crest forage, though both decrease in quality as the growing season proceeds, though regularly defoliated swards produce higher quality forage than swards allowed to accumulate biomass.

In the KNP, forage quality – and not quantity – at the patch scale determines utilisation distribution. Utilisation is higher in patches with higher forage quality, relating specifically to higher foliar levels of N, P and Na (Grant & Scholes 2006). In east Africa, it was found that plant-available N and Na were higher in soils that were highly grazed, and that areas producing forage with higher-Na are selected for (McNaughton et al. 1997).

Carbon/nitrogen ratios are generally lower in the immature stage of a grass plant – or in grass plants which are kept short by regular defoliation (Grant & Scholes 2006, McNaughton 1985). It has been established by previous discussion and in the literature review that sodic forage experience more intense defoliation than crests.

Nitrogen and Na appear to be the most important nutrients that determine forage selection in this study, while phosphorus seems to be of relatively less importance, even though sodic forage has higher levels of phosphorus.

CHAPTER 6: CONCLUSIONS AND RECOMMENDATION

Findings from east African studies of grass biomass productivity in response to utilisation by grazing mammals and the observed difference in utilisation and standing crop disparities between sodic patches and crest patches lend initial credence to an hypothesis that grass biomass production (at a $1m^2$ scale) would be higher on sodic patches than on crest patches of the Skukuza land system in a semi-arid granitic savanna. This hypothesis was disproved as no significant difference was found between sodic and crest forage productivity. This study represents the first quantitative reporting of monthly and seasonal grass production data for sodic patches, hopefully dispelling paradigms that all naturally occurring sodic patches are problem areas with low productivity. In contrast to east African savannas, it was found – in both crests and sodic patches – that regular defoliation did not stimulate production, but resulted in lower biomass production when compared to an unclipped sward allowed to accumulate biomass. It was not possible to calculate inferential statistics when comparing the total grass production areas of the sodic and crest patches within the study site, and the $1m^2$ scale of comparison remained the most useful in this study.

Forage quality is higher in sodic patches than on crests, which possibly leads to higher utilisation by herbivores. Foliar nitrogen and sodium may be the most important nutrients influencing foraging choices between the two patch types. Higher foliar nitrogen in sodic forage has been linked to relatively higher soil-N availability in sodic soils than crest soils, as revealed by measuring total N and investigating co-occurring $\delta^{15}N$ soil and foliar values along the nutrient gradient. Using $\delta^{13}C$ values, it is shown that more water use efficient grasses were to be found on the crest, with less water use efficient grasses on the sodic site. Crest grass production seems to be largely affected by water availability, while sodic grass production is affected more by soil-N.

Both the use of $\delta^{15}N$ and $\delta^{13}C$ natural abundance stable isotopes in this study has proved very useful as an auxiliary data set for investigating production strategies, and their use in monitoring should be investigated for the region.

In the KNP, the VCA system was put in place to assess veld condition in terms of its potential to produce (1) forage for consumption by herbivores and (2) fine fuels for veld burning (Trollope 1990; Trollope et al 1989). None of the 533 permanent VCA points were placed on sodic sites, as they were not deemed to be representative of the respective landscapes which were being sampled. This is an anomaly, as sodic sites are a ubiquitous feature of the larger, granitic landscape of the Lowveld. Therefore, the VCA method ignores the inherent heterogeneity of savanna landscapes, specifically in terms of forage production in patches that might be preferred; more utilised, or produce more forage than patches that may be more representative of the spatially defined matrix that seemingly comprises a given landscape. In reality, patches are not utilised evenly, as some patches will always remain "under-utilised", while other "hotspots" will always be "overstocked" (Peel et al 1999). Therefore, the VCA network by omitting sodic sites, casts doubt on the presumed accuracy of the current estimating method (the composition and biomass of standing crop) for the forage production potential of a given landscape in the KNP, i.e. using standing crop at the end of the growing season. Methods of forage production assessment should be linked to the appropriate spatial and temporal scales at which herbivores impact the vegetation.

Management recommendations of this study include increased monitoring of sodic sites, highlighting the importance of sodic sites in the landscape and revisiting current methodology in terms of assessing accurately the forage production potential of the various landscapes (at the catena scale), and indeed, in highly grazed systems.

