

**EFFECTS OF CATTLE BROWSING ON *TERMINALIA SERICEA*-DOMINATED
WOODLANDS IN A SEMI-ARID REGION OF THE KALAHARI, NAMIBIA**

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at the University of Stellenbosch.



Promoter; Prof. David Ward

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

20 June 2006

ABSTRACT

Livestock farming affect plant growth and soil condition around artificial water points in arid and semi-arid environments. This study investigated the following, in the northern Kalahari, Namibia: 1) the impact of livestock on soil condition, vegetation structure and composition with reference to artificial water points; 2) cattle browsing preference on pre-rain flush during the hot-dry season; 3) the independent and interactive effects of plant damage, soil nutrients and moisture content on tolerance and resistance traits of *Terminalia sericea*. Condensed tannin was used as a measure of resistance trait, while growth parameters were used to measure tolerance of (herbivore) damage. This experiment was carried out in small camps in the field where plant damage and soil nutrients were controlled, and (4) under nursery conditions where in addition to plant damage and soil nutrients, soil moisture was also controlled. The nursery experiment was carried out on 19 month-old seedlings of *Terminalia sericea*; and 5) the perception and knowledge of local pastoralists on vegetation change and utilization of woody plants was assessed. The key results of the study are summarised in the sections below:

Impacts of livestock around artificial water points in the northern Kalahari

Livestock activities near artificial water points had significant impacts on vegetation and soils. Fewer, but tall trees with broader canopy areas grew near the water points. Herbaceous abundance increased with proximity to the water points, but species diversity of both herbaceous and woody plants was 55 and 29 % respectively of the diversity measured from 600 – 4000 m from the water points. Soil organic carbon and nitrogen content was generally higher at 10 – 20 cm depth near the water points than at lower depths, while soil moisture changed little across the soil profile and farther away from water points. Available phosphorus in the 10 – 20 cm soil layer was significantly higher at 200 m from water points than at any other depth and distance from water points. This may have resulted from livestock dung deposition. Long-term observations by pastoralists revealed that the density of woody vegetation

and composition of plant community have changed substantially all over the rangelands since the commencement of sedentary settlements around the artificial permanent water points some 32 to 51 years ago.

Cattle diet selection during the hot-dry season

Cattle consumed more browse than grass during the hot-dry season because of low grass availability during that period. This confirmed pastoralists' impressions that cattle browse more than they graze during the hot-dry season in the northern Kalahari. Cattle fed on a variety of browse during the hot-dry season, but three species, *Bauhinia petersiana*, *Philenoptera nelsii* and *Terminalia sericea*, accounted for three-quarters of dry matter intake. Browse quality and availability influence the consumption pattern of herbivores. In this regard, cattle avoided *Ochna pulchra*, which had consistently high levels of fibre and condensed tannins, while they browsed heavily on the preferred *P. nelsii*, which contained low concentrations of fibre and condensed tannins, but a high crude protein content. We found that diet selection was best explained by a multiple linear regression model ($Forage\ ratio = 0.522 + 1.55 \times CP - 1.6 \times P - 0.60 \times ADL$; $R^2 = 0.9385$, $P = 0.0019$).

Plant resource-partitioning between resistance and tolerance traits along a resource availability gradient

The field and the controlled (seedling) experiments both supported the Resource Availability Hypothesis. Fertilizer addition increased the tolerance traits of seedlings, i.e. leaf area, leaf dry mass, height, number of branches, number of branches:height ratio and above:below ground biomass ratio. Seedlings in the nutrient-poor environments and under limited soil-moisture had 22.5% and 21.7% higher condensed tannin concentrations than those seedlings grown in nutrient-rich environments and under high soil-moisture. The strategy of plants in the low resource environments to deter rather than to tolerate herbivores was not supported by this study because tolerance and resistance traits occurred concurrently, and with no indication of trade-offs between investments into resistance traits (e.g. tannin

synthesis) and tolerance traits (e.g. leaf area and plant height). Furthermore, the high constitutive defence levels in low resource environments appeared to result from constrained plant growth rather than as a response to herbivory. Leaf production was resource-dependent. *Terminalia sericea* produced more leaves per cluster under nutrient-poor soils than under fertilizer-enriched soils. Heavy browsing and complete defoliation reduced cluster size, but improved soil nutrient status negated the negative effects of complete defoliation and high browsing pressure on cluster size.

Compensatory responses of resistance and tolerance traits to (herbivore) damage

The effects of fertilizer and defoliation on condensed tannin were complex and dependent on the temporal scale. Foliar damage under natural soil conditions promoted overcompensation of resistance and tolerance traits, while fertilizer addition reduced condensed tannin concentrations. However, the interaction effect of foliar damage and fertilizer treatments promoted full compensation. The results suggested that compensatory responses of tolerance and resistance traits upon damage result from the high accumulation of photosynthetic products in excess of constrained growth requirement under low resource conditions. In this study, a 31.3 % lower above:below-ground biomass ratio was found in seedlings grown on the low-resource environment than in the high-resource environment. Thus, compensatory ability of *T. sericea* reflected the degree to which growth in the low resource environments was constrained and, subsequently, the amount of photosynthetic products allocated to storage and secondary metabolites. Furthermore, the compensatory ability of *T. sericea* revealed the adaptability of the plant to environmental stress in its struggle to maintain fitness.

Responses of resistance and tolerance traits over time

There was no evidence for increased condensed tannin (resistance trait) as a result of cattle herbivory early in the growing season across a soil nutrient gradient. However, the concentration of condensed tannins increased as the seasons progressed from early hot-dry season (October) to mid hot-wet season (February). In contrast, repeated early-season manual defoliation induced condensed tannin by 89.9% in

nutrient-poor environments. Resource allocation to phytochemical substances and (perhaps) the ability of *T. sericea* to restore its internal resource balance over the growing season, was influenced by the interactive effects of soil fertility and (the degree of) plant damage. The compensatory ability of *T. sericea* may have ensured that the negative effects of early-season damage did not endure for the entire growing season.

Pastoralists of the Otjinene constituency

Historically, the OvaHerero kept cattle for consumptive uses, religious rituals and as a symbol of one's status in society. In this study, the respondents clearly raised cattle primarily for consumption of milk and milk by-products (93 % of respondents) and equally so to generate cash income (82 % of respondents). The high offtake of male weaners (calves) and young adults in particular was an indication that the pastoralists have commercialized their production system. An estimated annual cattle offtake of about 15.3 – 16.5 % in the study area was above the national offtake (12.6 %) for all herds in 2004. The second priority for raising cattle was to retain a cultural identity (35 % of respondents), achieve a good social standing by possessing a sizeable number of cattle (33 % of respondents) and to ensure that the younger generation continue with pastoralism (31 % of respondents). Goats and sheep were primarily used for meat consumption (77 % and 69 % of respondents, respectively).

The current state of vegetation change in the northern Kalahari had beneficial outcomes for the livelihoods of pastoralists, because encroaching woody vegetation presented opportunities for browse consumption, firewood and timber for construction of houses and livestock pens. Pastoralists regarded *T. sericea*, *P. nelsii* and *Combretum collinum* as the key browse species during the hot-dry season. The pastoralists' knowledge of cattle browse consumption compared well with the actual browse consumption based on observations of foraging cows ($r = 0.70$, $P < 0.05$). Integration of indigenous and scientific knowledge, methods of natural resource inventurisation, evaluation of land use impacts and

management practices in pastoral systems may not only enhance local-level (community-based) adaptive range resource management, but will also enrich ecological research outputs.

Keywords; bush encroachment, soil hydrochemistry, diet selection, plant defences, traditional ecological knowledge, Kalahari

SAMEVATTING

Diere boerdery in die noordelike Kalahari het invloed op plantegroei en grond toestand, veral rondom water-boorgate wat gesink is vir water voorsiening aan mense en diere. Die volgende was ondersoek: 1) die effek van beweiding op grond minerale, plantegroei, bosverdigging en plant verskeidenheid (spesies) met afstand vanaf die water punte; 2) beweiding van bome gedurende die droë seisoen wanneer blaar-wisselende bome hul blare hergroeï het. Koeie was agtervolg in die veld om hul beweïdings patroon te ondersoek; 3) die onafhanklike en interaktiewe effek van beweïdingskade en grond vrugbaarheid op plantegroei (in terme van die verdraagbaarheid van beweïdingskade) en weerstand van *Terminalia sericea* teen beweïding. Weerstand teen beweïding was in terme van tannin gemeet. Vir hierdie eksperiment was klein kampe in die veld opgerig en gekontroleer vir die getal beeste en grond bemisting; 4) die effek van die hoeveelheid water, grond vrugbaarheid, beweïdingskade en hul interaksies op die groei, verdraagbaarheid van skade, en weerstand van *T. sericea* teen beweïding. Hierdie eksperiment was in 'n kwekery uitgevoer op 19 maande-oud saailinge; en 5) die persepsie en ervaring van plaaslike boere ten opsigte van die invloed van diere boerdery op plantegroei, en die benuttigingswaarde van bome en bosse vir diere asook mense. Die studie bring navore die volgende resultate: 1) die effek van diere boerdery op grond minerale en plantegroei was beperk tot 200 m en 600 m vanaf die water punte onderskeidelik. Plant spesies was verminderd onder die invloed van intensiewe diere aktiviteite naby die water punte. 'n Paar kruie soos *Sida cordifolia* het hierdie area domineer; 2) Beeste het meeste van die tyd (71%) aan bome en bosse gewei gedurende die droë seisoen. *Terminalia sericea*, *Bauhinia petersiana* en *Philenoptera nelsii* het 74.5 % van die total inname van bome en bosse uitgemaak. *Philenoptera nelsii* was die mees verkiesde plant; 3) Beweïdingskade en grond vrugbaarheid het groot invloed op *T. sericea* se groei, verdraagbaarheid van skade en weerstand teen beweïding gehad. *Terminalia sericea* het baie gegroeï wanneer die grond se vrugbaarheid was verhoog. Hoë beweïding het groei punte verkort, aantal blare en blaargrote verminder. In hierdie verband het hoë grond vrugbaarheid die effek van beweïding geneutraliseer. Weerstand teen beweïding was hoog onder lae grond vrugbaarheid, maar was verminderd as grond vrugbaarheid verhoog was.