Sodic patches are important resource elements in the semi-arid granitic savanna landscape in terms of high quantity and quality forage supply. The select use of standing crop is inadequate for the assessment of grass biomass productivity in highly grazed systems. However, standing crop indices used in conjunction with values sampled from areas excluding herbivory allow for rigorous assessment of grass biomass productivity and utilisation in the landscape. Spatially, sodic patches occupy a much smaller proportion of the landscape than the extensive crest patches. Significantly higher sodic

patch forage quality possibly underpins the distinct disparity in patch utilisation. As such, sodic sites may act as “hot spots” in the landscape and may be crucial in supplying forage to fulfil the dietary requirements of both migrant and resident large mammalian herbivores in a semi-arid environment.

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APPENDICES

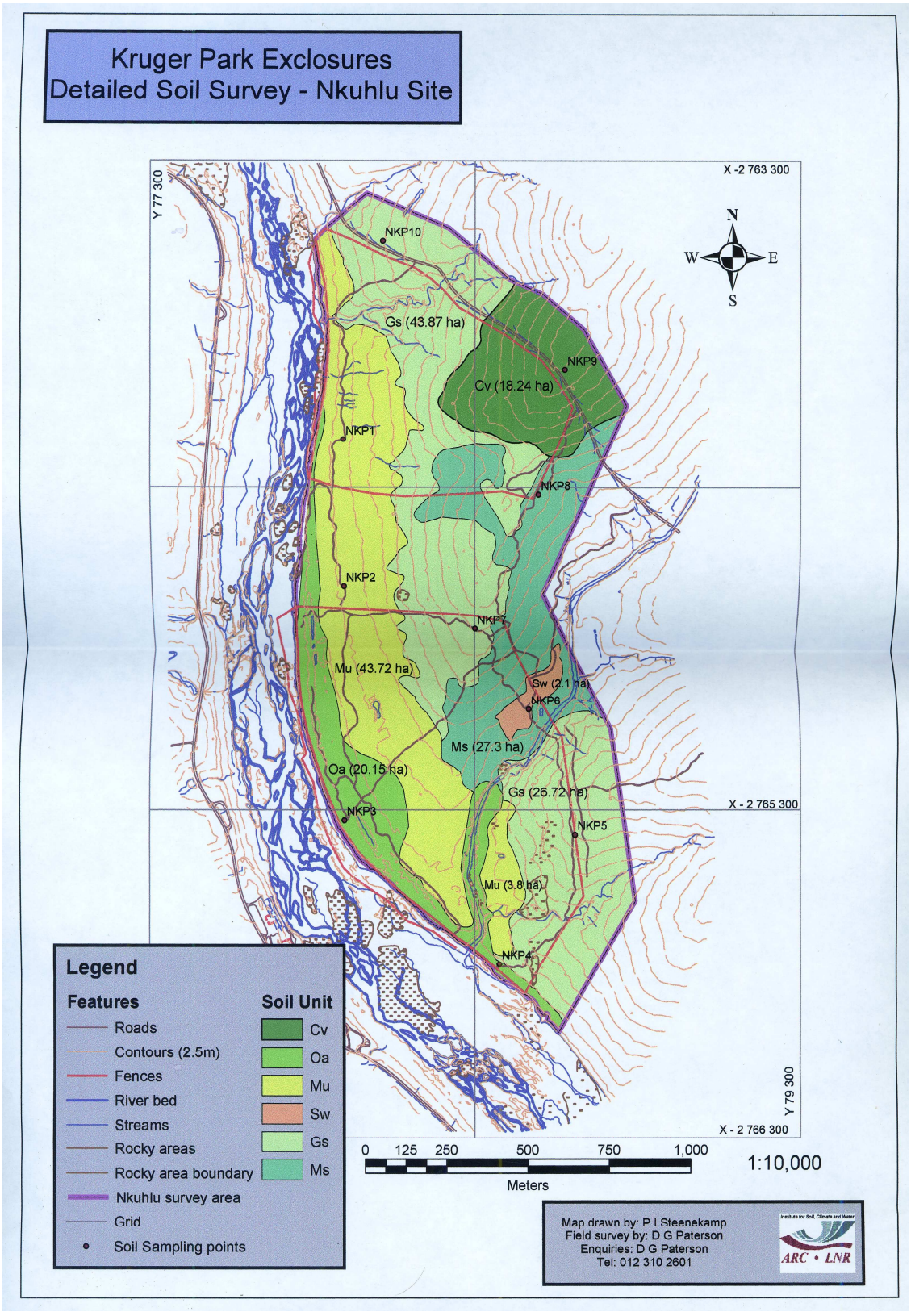
Appendix I: Confusion matrix of classified terrain units

			Classified				
Terrain Sub-unit		Classes	Bare	Grass	Brown Tree	Green Tree	Yellow Tree
Crest 1	**Observed**	Bare	94	4	0	0	2
		Grass	0	83	5	0	12
		Brown Tree	0	13	84	2	1
		Green Tree	0	0	15	80	5
		Yellow Tree	9	3	1	1	86
Crest 2		Bare	91	2	0	*	7
		Grass	0	91	3	*	6
		Brown Tree	0	21	79	*	0
		Green Tree	*	*	*	*	*
		Yellow Tree	2	7	1	*	90
Sodic 1		Bare	99	1	0	0	*
		Grass	0	98	1	1	*
		Brown Tree	0	1	98	1	*
		Green Tree	0	0	3	97	*
		Yellow Tree	*	*	*	*	*
Sodic 2		Bare	99	1	0	0	*
		Grass	0	98	1	1	*
		Brown Tree	0	0	98	2	*
		Green Tree	0	0	3	97	*
		Yellow Tree	*	*	*	*	*

Appendix II: Area and proportions of each terrain class per sub-unit

Terrain Sub-unit	Classes	Proportion	Area (ha)
Crest 1	Bare	0.06	0.58
	Grass	0.40	4.19
	Brown Tree	0.48	5.00
	Green Tree	0.01	0.13
	Yellow Tree	0.06	0.61
Crest 2	Bare	0.04	0.45
	Grass	0.65	7.60
	Brown Tree	0.24	2.81
	Yellow Tree	0.07	0.86
Sodic 1	Bare	0.09	1.18
	Grass	0.52	6.91
	Brown Tree	0.26	3.48
	Green Tree	0.13	1.74
Sodic 2	Bare	0.07	0.03
	Grass	0.77	0.29
	Brown Tree	0.10	0.04
	Green Tree	0.06	0.02

Appendix III: Soil Map of Nkuhlu Exclosure site and profile descriptions



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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15023

Map/photo : 2431DD Tshokwana

Latitude + Longitude: 24° 58' 58.4" / 31° 46' 17.3"

Land Type No :

Climate Zone :

Altitude : 217 m

Terrain Unit: Lower Footslope

Slope: 2 %

Slope Shape : Convex

Aspect : West

Microrelief :

Parent Material Solum : Origin binary, solid rock, lacustrine

Underlying Material : Gneiss

Geological Group / Formation : Nelspruit Suite

Soil form and family Valsrivier luckhoff

Surface rockiness :

Surface stoniness :

Occurence of flooding : Occasional

Wind erosion :

Water Erosion : Sheet slight, partially stabilized

Vegetation / Land use : Shrubveld, open

Water table : None

Described by : D.G. Paterson

Date Described : 9/2003

Weathering of underlying material: Unknown

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Dry state; horizon undisturbed; dry colour: brown 10YR5/3; texture: medium sandy loam; few fine faint grey unknown mottles; structure: weak coarse subangular blocky; consistence: slightly hard; common fine normal pores; few clay cutans; water absorption: 2 second(s); common roots; clear smooth transition.	Orthic
B1	250 - 500	Moist state; horizon undisturbed; moist colour: dark brown 10YR3/3; texture: medium sandy clay loam; common medium distinct grey and yellow unknown mottles; structure: moderate coarse subangular blocky; consistence: very firm; few fine normal pores; non-hardened free lime, moderate effervescence; common clay cutans; water absorption: 5 second(s); few roots; gradual smooth transition.	Pedocutanic
B2	500 - 1000	Moist state; horizon undisturbed; moist colour: olive brown 2.5Y4/4; texture: medium sandy clay loam; many medium prominent yellow and brown lime mottles; structure: weak coarse subangular blocky; consistence: slightly firm; common fine normal pores; non-hardened free lime, strong effervescence; few clay cutans; very few fine <2-6mm lime concretions; water absorption: 4 second(s); few roots; gradual wavy transition.	Neocarbonate
C	1000 - 1500		Unspecified material, with signs of wetness

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15024

Map/photo : 2431DD Tshokwana

Latitude + Longitude: 24° 59' 13" / 31° 46' 17.4"

Land Type No :

Climate Zone :