Grond armoede het *Terminalia sericea* instand gehou om beweiding te verdra en ook meer tannin te produseer na beweiding. Daar was groot ooreenkoms tussen die eksperimente in die natuurlike veld en in die kwekery. 4) Die plaaslike boere besit goeie kennis van die verandering in hul omgewing. Hulle beskou die huidige situasie van bosverdigging as voordelig vir hul bestaan, omdat dit voeding aan hul diere verskaaf; vuurhoud vir kook en verhitting, asook material vir die bou van krale en huise. Dus, restoureer werk op oorbebosde weivelde moet inagneem die bydrae van bome en bosse tot die welvaart van plaaslike boere en die voeding van diere. Beweiding van bome en bosse kan tot voordeel wees vir diere as grond vrugbaarheid behou of verbeter word, omdat bome en bosse dan lae weerstand teen beweiding bied. Verder moet ervaring en kennis van die plaaslike ekologie inageneem word vir die daarstelling van volhoubare boerdery praktyke.

Sleutelwoorde; bosverdigging, grond minerale, diët voorkeer, plant verdediging, tradisionele ekologiese kennis, Kalahari

DEDICATION

To my spouse Ngurimuje and the children: Ndjoura, Mekukuje and Vandipara
for gifts of love, support and understanding.

“TJI TJIHA JANDA TJIHUNA, NU PUPENOMBANGO PENONDJIRA”.

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CHAPTER 1

BACKGROUND TO THE STUDY

1.1 INTRODUCTION

This dissertation is a study about the nature of the effects of grazing and browsing on community structure and composition of *Terminalia sericea* woodlands in the Otjinene Constituency of the Omaheke Region, a part of the northern Kalahari (Fig. 1.1). It utilizes the piosphere approach to investigate livestock impact along grazing and browsing intensity gradients around artificial water points in a semi-arid environment. A critical element of studying piospheres is to minimize habitat heterogeneity around the water points; otherwise the assumption that livestock impact is radial from water points would not be met. Concerted effort was made to ensure that this condition was met for the selected sites. Secondly, the study investigated the contribution of woody species to the diet of cattle during the hot-dry season when grass biomass is overgrazed. Thirdly, the effects of plant damage on regrowth and condensed tannin (a chemical defence trait) of one of the most abundant woody browse species, *T. sericea*, was investigated under varying soil nutrients and moisture conditions. Woody plants are usually heavily defended against herbivore attack particularly under poor soil nutrient and moisture conditions (Osier and Lindroth 2001; Kouki and Manetas 2002) Finally, an attempt was made to determine and match findings of vegetation change and browse consumption with managers' (pastoralists') perceptions of landscape change and the value of browse to cattle. The value of range resources to the pastoralists' daily livelihood needs was also assessed. The pastoralists studied were OvaHerero, who are predominantly cattle herders, like the Maasai of East Africa. This introductory chapter briefly reviews the pertinent literature and sets the scene for the research rationale, thereafter presents the general objectives and the outline of the dissertation.



Figure 1.1. Otjinene constituency in the Omaheke region of eastern Namibia, indicating the Otjinene settlement, the four study sites and numerous artificial water points scattered in the constituency. The constituency falls within the northern Kalahari vegetation type.

1.2 THE PROBLEM

Arid and semi-arid environments are characterized by scarce resources, which vary widely in space and time (Vetter 2003). Historically, transhumance between ephemeral and perennial range resources has allowed exploitation of seasonal resources over a large space and as a result minimized the degradation of resources in one locality (Ellis and Swift 1988). The provision of permanent water sources for human and livestock production in arid and semi-arid environments has resulted in sedentary livestock production, and with increasing human populations, this has led to the proliferation of permanent settlements around artificial water points (Vetter 2003). Livestock activities around water points improves soil nutrients through dung and urine deposition, but may impact negatively on soils and vegetation (Tolsma et al. 1987; Strohbach 1992) as manifested by loss of biodiversity, declining ratio of perennial/annual grass species increase of bush density and soil erosion (Coppock 1993; Moleele 1998). There is contradicting evidence about the extent of livestock impacts around artificial water points in the Kalahari. A number of studies have documented that changes resulting from livestock production are only confined to the area near the water points, usually within 200 m from the water points (Tolsma et al. 1987; Thrash 1998; Makhabu et al. 2002). These empirical studies depicted a state of vegetation as it appeared at the time of investigation, without a long-term overview of changes that might have occurred since the establishment of settlements. Another view, based on simulation models, argues that changes brought by livestock activities over the years of range utilization extend far into their home ranges. Cattle in the northern Kalahari can easily graze beyond 7 000 m from water points (personal observations), but must return to water points every other day to drink. The absence of long-term data limits the validation of these contradictory results. However, the use of long-term observations by local pastoralists may provide insights into the dynamics of vegetation change since the beginning of the settlements.

The change in vegetation composition and density has implications for herbivores in terms of the available and accessible of forage resources. Vegetation change in the form of bush encroachment diminishes grass production, and hence its availability to grazing livestock (DeKlerk 2004). In Namibia bush encroachment has reduced the carrying capacity of rangelands for beef production, with a concomitant loss in income of more than N\$ 700 million per annum (Quan et al. 1994). Mechanical and chemical treatment of encroaching species is being applied in Namibia to reverse the situation (De Klerk 2004). In doing this, there is a need for selective debushing because some species provide fodder for livestock. In the current study, cattle are said to depend on browse during the hot-dry season when grass biomass is overgrazed. The absence of knowledge about key browse species may lead to debushing of such species which may increase livestock vulnerability to droughts in continually overgrazed communal areas.

The consumption of browse species may be constrained by physical and chemical anti-herbivory traits (Watson and Owen-Smith 2000; Shipley and Yanish 2001). Physical traits such as high fibre content may reduce digestibility of dietary items (Woodward and Coppock 1995; Shipley and Yanish 2001), while chemical traits such as condensed tannins binds with protein in the rumen and precipitate the proteins (Kaitho et al. 1998; Aerts et al. 1999). Browse often contains sufficient tannin to reduce protein digestibility upto 50% (Beck and Reed 2001). High levels of condensed tannin decrease the acceptability and nutritional value of browse (Aerts et al. 1999; Shipley and Yanish 2001). Mosaic patches of natural vegetation differing in quality, accessibility and acceptability to foraging herbivores, necessitates that herbivore excercises selective browsing. Selective browsing allows for maximization of energy intake (Owen-Smith 1994; Illius et al. 1999).

The quality of browse also depends on the plant's phenophase, the frequency of herbivory and the resources available to the plant. Deciduous trees in southern African savannas may become more palatable during pre-rain flush than later in the growing season (Owen-Smith 1994; Augustine and

McNaughton 1998). Herbivores may therefore shift their diet and spend more time foraging on the new leaves to maximize energy intake (Owen-Smith 1994). Frequent and heavy plant damage may lead to elevated nutrient content of browsed plants (Du Toit et al. 1990; Ward and Young 2002), while in some instances browsing may increase plant defenses (Strauss and Agrawal 1999). Soil moisture and nutrients affect the allocation of photosynthates to anti-herbivory traits and plant growth (Kouki and Manetas 2002). In the poor resource conditions plants invest more in anti-herbivory traits presumably to deter herbivores (Coley et al. 1985; Gebauer et al. 1998; Osier and Lindroth 2001), while in high resource environments plants allocate greater part of photosynthates to growth and regrowth (Hochwender et al. 2000). Thus plants may tolerate herbivore damage in high resource environments by growing at a faster rate (Milewski et al. 1991). The northern Kalahari is resource poor in terms of soil nutrients and moisture content, thus woody plants would be expected to be more defended against herbivore attack.

Living in arid and semi-arid environments requires that pastoralists adapt to the variability and unpredictability of rainfall and drought events (see review by Vetter 2003). Thus they need to exploit resources maximally when such resources are available, and diversify uses such as for livestock production, construction of houses and livestock pens, cooking and heating, medicinal use, and for religious uses. In turn livestock are also kept for a variety of uses: viz milk and meat consumption, sales for cash income, a symbol of social status and for religious rituals (Pool 1991). Balancing between these uses may be complex particularly when some uses are not necessarily compatible. Hence, a combination of uses may provide insights to understand the perceptions of pastoralists as may be influenced by the trade-offs associated with the various uses.

There is a need to quantify the effects of grazing and browsing activities on the soil and vegetation around artificial water points in the northern Kalahari to facilitate better planning of water-point distribution and livestock densities. The response of woody plants to herbivore damage, in terms of

regrowth capacities and production of secondary compounds, needs investigation to determine the impact it has on diet selection. Managing the diversity and proliferation of woody plants on rangelands requires knowledge about the utility of woody species to humans and their livestock. The integration of local knowledge and science-based ecological knowledge has advantages for improved local-level adaptive resource management.

1.3 RESEARCH OBJECTIVES

The general research objectives are to:

1. Investigate soil and vegetation changes with reference to distance from artificial permanent water points in the *Terminalia sericea* open woodland of the Omaheke region in the northern Kalahari desert;
2. Determine the contribution of woody plants (particularly *Terminalia sericea*) to cattle diet during the hot-dry season (September to November) in a semi-arid region of the northern Kalahari desert;
3. Investigate the defensive strategies of one of the most browsed woody plant, *Terminalia sericea*, to herbivore damage under field and controlled conditions; and
4. Quantify pastoralists' knowledge and perceptions regarding vegetation change, cattle browse utilization, livestock production and pastoral use of range resources in *Terminalia*-dominated woodland.

1.4 OUTLINE OF DISSERTATION

The specific hypotheses of the study relating to the general objectives above are presented in each chapter following a succinct literature review. Thus, each chapter is a stand-alone manuscript testing a set of specific hypotheses. Hence, Chapter 2 tests hypotheses relating to the extent of soil and vegetation change with distance from water points; Chapter 3 deals with cattle diet selection during the hot-dry season; Chapter 4 investigates the defensive strategies of *Terminalia sericea* bushes grown naturally under field conditions, but additionally exposed to either simulated or actual cattle herbivory in combination with graded soil nutrient conditions; similarly, Chapter 5 investigates the defensive strategies of *T. sericea* seedlings to simulated herbivore damage under controlled soil nutrient and moisture conditions; Chapter 6 quantifies pastoral knowledge and perceptions of vegetation change, livestock production and range resource utilization; and Chapter 7 presents a synopsis of the main findings and the implications for management.

Chapters 2 to 6 are all written for publication in appropriate journals. Consequently, they differ considerably in style and format as appropriate for those journals. A further consequence of writing the chapters for publication in journals is that there is considerable repetition of the *Material and Methods* sections. For this, I apologize to the reader.

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CHAPTER 2

SOIL AND VEGETATION CHANGES UNDER LIVESTOCK PRODUCTION IN THE NORTHERN KALAHARI, NAMIBIA

ABSTRACT

The spatial scale and intensity of rangeland degradation around water points in arid and semi-arid environments depend on the population density of livestock, the duration of water point use and the distance livestock travel from water points. We visually established a broadscale pattern of vegetation zonation along a grazing gradient on 28 settlements in the Kalahari to place five sampling points from artificial water points. We selected four settlements for a more intense study of vegetation and soil changes under livestock production. We tested the effect of livestock on species diversity of herbaceous and woody plants, structural parameters of woody plants, and soil moisture and nutrient contents. We found that the effect of livestock on vegetation was confined to the area within 200 m from the artificial water points. The diversity of herbaceous and woody species decreased under high livestock pressure, but the abundance of herbaceous species increased significantly at 200 m from the water points. The woody *Acacia hebeclada*, *A. erioloba* and *Kleinia longiflora*, and herbaceous species such as *Dactyloctenium aegyptium*, *Tribulus terrestris*, *Sida cordifolia*, *Tragus berteronianus* and *Amaranthus thunbergii* were most abundant at 200 m from the water points. Soil parameters were not influenced significantly by livestock activities along the grazing gradient at comparable soil depth; however the upper soil layer had generally higher organic carbon, available phosphorus and total nitrogen near the water points than at lower depths away from water points. It appeared that livestock impact around artificial water points in the northern Kalahari was generally confined to the distance within 200 m from the water points. In contrast, livestock impact may also have resulted in a relatively uniform vegetation and soil changes beyond the 200 m distance from the water points.

Key Words: arid environments, bush encroachment, dryland pastoralism, land degradation, soil hydrochemistry, range management, Africa.

INTRODUCTION

Arid and semi-arid environments are inherently variable, and largely driven by rainfall events (Ellis and Swift 1988, Ward et al. 1998, Illius and O'Connor 1999). To cope with this natural variability, pastoralists have been able to: 1) migrate to ephemeral water sources where forage could be utilised during the wet seasons, while resting forage resources in areas with perennial water sources; 2) keep a variety of livestock to utilise both browse and grazing resources; and 3) utilise a wide land area to minimise localised negative impacts on resources (Ellis and Swift 1988). Much of Namibia (in southwestern Africa) is semi-arid to extremely arid (Van der Merwe 1983, Aharoni & Ward 1997), thus pastoralists have traditionally used the abovementioned flexible grazing system described by Ellis and Swift (1988) for the arid Turkana region of Kenya. However, this system of range and livestock management has changed in Namibia because current land tenure systems have confined pastoralists to specified land areas, and the provision of artificial permanent water sources has created permanent settlements. Elsewhere in arid and semi-arid Sub-Saharan Africa, the creation of permanent pastoral settlements, the high proportion of domestic grazers (cattle) to browsers (goats) and the decline of wild ungulate browsers in agricultural lands have tilted the balance between woody species and grasses into woody plant-dominated rangelands (Coppock 1993, Moleele 1998). In addition, livestock pressure in the vicinity of water points reduces species diversity, increases the prevalence of invasive herbaceous species, reduces the abundance of palatable grass species, but favours unpalatable species (Tolsma et al. 1987, Strohbach 1992). The impacts on soils are multiple, but depend mainly on the soil type and the topography of the affected landscape (Behnke and Scoones 1993, Stafford-Smith and Pickup 1993). Trampling and overgrazing can lead to soil erosion, compaction and reduced moisture infiltration on slopes (De Klerk 2004). However, sandy Kalahari soils are less affected by these factors (Dougill et al. 1999). Nonetheless, irrespective of soil type, the concentration of livestock around water points leads to increased nutrient accumulation in the soil as a result of urine and dung deposition (Tolsma et al. 1987).

A distinctive pattern of vegetation and soil changes develops around artificial water points (Lange 1969,

Jeltsch et al. 1997), of which the extent is determined by the age of the water point, livestock densities and the capacity of animals to forage away from the water points (Andrew 1988). Lange (1969) termed this unique ecological system centred around artificial permanent water points, 'piosphere' (derived from a Greek word: '*pios*', meaning 'to drink'). The area closest to the water points experiences severe pressures such that only few herbaceous plants can survive. This area is referred as the "sacrifice" zone (Graetz and Ludwig 1978). The sacrifice zone is characterised by extensive bare ground, particularly during the dry season, and is dominated by annual invasive herbs (Thrash 1998, Brits et al. 2002) that are mostly unpalatable to livestock (James et al. 1999, Ward 2004). Beyond the sacrifice area, is the second zone where the impact of large herbivores tapers off, until an upper asymptote of basal cover is reached (Thrash et al. 1993). The second zone is characterised by a rapidly-increasing standing crop, while the third has a relatively constant standing crop (Thrash 1998). Thus, the impact of large herbivores on vegetation and soils parameters forms a sigmoid relationship with distance from water points (Thrash 1998, Britz et al. 2000). Thrash (1998) used a 2000 m transect to arrive at this sigmoid curve. Tolsma et al. (1987) reported thickets of *Acacia* spp. and *Dichrostachys cinerea* from 800-1500 m of water points in a semi-arid district of eastern Botswana, and that these thickets were transitional to a tree savanna at 3000 m from the water points. Cattle in our study area were occasionally observed at about 7000 m from water points (personal observations). Pickup (1994), using a model based on the Australian semi-arid rangelands, demonstrated that the effect of cattle on vegetation might extend beyond 7000 m from water points.

The objective of this study was to investigate the extent of vegetation and soil changes in relatively homogenous flat landscapes of the northern Kalahari communal rangelands dominated by *Terminalia sericea*. We specifically tested the effects of livestock on species diversity, the structural parameters of woody plants, soil moisture and nutrients.

MATERIALS AND METHODS

SITE SELECTION

We drove through 28 pastoral settlements and observed the pattern of vegetation distribution and abundance with increasing distance from artificial water points. We combined our observation with 30-year-old and current aerial photographs (1:60 000) to select four settlements with homogenous landscapes in all directions from the water points. All settlements located on calcrete outcrops and those dominated by *Acacia* species were excluded because of their limited distribution, and unusual vegetation composition to most of the northern Kalahari (Makhabu et al. 2002). All selected settlements had a flat landscape and were situated away from low-lying areas. The selection criteria met the requirement of our assumption that the impact of livestock on vegetation and soil is radial in relation to the locations of artificial water points in homogenous flat landscapes and that the impact is most intense at water points. This assumption is consistent with that adopted in related studies in arid and semi-arid environments (Lange 1969, Thrash 1998, Ward et al. 1998, Makhabu et al. 2002). In this study the distance between the selected or any other neighboring settlements ranged between 8000 and 9000 m. This distance was selected to minimize overlaps in livestock home ranges between the settlements and to allow for a maximum possible distance between settlements such that the full extent of livestock impacts could be determined around the water points. The longest mean \pm SD distance between any two settlements in the study area was 14 ± 11.95 km ($n = 44$), while the shortest mean \pm SD distance was 6.6 ± 4.5 km (Ministry of Agriculture, Water and Forestry, unpublished data). The age of the selected settlements ranged from 32-51 y, and with cattle production as the main form of land use (Table 2.1).