Altitude : 215 m

Terrain Unit: Lower Footslope

Slope: 1 %

Slope Shape : Straight

Aspect : West

Microrelief :

Parent Material Solum : Origin binary, solid rock, alluvium

Underlying Material : Gneiss

Geological Group / Formation : Nelspruit Suite

Soil form and family Montagu esperanza

Surface rockiness :

Surface stoniness :

Occurence of flooding : Occasional

Wind erosion :

Water Erosion :

Vegetation / Land use : Shrubveld, open

Water table : None

Described by : D.G. Paterson

Date Described : 9/2003

Weathering of underlying material: Unknown

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 400	Dry state; horizon undisturbed; dry colour: brown 10YR5/3; texture: medium sandy loam; few medium faint grey unknown mottles; structure: weak coarse subangular blocky; consistence: hard; common fine pores; non-hardened free lime, slight effervescence; few clay cutans; very few mixed-shape gravel 2-6mm; very few fine <2-6mm lime concretions; water absorption: 3 second(s); common roots; clear smooth transition.	Orthic
B1	400 - 900	Moist state; horizon undisturbed; moist colour: yellowish brown 10YR5/4; texture: medium sandy clay loam; common medium distinct grey and yellow lime mottles; structure: weak medium subangular blocky; consistence: slightly firm; few fine pores; non-hardened free lime, moderate effervescence; common clay cutans; water absorption: 4 second(s); few roots; gradual wavy transition.	Neocarbonate
C	900 - 1200+		Unspecified material, with signs of wetness

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15025

Map/photo : 2431DD Tshokwana

Latitude + Longitude: 24° 59' 36.7" / 31° 46' 17.7"

Land Type No :

Climate Zone :

Altitude : 215 m

Terrain Unit: Lower Footslope

Slope: 2 %

Slope Shape : Convex

Aspect : West

Microrelief :

Parent Material Solum : Origin binary, solid rock, alluvium

Underlying Material : Gneiss

Geological Group / Formation : Nelspruit Suite

Soil form and family Oakleaf ritchie

Surface rockiness :

Surface stoniness :

Occurence of flooding : Occasional

Wind erosion :

Water Erosion :

Vegetation / Land use : Treeveld, closed

Water table : None

Described by : D.G. Paterson

Date Described : 9/2003

Weathering of underlying material: Unknown

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 350	Moist state; horizon undisturbed; moist colour: brown 10YR5/3; texture: fine sand; few fine faint brown unknown mottles; structure: weak medium subangular blocky; consistence: slightly firm; common fine normal pores; few clay cutans; water absorption: 2 second(s); many roots; gradual smooth transition.	Orthic
B1	350 - 1200+	Moist state; horizon undisturbed; moist colour: brown to dark brown 10YR4/3; texture: fine sandy loam; few fine faint brown unknown mottles; structure: weak medium subangular blocky; consistence: slightly firm; common fine normal pores; few clay cutans; water absorption: 2 second(s); common roots; no observed transition.	Neocutanic

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15026

Map/photo : 2431DD Tshokwana

Latitude + Longitude: 24° 59' 50.9" / 31° 46' 34.8"

Land Type No :

Climate Zone :

Altitude : 211 m

Terrain Unit: Lower Footslope

Slope: 1 %

Slope Shape : Concave

Aspect : West

Microrelief :

Parent Material Solum : Origin binary, solid rock, alluvium

Underlying Material : Gneiss

Geological Group / Formation : Nelspruit Suite

Soil form and family Oakleaf ritchie

Surface rockiness : 2-10% exposed surface

Surface stoniness :

Occurence of flooding : Occasional

Wind erosion :

Water Erosion :

Vegetation / Land use : Treeveld, open

Water table : None

Described by : D.G. Paterson

Date Described : 9/2003

Weathering of underlying material: Weak physical, weak chemical

Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Moist state; horizon undisturbed; moist colour: brown 10YR5/3; texture: fine sandy loam; few fine faint brown unknown mottles; structure: apedal massive; consistence: slightly firm; common fine normal pores; few type unknown cutans; water absorption: 2 second(s); common roots; clear smooth transition.	Orthic
B1	250 - 600	Moist state; horizon undisturbed; moist colour: dark yellowish brown 10YR4/6; texture: fine sandy loam; common fine faint reddish brown unknown mottles; structure: moderate massive; consistence: slightly firm; few fine normal pores; few type unknown cutans; water absorption: 2 second(s); few roots; abrupt wavy transition.	Neocutanic
R	600 - 750+		Hard rock

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15027

Map/photo : 2431DD Tshokwana

Latitude + Longitude: 24° 59' 38" / 31° 46' 43"

Land Type No :

Climate Zone :

Altitude : 229 m

Terrain Unit: Crest

Slope: 1 %

Slope Shape : Convex

Aspect : South-west

Microrelief :

Parent Material Solum : Origin single, solid rock

Underlying Material : Gneiss

Geological Group / Formation : Nelspruit Suite

Soil form and family Mispah myhill

Surface rockiness : 2-10% exposed surface

Surface stoniness : 2-10% exposed surface, round & flat, gravel

Occurence of flooding :

Wind erosion :

Water Erosion :

Vegetation / Land use : Treeveld, sparse

Water table : None

Described by : D.G. Paterson

Date Described : 9/2003

Weathering of underlying material: Weak physical, weak chemical

Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Dry state; horizon undisturbed; dry colour: brown to dark brown 10YR4/3; texture: coarse sandy loam; common fine faint reddish brown geogenic mottles; structure: apedal massive; consistence: slightly hard; common fine normal pores; few clay cutans; few angular gravel 2-6mm; water absorption: 2 second(s); common roots; abrupt wavy transition.	Orthic
R	250 - 500+		Hard rock

ARC • LNR

SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15027
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 59' 38" / 31° 46' 43"
Land Type No :
Climate Zone :
Altitude : 229 m
Terrain Unit: Crest
Slope: 1 %
Slope Shape : Convex
Aspect : South-west
Microrelief :
Parent Material Solum : Origin single, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Nelspruit Suite

Soil form and family Mispah myhill
Surface rockiness : 2-10% exposed surface
Surface stoniness : 2-10% exposed surface, round & flat, gravel
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Treeveld, sparse
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Weak physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Dry state; horizon undisturbed; dry colour: brown to dark brown 10YR4/3; texture: coarse sandy loam; common fine faint reddish brown geogenic mottles; structure: apedal massive; consistence: slightly hard; common fine normal pores; few clay cutans; few angular gravel 2-6mm; water absorption: 2 second(s); common roots; abrupt wavy transition.	Orthic
R	250 - 500+		Hard rock

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15028
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 59' 25.5" / 31° 46' 37.9"
Land Type No :
Climate Zone :
Altitude : 222 m
Terrain Unit: Footslope
Slope: 2 %
Slope Shape : Straight
Aspect : South
Microrelief :
Parent Material Solum : Origin binary suspected, solid rock, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Basic intrusion (dolerite) into Nelspruit Suite

Soil form and family Swartland breipaal
Surface rockiness :
Surface stoniness :
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Shrubveld, sparse
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Moderate physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Moist state; horizon undisturbed; moist colour: very dark greyish brown 10YR3/2; texture: medium sandy loam; common fine faint black and brown unknown mottles; structure: weak medium subangular blocky; consistence: firm; common fine normal pores; non-hardened free lime, slight effervescence; common clay cutans; very few mixed-shape gravel 2-6mm; water absorption: 4 second(s); many roots; clear smooth transition.	Orthic
B1	250 - 700	Moist state; horizon undisturbed; moist colour: very dark grey 10YR3/1; texture: medium sandy clay loam; common fine distinct black and brown unknown mottles; common fine distinct grey lime mottles; structure: moderate medium subangular blocky; consistence: very firm; few fine normal pores, fine cracks; non-hardened free lime, moderate effervescence; common clay cutans; very few mixed-shape gravel 2-6mm; very few fine <2-6mm lime concretions; water absorption: 5 second(s); few roots; clear wavy transition.	Pedocutanic
C	700 - 900+		Saprolite

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15029
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 59' 17.2" / 31° 46' 31.9"
Land Type No :
Climate Zone :
Altitude : 240 m
Terrain Unit: Upper Midslope
Slope: 2 %
Slope Shape : Convex
Aspect : South-west
Microrelief :
Parent Material Solum : Origin single, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Nelspruit Suite

Soil form and family Glenrosa tsende
Surface rockiness : <2% exposed surface
Surface stoniness : 2-10% exposed surface, round & flat, gravel
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Shrubveld, open
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Weak physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 400	Dry state; horizon undisturbed; dry colour: brown to dark brown 7.5YR4/4; texture: coarse sandy loam; few medium faint many coloured geogenic mottles; structure: apedal single grain; consistence: slightly hard; common fine normal pores; few clay cutans; few mixed-shape gravel 2-6mm; water absorption: 2 second(s); common roots; clear wavy transition.	Orthic
C	400 - 500+	horizon undisturbed.	Lithocutanic