SITE DESCRIPTION

The long-term mean rainfall in the study area ranges from 250-400 mm per annum (Dealie *et al.* 1993). The coefficient of variation of the annual rainfall varies between 30-40% of the long-term mean rainfall (Mendelsohn et al. 2002). The general area consists of a large undulating landscape covered with sand

dunes traversed by low-lying inter-dunal valleys (pl.: *omiramba* in the local Otjiherero language) (Köhler 1959). The sandy soils have low phosphorus and nitrogen contents (Mendelsohn et al. 2002). The study sites were located between the Epukiro Omuramba and Eiseb Omuramba in the Otjinene communal area (S21°E19°). The vegetation of the area is classified as northern Kalahari bush savanna and is characterised by dense stands of edible bush covering the dunes, of which *Croton gratissimus*, *Combretum apiculatum*, *Terminalia sericea* and *Philenoptera nelsii*, and shrubs such as *Bauhinia petersiana* and *Grewia* species are the most common (Rawlinson 1994). In the dune valleys, *Acacia* species such as *A. erioloba*, *A. mellifera* occur together with *Boscia albitrunca* (Rawlinson 1994).

Oukango and Otjirarua were the oldest of the four settlements (Table 2.1). According to Mr. Naftalie Mukungu, one of the first permanent residents of Oukango, the settlement water point was sunk at the end of 1951. The borehole at Otjirarua was drilled in 1960 (Mr. Alfeus Kauta, pers. comm. 2002). The water points at Okatjana and Ombujonjama were both drilled at the end of 1969. Prior to this date, only a few Khoi San families roamed the area (settlement elder, Chief Ben Hembapu, pers. comm. 2002).

Table 2.1 Four study sites showing the dates when boreholes were sunk, and also the type of livestock and their numbers for the year 2002.

Settlement	Geographical coordinates	Borehole drilled (year)	Cattle no. (2002)	Goats no. (2002)	Sheep no. (2002)
Oukango	S21°16.509'; E19°04.904	1950	561	237	73
Otjirarua	S21°12.714'; E19°13.871'	(+-1960)	916	356	135
Okatjana	S21°02.402'; E19°04.958'	1970	480	202	31
Ombujonjama	S21°00.421'; E19°08.987'	1970	734	157	48

DATA COLLECTION

OBSERVATION OF VEGETATION AWAY FROM WATER POINTS

A consistent vegetation zonation away from the artificial water points was observed during field reconnaissance and site selection exercise, across 28 settlements in June of 2001. We subdivided the observed vegetation pattern into five zones, on the basis of the extent of herbaceous invasive plants, clarity of browse line, shrub and bush density, and the proportion of tree and grass abundance (Table 2.2). Plant species distribution and abundance were not evenly distributed across the distances from the water points. Nothing grew within about 30 m radius around the water points. Areas closest to the water points, but beyond 30 m, had the most sparse woody plant cover due to livestock impacts. The dominant tree *Terminalia sericea* rarely occurred in this zone. This zone (Zone I) extended to about 850 m from the water points. It was dominated by *Sida cordifolia* (Malvaceae), a native unpalatable invasive herb, and few scattered tall trees (mainly *Acacia erioloba* and *Combretum collinum* subsp. *gazenze*) with a clear browse line. Homesteads and livestock pens were located in this zone - ranging from 300-600 m from the water points. A disappearing browse line and declining herbaceous-layer, but increasing shrub-layer characterized Zone II. This zone stretched from approximately 850 – 2000 m from the water points. Following Zone II, the woody vegetation became denser and dominated by woody species such as *Terminalia sericea*, *Grewia flava*, *Bauhinia petersiana*, *Acacia fleckii* and *Acacia mellifera*. This we classified as Zone III, which extended approximately 3000 m from the water points. This appeared to be the bush proliferation zone. Zone IV, 3000 – 4000 m was more of a transitional zone showing varying features of Zone III at some sites, and also becoming more of a savanna vegetation type (sparse trees interspersed with herbage) at other sites. Zone V, from 4000 – 5000 m from water points, appeared to be the least bushy.

Table 2.2 Observed vegetation zonation along a livestock pressure gradient. Zone I experienced the greatest pressure at the water point, while Zone V suffered the least pressure on soils and vegetation.

This pattern is based on field observations of 28 settlements in the northern Kalahari.

Zone	I	II	III	IV	V
Distance	30–850 m from water points (WPs).	± 850-2000 m from WPs.	± 2000-3000 m from WPs.	± 3000-4000 m from WPs.	+ 4000-5000 m from WPs
Vegetation	Mainly invasive herbs – i.e. <i>Sida cordifolia</i> and <i>Acanthospermum hispidum</i> ; few big trees: <i>A. erioloba</i> , <i>Combretum collium subsp. gazeze</i> , and shrubby <i>A. hebaclada</i>	Increasing shrub layer; greater tree abundance and lesser invasive herbs compared to Zone I.	Dense woody plants dominated by <i>T. sericea</i> ; <i>A. flecki</i> , <i>A. mellifera</i> , <i>G. flava</i> and <i>Bauhinia petersiana</i> seemed to occur frequently	This seem to be a transitional zone between zone III and V, at some sites it was becoming less dense, while at others it was more of a savanna dominated by <i>T. sericea</i> and tall perennial grass cover.	Woody species interspersed with herbage layer
Other observations	Clear browse line. <i>Combretum collium subsp. gazeze</i> was more abundant than <i>A. erioloba</i> .	Diminishing browse line. <i>Terminalia sericea</i> started to be more abundant in this zone.	Bush proliferation zone.	It is possible that the age of the water points and cattle density may play a defining role in this zone. (older sites = more dense woody plants in this zone, meaning expansion of piosphere on older WPs)	This zone could not clearly be established as only few villages had inter-village distance exceeding 10 km.

QUANTITATIVE ANALYSIS OF VEGETATION AND SOIL PARAMETERS ALONG A GRAZING GRADIENT

We sampled woody vegetation, herbs and soil parameters at 200, 600, 1200, 2500 and 4000 m along two transects in random directions from the artificial water points. These sampling distances were selected as such to match and test the observed vegetation zonation. No sampling was done in the sacrificial zone.

Woody Vegetation Sampling. We recorded woody species richness, basal circumference, height and canopy diameter in the 50 m x 10 m plots. Canopy diameter was measured in two perpendicular directions, that is the longest and the shortest diameters of the canopy. Average canopy diameter was then obtained for each tree measured and then the area of the canopy cover was calculated, assuming a circular spread. Basal area was measured above the buttress swelling, and in the case of multi-stemmed trees, where the stems are separated at the ground level, each was measured separately, but summed to give the total stem basal for the tree. In the majority of cases, plant height was measured directly with a tape, but in a limited number of cases where trees were too high, a clinometer was used to calculate tree height (Brower and Zar 1984). Only one observer was consistently used throughout this exercise. The density of woody species was estimated by the *T*-square method (Greenwood 1996). The *T*-square sampling method is based on the point-to-object and nearest neighbour methods. At each sampling distance, a random point (Y) is selected and the distance (D_1) to the nearest individual species (S_1) is measured (Fig. 2.1); then an imaginary line (dashed) is laid at S_1 perpendicular to the random point (Y) and distance D_2 is measured from S_1 to the nearest neighbour S_2 on the opposite side of the dashed line with reference to Y . Twenty (20) random points (Y_i) at each sampling distance were sampled. These random points were more than the 10 recommended by Greenwood (1996).

Herbaceous-layer Sampling. Herbaceous species were sampled in the 50 m x 10 m plots along six imaginary lines perpendicular to the 50 m tape at 0, 10, 20, 30, 40 and 50 m intervals, and along each of

these lines four random quadrats (1 m²) were placed to sample the herbaceous species. A total of 24 restricted random samples were collected on each plot to record species abundance. Sampling was carried out at the beginning of April 2002 during the growing season when herbaceous species were easily identifiable. Species that could not be identified in the field were identified at the National Botanical Research Institute in Windhoek.

Soil Parameters. The top loose-sandy soil containing litter was removed and samples were taken from three depths: 10-20, 50-60 and 90-100 cm during May 2002. Soil moisture was recorded with a moisture probe (HydroSense, Campbell Scientific Australia) at each depth. A total of 120 samples were collected, air-dried and delivered to the Agricultural Laboratories of the Ministry of Agriculture, Water and Forestry (Government of Namibia) in Windhoek. The samples were further dried at 65°C and passed through 2 mm sieve. Available phosphorus was extracted following the Ohlsen method – measured with a UV/VIS spectrophotometer, organic carbon by the Walkley-Black method (Walkley 1947) and total nitrogen by the Kjeldahl digestion method.