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SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15030
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 59' 3.8" / 31° 46' 38.8"
Land Type No :
Climate Zone :
Altitude : 237 m
Terrain Unit: Upper Midslope
Slope: 2 %
Slope Shape : Straight
Aspect : North-east
Microrelief :
Parent Material Solum : Origin binary suspected, solid rock, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Basic intrusions (dolerite) into Nelspruit Suite

Soil form and family Cartref egolomi
Surface rockiness :
Surface stoniness : 2-10% exposed surface, round & flat, gravel
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Treeveld, open
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Weak physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 300	Dry state; horizon undisturbed; dry colour: dark greyish brown 10YR4/2; texture: loamy coarse sand; structure: apedal single grain; consistence: soft; common fine normal pores; very few mixed-shape gravel 2-6mm; water absorption: 1 second(s); common roots; gradual smooth transition.	Orthic
E	300 - 600	Dry state; horizon undisturbed; dry colour: light brownish grey 10YR6/2; moist colour: brown 10YR5/3; texture: loamy coarse sand; few medium distinct grey unknown mottles; structure: apedal single grain; consistence: soft; common fine normal pores; few mixed-shape gravel 2-6mm; water absorption: 1 second(s); many roots; abrupt wavy transition.	E-horizon
B1	600 - 900+		Lithocutanic

ARC • LNR

SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15031
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 58' 51.4" / 31° 46' 41.6"
Land Type No :
Climate Zone :
Altitude : 250 m
Terrain Unit: Crest
Slope: 1 %
Slope Shape : Convex
Aspect : South
Microrelief :
Parent Material Solum : Origin single, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Nelspruit Suite

Soil form and family Clovelly setlagole
Surface rockiness :
Surface stoniness : 2-10% exposed surface, round & flat, coarse gravel
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Treeveld, sparse
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Weak physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 250	Dry state; horizon undisturbed; dry colour: brown to dark brown 7.5YR4/2; texture: coarse sandy loam; few fine faint brown unknown mottles; structure: apedal single grain; consistence: soft; few fine pores; few clay cutans; very few mixed-shape gravel 2-6mm; water absorption: 2 second(s); common roots; clear smooth transition.	Orthic
B1	250 - 550	Dry state; horizon undisturbed; dry colour: strong brown 7.5YR4/6; texture: loamy coarse sand; few fine faint brown unknown mottles; structure: apedal single grain; consistence: soft; few fine pores; few clay cutans; very few mixed-shape gravel 2-6mm; water absorption: 2 second(s); few roots; abrupt wavy transition.	Yellow-brown apedal
R	550 - 750+		Hard rock

ARC • LNR

SOIL PROFILE DESCRIPTION

NATIONAL SOIL PROFILE NO : 15032
Map/photo : 2431DD Tshokwana
Latitude + Longitude: 24° 58' 38.6" / 31° 46' 21.5"
Land Type No :
Climate Zone :
Altitude : 226 m
Terrain Unit: Lower Midslope
Slope: 3 %
Slope Shape : Straight
Aspect : West
Microrelief :
Parent Material Solum : Origin single, solid rock
Underlying Material : Gneiss
Geological Group / Formation : Nelspruit Suite

Soil form and family Mispah myhill
Surface rockiness :
Surface stoniness : 10-25% exposed surface, angular, coarse gravel
Occurence of flooding :
Wind erosion :
Water Erosion :
Vegetation / Land use : Treeveld, open
Water table : None
Described by : D.G. Paterson
Date Described : 9/2003
Weathering of underlying material: Weak physical, weak chemical
Alteration of underlying material : Normal weathering

Horizon	Depth (mm)	Description	Diagnostic horizon
A1	0 - 200	Dry state; horizon undisturbed; dry colour: brown to dark brown 7.5YR4/4; texture: coarse sandy loam; few fine faint brown unknown mottles; structure: apedal massive; consistence: slightly hard; few fine normal pores; few clay cutans; few angular gravel 2-6mm; water absorption: 2 second(s); common roots; abrupt wavy transition.	Orthic
R	200 - 500+		Hard rock