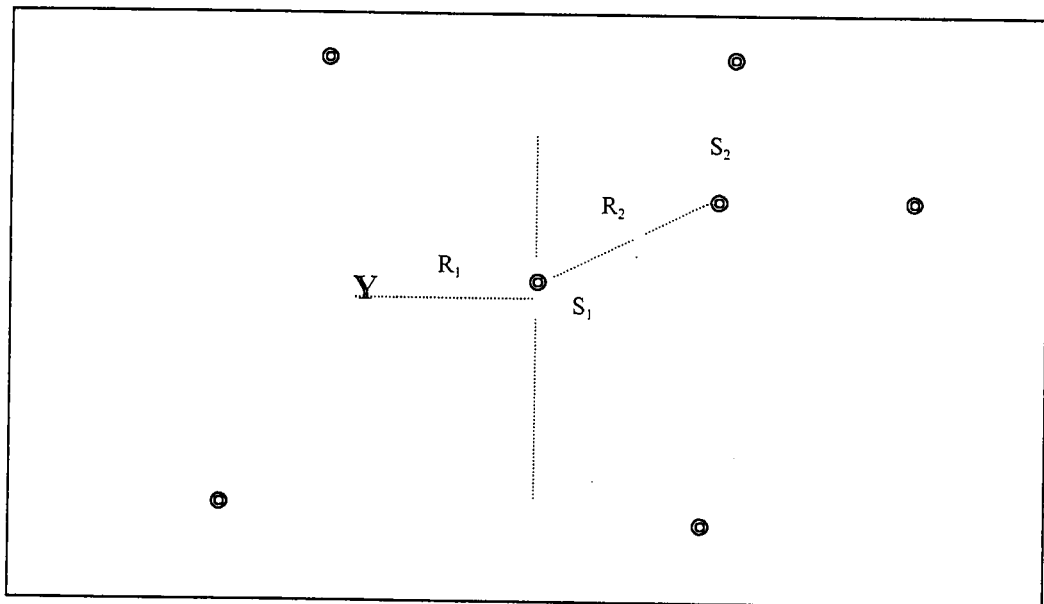


Figure 2.1. The *T*-square method, showing the black dots as the woody plant species, Y : random point; R_1 : the distance to the nearest individual S_j ; S_2 is S_j 's nearest neighbour on opposite the side of the dashed line, which is perpendicular to YS_j .

DATA ANALYSES

VEGETATION COMMUNITY ANALYSES

We used detrended correspondence analysis (DECORANA) for the analysis of differences in woody and herbaceous plant communities, using total counts of each species encountered at the 40 sampling localities along a decreasing livestock pressure gradient from the water points. DECORANA groups vegetation into one or more composite dimensions (axes) on the basis of floristic similarities, that generally correspond to major influencing factors in the environment (Ward and Olsvig-Whittaker 1993). It is an improved multivariate eigenvector technique based on reciprocal averaging (also called 'correspondence analysis') but correcting its main faults (Hill and Gauch 1980). The ordination was performed on the 40 sampling localities and 31 woody or 65 herbaceous species. The data were log transformed and rare species were downweighted using Multi Variate Statistical Package (Kovach Computing Services 2003). Pearson product-moment correlations were used to determine correlations between Shannon-Wiener species diversity index values and eigenvalues of species abundance for axis 1 (DC1) and axis 2 scores (DC2) to determine whether species diversity was in any way correlated with the degradation gradient from the water points.

Furthermore, a two-factorial mixed model ANOVA was performed to compare differences in woody plant species richness and diversity, basal area, density, height and canopy area, using distance from water points as a fixed factor and sites as a random factor. Basal area, canopy area and height data were log-transformed. Species richness was not transformed. A nested ANOVA with distance nested in site and depth nested in distance was used to compare the effects of soil depth and distance from water points on soil parameters (organic carbon, total nitrogen, available phosphorus and soil moisture). Transects from water points were treated as replicates. Organic carbon and total nitrogen data were transformed using the arcsine and square-root transformations respectively to normalize the data. Soil moisture was also arcsine-transformed, while available phosphorous was untransformed. A Scheffe *post*

hoc test ($\alpha = 0.05$) was carried out to determine where significant differences occurred when the treatment effects were significant in ANOVA unless otherwise stated; means were listed with standard errors.

RESULTS

QUANTITATIVE ANALYSIS OF VEGETATION

Species composition. Distance from water points affected woody species richness and diversity significantly ($F = 16.21$, $P < 0.0001$, d.f. = 4, 12; $F = 13.46$, $P < 0.001$, d.f. = 4, 12 respectively). Scheffe *post hoc* test showed that mean woody species richness and diversity were significantly lower at 200 m ($P < 0.05$), compared to further away from the water points (Table 2.3). There were no significant differences among woody species richness and diversity further away from water points ($P > 0.05$). The pattern of herbaceous species richness and diversity resembled that of woody plants ($F = 7.61$, $P < 0.05$, d.f. = 4,12). Mean herbaceous species richness and diversity were significantly lower at 200 m than further away from the water points ($P < 0.05$, Table 2.3). No significant differences existed in herbaceous species richness and diversity at the remaining distance from water points.

Table 2.3 Mean±SE woody and herbaceous species richness and diversity at distances from water points. The Shannon-Wiener index was used to express species diversity. Different letters indicate significant differences in mean values at $P < 0.05$. The H' and DC1 values denote the Shannon-Wiener species diversity index and the first axis in the DECORANA representing the eigenvalues of species abundance.

Distance (m)	Woody species richness	Woody species diversity (H')	Herbaceous species richness	Herbaceous species diversity (H')	Woody plants DC 1 values	Herbaceous plants DC 1 values
200	2.5 ± 0.45 a	0.219 ± 0.0805 a	8.4 ± 0.84 a	0.448 ± 0.4844 a	0.375 ± 0.4678 a	4.079 ± 0.3643 a
600	9.9 ± 1.95 b	0.726 ± 0.1022 b	17.3 ± 1.44 b	0.758 ± 0.0576 b	2.073 ± 0.5723 b	2.678 ± 0.1443 b
1200	13.1 ± 1.19 b	0.813 ± 0.0496 b	20.4 ± 2.63 b	0.858 ± 0.0731 b	2.814 ± 0.2849 bc	0.824 ± 0.5013 c
2500	10.9 ± 0.97 b	0.723 ± 0.0428 b	18.3 ± 1.56 b	0.839 ± 0.0596 b	3.441 ± 0.2722 bc	0.244 ± 0.2624 c
4000	10.9 ± 1.33 b	0.731 ± 0.0426 b	18.3 ± 1.38 b	0.785 ± 0.0346 b	3.644 ± 0.3357 c	0.655 ± 0.1729 c

We used DECORANA to compare woody vegetation parameters sampled at 40 localities with increasing distance from water points. The percentage of variance in woody plant species abundance explained by the first two axes in the DECORANA was low (DC1 = 20.6%, DC2 = 10.5%), but much higher relative to the values of DC3 (5.7%) and DC4 (3.6%). There was a positive significant correlation between DC1 values and woody species diversity along the livestock pressure gradient ($r = 0.42$, $P = 0.0068$, $n = 40$), the correlation between DC2 values and woody species diversity was non-significant ($r = 0.05$, $P = 0.7646$, $n = 40$). The positive significant correlations implied that livestock pressure gradient affected the abundance and diversity of woody plants. We found a highly significant difference in DC1 values between sampling distances from the water points ($F = 17.65$, $P < 0.0001$, d.f. = 4, 12). DC1 values at 200 were significantly lower than at any other distance from the water points, but generally increased with distance from the water points ($P < 0.05$, Table 2.3). There were no significant differences in DC2 values between sampling distances from water points ($F = 0.53$, $P = 0.7160$, d.f. = 4, 12). Livestock pressure gradient affected the distribution of woody plants (Fig. 2.2). *Acacia hebeclada* and *A. erioloba* were most abundant at 200 m from water points. *Kleinia longiflora* also occurred at this distance but in the understory of *A. hebeclada*. No clear separation of species distribution occurred at 600 – 4000 m from the water points. This was demonstrated by the ordination of sampling plots (Fig. 2.3). These results demonstrate that the most important axis in the ordination of woody species was the livestock pressure gradient around the water points.

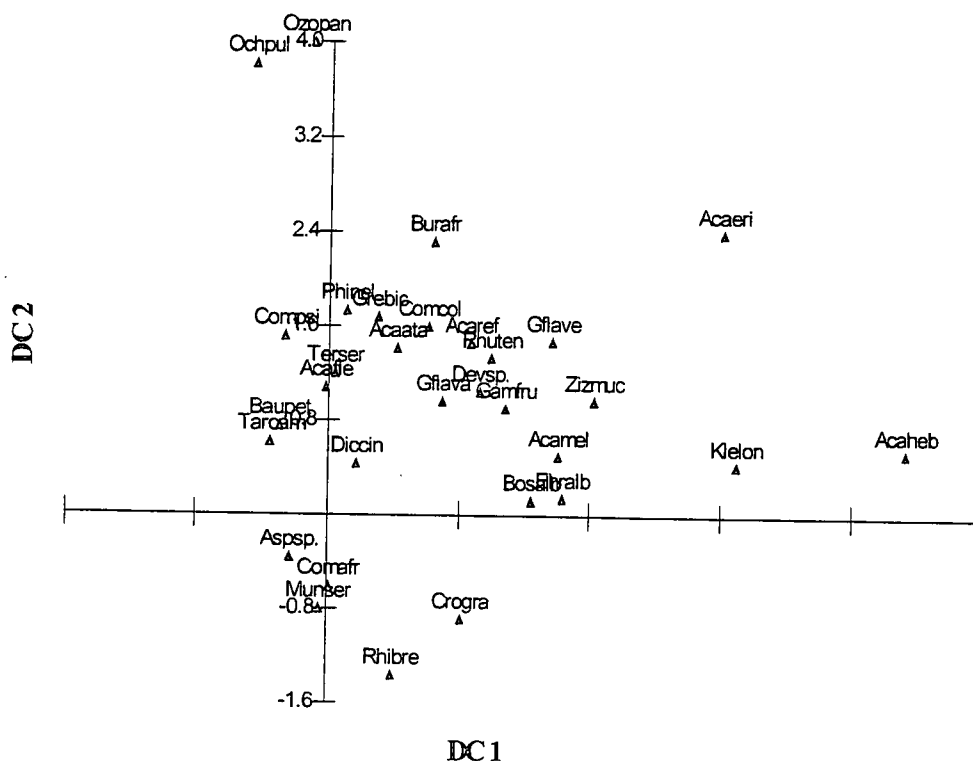


Figure 2.2 Detrended correspondence analysis of woody species sampled at varying distance from water points. DC1 represents the livestock pressure gradient.

(Acaheb = *Acacia hebeclada*; Klelon = *Kleinia longiflora*, Acaeri = *Acacia erioloba*, Acamel = *Acacia mellifera*, Zizmuc = *Ziziphus mucronata*, Gflave = *Grewia flavescens*, Ehralb = *Ehretia cf. alba*, Bosalb = *Boscia albitrunca*, Gamfru = *Gamphocarpus fruticosus*, Devsp = *Deverra sp.*, Rhuten = *Rhus tenuinervis*, Acaref = *Acacia reficiens*, Gflava = *Grewia flava*, Comcol = *Combretum collinum*, Burafr = *Burkea africana*, Acaata = *Acacia ataxacantha*, Crogra = *Croton gratissimus*, Rhibre = *Rhigozum brevispinosum*, Munser = *Mundulea sericea*, Comafri = *Commiphora africana*, Diccin = *Dichrostachys cinerea*, Acafle = *Acacia fleckii*, Terser = *Terminalia sericea*, Grebic = *Grewia bicolor*, Phinel = *Philenoptera nelsii*, Aspsp. = *Asparagus sp.*, Tarcam = *Tarchonanthus camphoratus*, Baupet = *Bauhinia petersiana*, Compsi = *Combretum psiodioides*, Ozopan = *Ozoroa paniculosa*, Ochpul = *Ochna pulchra*).

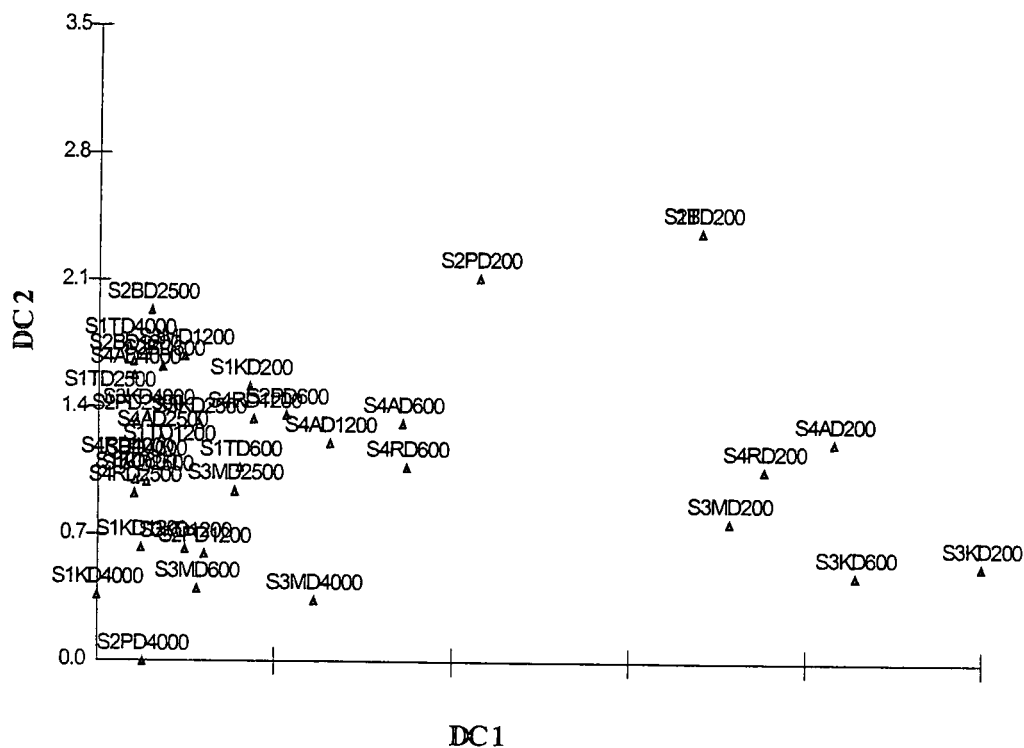


Figure 2.3 Detrended correspondence analysis of sampling plots for woody plants at varying distance from water points. DC1 represents the livestock pressure gradient showing a clear distinction of plots near water plots at the right end along DC1, while plots away from water points are clumped at the left end. Each point indicates a plot (e.g. S3KD200 : S3 = Site 3; K = name of transect; D200 = distance 200 m).

The percentage of variance in herbaceous plant species abundance explained by the first two axes in the DECORANA was low (DC1 = 21.3%, DC2 = 7.5%). However, this was higher than the variance explained by DC3 (5.3%) and DC4 (3.9%). There was a negative significant correlation between DC1 values and herbaceous species diversity along the grazing gradient ($r = -0.66$, $P < 0.0001$, $n = 40$), however, the correlation between DC2 values and herbaceous species diversity was non-significant ($r = 0.002$, $P = 0.9882$, $n = 40$). We found highly significant differences in DC1 values between sampling distances from the water points ($F = 35.06$, $P < 0.0001$, d.f. = 4, 12). DC1 values at 200 and 600 m were significantly higher than those at the remaining distances ($P < 0.05$, Table 2.3), while values at 200 m were significantly higher than at 600 m. There was no significant difference in DC2 values between sampling points from water points ($F = 0.60$, $P = 0.6666$, d.f. = 4, 12). Livestock pressure gradient, represented by DC1, affected the distribution of herbaceous species (Fig. 2.4). *Dactyloctenium aegyptium* and *Tribulus terrestris* occurred mainly within 200 m from the water points, while *Sida cordifolia*, *Tragus berteronianus*, *Amaranthus thunbergii*, *Indigofera spp.*, *Acanthospermum hispidum*, *Chloris virgata* and *Setaria verticillata* mostly occurred around the 600 m distance from the water points. No clear separation of species distribution occurred at 1200 – 4000 m from the water points. This is demonstrated by the ordination of sampling plots (Fig. 2.5). Perennial grass species such as *Eragrostis pallens*, *Melinis repens*, *Aristida meridionalis*, *E. jeffreysii*, *Digitaria seriata*, *D. sanguinalis*, and herb species such as *Chamaecrista biensis*, *Acanthosicyos naudinianus* and *Oxygonum alatum* were more common at 4000 m from the water points. Again, these results show that the most important factor in the ordination of herbaceous species is primarily the grazing pressure gradient (DC1). Herb abundance increased with declining diversity towards the water points.

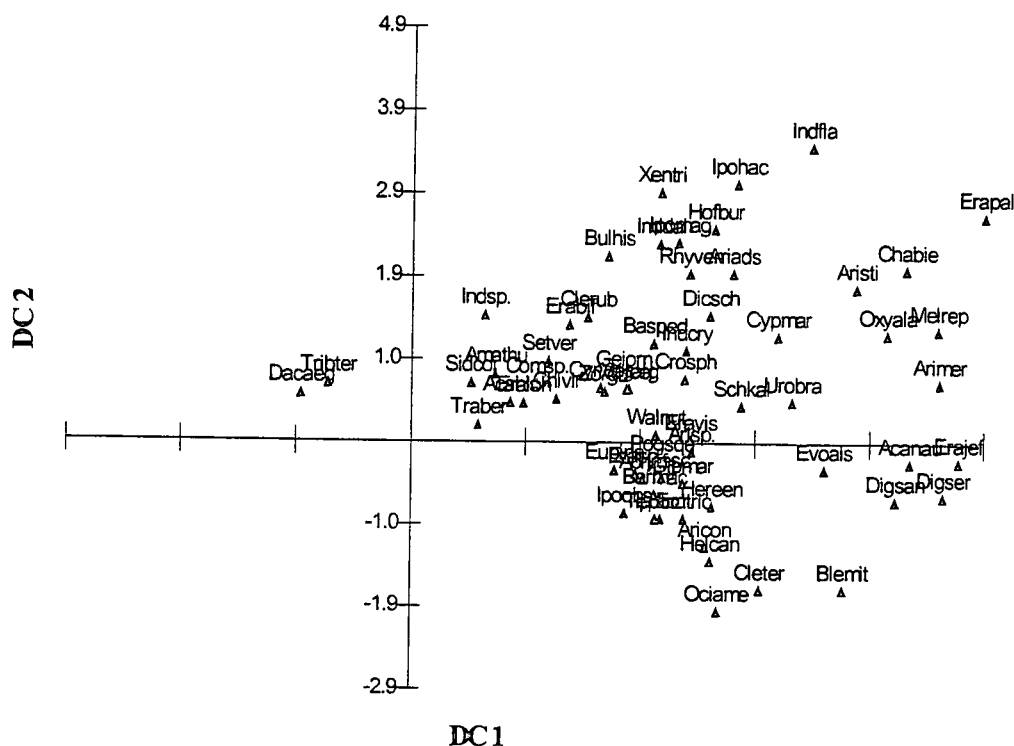


Figure 2.4 Detrended correspondence analysis of herbaceous species sampled at varying distance from water points. DC1 represents the livestock pressure gradient.

(Herbs/forbs: Triter = *Tribulus terrestris*, Sidcor = *Sida cordifolia*, Amathu = *Amaranthus thunbergii*, Indsp. = *Indigofera* spp., Inddal = *Indigofera daleoides*, Indcry = *I. cryptantha*, Acahis = *Acanthospermum hispidium*, Comsp. = *Commelina* sp., Clerub = *Cleome rubela*, Bulhis = *Bulbostylis hispidula*, Geiorn = *Geigeria ornativa*, Cleter = *Clerodendrum ternatum*, Acanau = *Acanthosicyos naudinianus*, Cyaser = *Cyamopsis serrata*, Rhyven = *Rhynchosia venulosa*, Evoals = *Evolvulus alsinoides*, Hereen = *Hermannia eenii*, Oxyala = *Oxygonum alatum*, Ociame = *Ocimum americanum*, Ipobol = *I. bolusiana*, Ipohac = *I. hackeliana*, Ipools = *I. obscura*, Ipomag = *I. magnusiana*, Barmac = *Barleria macrostegia*, Crosph = *Crotolaria sphaerocarpa*, Molcer = *Mollugo cerviana*, Zorglo = *Zornia glochidiata*, Blemit = *Blepharis mitrata*, Acrinf = *Acrotome inflata*, Xentri = *Xenostegia tridentata*, Hofbur = *Hoffmannsegia burchellii*, Dipmar = *Dipcadi marlothii*, Walnut = *Walleria nutans*, Tepbur = *Tephrosia burchellii*, Chabie = *Chamaecrista biensis*, Basped = *Basananthe pedata*, Herarg = *Hermbsiaedtia argenteiformis*, Cypmar = *Cyperus* cf. *margaritaceus*, Dicsch = *Dicoma schinzii*, Helcan = *Helichrysum* cf. *candolleianum*, Eupina = *Euphorbia inaequilatera*;

Graminoids: Daccaeg = *Dactyloctenium aegyptium*, Erapal = *Eragrostis pallens*, Erajef = *E. jeffreysii*, Erabif = *E. biflora*, Eraleh = *E. lehmanniana*, Eratric = *E. trichophora*, Eravis = *E. viscosa*, Erasp. = *Eragrostis* sp., Digser = *Digitaria seriata*, Digsan = *D. sanguinalis*, Setver = *Setaria verticillata*, Melrep = *Melinis repens*, Arimer = *Aristida meridionalis*, Aricon = *A. congesta*, Aristi = *A. stipitata*, Ariads = *A. adscensionis*, Arisp. = *Aristida* sp., Chlvir = *Chloris virgata*, Cyndac = *Cynodon dactylon*, Traber = *Tragus berteronianus*, Schkal = *Schmidtia kalihariensis*, Urobra = *Urochloa brachyura*, Pogsqu = *Pogonarthria squarrosa*).

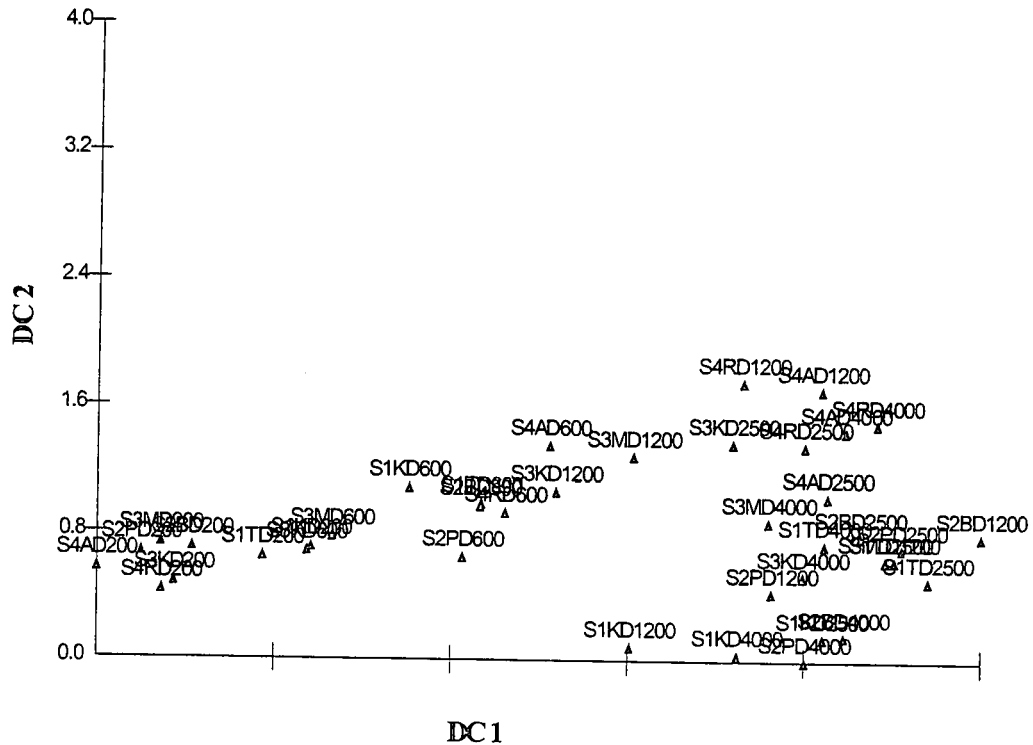


Figure 2.5 Detrended correspondence analysis of sampling plots for herbaceous plants at varying distance from water points. DC1 represents the livestock pressure gradient. Each point indicates a plot (e.g. S3KD200 : S3 = Site 3; K = name of transect; D200 = distance 200 m).

Basal area. Basal area of woody plants varied significantly along a distance from water points ($F = 13.89$, $P < 0.001$, d.f. = 4, 12). Mean basal area declined with distance from water points (Table 2.4). Trees at 200 m had the biggest mean basal area, while it did not differ significantly at the remaining distances from the water points (Scheffe test, $P > 0.05$).

Plant height. Plant heights differed significantly with distance from water points ($F = 5.88$, $P < 0.05$, d.f. = 4, 12). Trees at 200 m were significantly taller (mean \pm SE, 2.43 ± 0.107 cm), while those further away from water points did not differ significantly in height (Scheffe test, $P > 0.05$) (Table 2.4).

Canopy area. Mean canopy area differed significantly along the grazing gradient ($F = 25.38$, $P < 0.0001$, d.f. = 4, 12). Trees in the vicinity of water points (200 m) had significantly the biggest canopy area (Table 2.4). Canopy area at 600 m and further away did not differ significantly (Scheffe test, $P > 0.05$).

Woody plant density. Livestock activities around water points affected plant density significantly ($F = 10.92$, $P < 0.001$, d.f. = 4, 12). Plants were sparsely distributed around 200 to 600 m from the water points, but increased gradually in density with increasing distance. Mean tree densities at 200 and 600 m (Table 2.4) did not differ significantly ($P > 0.05$), however only woody density at 200 m was significantly lower than at 1200, 2500 and 4000 m ($P < 0.05$). Thus mean tree density did not differ significantly at 600, 1200, 2500 and 4000 m from water points.

Fewer, but tall trees with broader canopy areas grew near the water points. Tree density declined with 91 %, while their height and canopy area increased with about 96 % and 16 % around the 200 m from the water points in comparison with farther distances (Table 2.4).

Table 2.4 Mean±SE woody plant basal area, height, canopy area and density at distances from water points. Different letters indicate significant differences in mean values at $P < 0.05$. Data were log-transformed.

Distance (m)	Basal area (cm ²)	Plant height (cm)	Canopy area (cm ²)	Woody density (m ⁻²)
200	2.59 ± 0.125 a	2.43 ± 0.107 a	5.1 ± 0.16 a	0.01 ± 0.005 a
600	1.90 ± 0.141 b	2.08 ± 0.053 b	4.5 ± 0.11 b	0.06 ± 0.017 ab
1200	1.65 ± 0.075 b	2.07 ± 0.043 b	4.2 ± 0.05 b	0.11 ± 0.014 b
2500	1.64 ± 0.121 b	2.09 ± 0.030 b	4.2 ± 0.07 b	0.15 ± 0.033 b
4000	1.75 ± 0.126 b	2.03 ± 0.046 b	4.2 ± 0.07 b	0.15 ± 0.024 b

SOIL PARAMETERS

The availability of organic carbon, nitrogen and phosphorus followed the same trend: generally higher nearer to the soil surface and with proximity to the water points.

SOIL ORGANIC CARBON

Soil organic carbon differed significantly across the soil profile at sampling distance from water points ($F = 5.75$, $P < 0.0001$, d.f. = 10, 90). Organic carbon content was significantly higher in the 10 – 20 cm depth at 200 m from water points than at all 90 -100 cm depths and at 50 – 60 cm depth at 1200 m and 4000 m from water points (Scheffe test, $P < 0.05$, Table 2.5). Mean organic carbon did not differ significantly at comparable soil depth across all sampling points away from water points (Scheffe test, $P > 0.05$).

TOTAL NITROGEN

Total nitrogen in the soil differed significantly across the soil profile at sampling distance from water points ($F = 2.87$, $P = 0.0038$, d.f. = 10, 90). However, Scheffe test did not show significant differences in total nitrogen between soil depths ($P > 0.05$), whilst Tukey HSD test showed that total nitrogen content in the 10 – 20 cm depth at 200 m was significantly higher than that measured at 90 – 100 cm depth at 600, 1200 and 2500 m from water points, and also higher than that measured in the 50 – 60 cm depth at 4000 from water points (Table 2.5). No significant differences existed between the 50 – 60 cm and 90 – 100 cm soil depths along the distance from water points (Scheffe test, $P > 0.05$).

AVAILABLE PHOSPHORUS

Available phosphorus differed significantly across the soil profile at sampling distance from water points ($F = 8.14$, $P < 0.0001$, d.f. = 10, 90). Available phosphorus content was significantly higher in the 10 -20 cm depth at 200 m from water points (Scheffe test, $P < 0.05$; Table 2.5). No significant differences existed between the 50 – 60 cm and 90 – 100 cm layers at 200 m and as well as at the remaining distances from from water points (Scheffe test, $P > 0.05$).

SOIL MOISTURE

Soil moisture differed significantly across the soil profile at sampling distance from water points ($F = 2.63$, $P = 0.0075$, d.f. = 10, 90). Scheffe test showed no significant difference in soil moisture across the soil profile away from water points ($P > 0.05$). However, Tukey HSD test showed significantly higher soil moisture content in the 90 – 100 cm depth at 200 and 600 m (0.545 ± 0.1046 % and 0.528 ± 0.0864 % respectively) than in the 10 – 20 cm depth (0.280 ± 0.0421 %) at 4000 m from water points (Table 2.5).

Table 2.5 Mean±SE soil organic carbon, total nitrogen, available phosphorus and soil moisture across the soil profile and distance from water points (n = 8). Different letters indicate significant difference in mean values at p < 0.05.

Distance (m)	Depth (cm)	Organic carbon (%)	Total nitrogen (%)	Available phosphorus (%)	Soil moisture (arcsine %)
200	10 – 20	0.327 ± 0.0763 a	15.555 ± 1.4525 a	4.279 ± 1.4108 a	0.318 ± 0.0134 ac
200	50 – 60	0.183 ± 0.0243 ab	12.792 ± 1.2715 ab	1.250 ± 0.5635 b	0.520 ± 0.0685 ac
200	90 – 100	0.123 ± 0.0184 b	10.023 ± 1.5267 ab	0.905 ± 0.4838 b	0.545 ± 0.1046 a
600	10 – 20	0.204 ± 0.0386 ab	13.121 ± 1.3429 ab	0.979 ± 0.6669 b	0.318 ± 0.0134 ac
600	50 – 60	0.137 ± 0.0285 ab	11.148 ± 1.4935 ab	0.271 ± 0.2090 b	0.404 ± 0.060 ac
600	90 – 100	0.104 ± 0.0198 b	8.387 ± 1.5141 b	0.179 ± 0.0945 b	0.528 ± 0.0864 a
1200	10 – 20	0.202 ± 0.0235 ab	11.581 ± 0.9460 ab	0.196 ± 0.0796 b	0.318 ± 0.0134 ac
1200	50 – 60	0.131 ± 0.0182 b	10.764 ± 0.4479 ab	0.104 ± 0.0443 b	0.359 ± 0.0291 ac
1200	90 – 100	0.091 ± 0.0108 b	9.060 ± 0.9746 b	0.029 ± 0.0137 b	0.385 ± 0.0272 ac
2500	10 – 20	0.208 ± 0.0255 ab	13.036 ± 1.0937 ab	0.116 ± 0.0564 b	0.305 ± 0.0 ac
2500	50 – 60	0.148 ± 0.0161 ab	10.121 ± 1.0572 ab	0.095 ± 0.0488 b	0.359 ± 0.0291 ac
2500	90 – 100	0.110 ± 0.0123 b	8.948 ± 1.4835 b	0.141 ± 0.0455 b	0.385 ± 0.0272 ac
4000	10 – 20	0.202 ± 0.0245 ab	12.591 ± 0.7350 ab	0.101 ± 0.0504 b	0.280 ± 0.0421 bc
4000	50 – 60	0.133 ± 0.0122 b	8.718 ± 2.0978 b	0.201 ± 0.1028 b	0.361 ± 0.0555 ac
4000	90 – 100	0.129 ± 0.0154 b	10.617 ± 1.4497 ab	0.093 ± 0.0502 b	0.337 ± 0.0755 ac

DISCUSSION

VEGETATION AND SOIL CHANGES ALONG A GRAZING GRADIENT

Sinking boreholes to tap groundwater resources facilitated all-year round livestock production in the semi-arid Kalahari, and high livestock pressure around the artificial water points often lead to undesirable vegetation and soil changes (Andrew 1988, Thrash 1998). We found that livestock activities near the water points had significant impacts on vegetation and soils. The status of vegetation and soil around the water points reflected the situation of range utilisation on relatively homogenous dune fields of the northern Kalahari after 32 to 51 y of livestock production.

Reduced competition for soil nutrients and moisture among the sparsely distributed trees may have been responsible for increased plant growth. Soil moisture, organic carbon and total nitrogen did not differ significantly at the comparable soil depth across the distance from water points ($P > 0.05$), but because of fewer trees near water points more resources could have been available for the individual trees. Hence, this might have promoted the growth of trees near water points. We found higher organic carbon and total nitrogen content at 10 – 20 cm depth than at lower depths, while available phosphorus in the upper soil layer was high in the 10 – 20 cm soil depth at 200 m from water points, and may have resulted from dung deposition by cattle supplemented with phosphorous licks. This may also be attributed to the predominant matrix flow of water movement in the Kalahari which allows nutrient adsorption onto soil particles and thus preventing leaching (Dougil et al. 1998). It is further suggested that high nitrogen and phosphorus would remain in the upper soil layer because of the low mineralization and adsorption onto soil particles (Dougil et al. 1998). Phosphorus is generally very low in the Kalahari environment (Mendelsohn et al. 2002).

Herbaceous abundance increased with proximity to the water points. These results suggest that disturbance decreased species diversity, but increased the population size of herb species in the vicinity of water points. Herbaceous species such as *Dactyloctenium aegyptium* and *Tribulus terrestris* were

most abundant at 200 m, while the abundance of *Sida cordifolia*, *Tragus berteronianus*, *Amaranthus thunbergii*, *Indigofera spp.*, *Acanthospermum hispidum*, *Commelina sp.*, *Chloris virgata* and *Setaria verticillata* was further extended and with greater prominence at 600 m from the water points. Two trees, *Acacia hebeclada* and *A. erioloba*, dominated the 200 m zone. These species may be indicators of land degradation due to livestock activities around water points. The combination of generally high soil fertility in the upper soil layer and reduced tree density may have increased the intensity of the above-ground herb interspecific competition which resulted in fewer species, but with high abundances (Wilson and Tilman 1991). In this system, selective herbivory may have altered community structure by enhancing the abundance of unpalatable species such as *Sida cordifolia*. Disturbance and low tree density favours the production of herbaceous species (Barker et al. 1990, James et al. 1999), while livestock activities may reduce the establishment of perennial species (Britz et al. 2002). This study showed that perennial grasses were more sensitive to livestock pressure and thus occurred mostly where grazing pressure was the least at 4000 m from water points.

SPATIAL AND TEMPORAL VEGETATION CHANGE UNDER GRAZING

This study showed that the current pattern of vegetation was significantly altered near the water points. However this result does not confirm with certainty that livestock impact is only confined to the areas near the water points, because it may as well be that the impact beyond the water points had resulted in a uniform pattern of vegetation. The absence of long-term data is a limitation; hence we cannot ascertain the nature of change. However, long-term observations by pastoralists revealed that the structure of plant community has change substantially all over the rangelands since the commencement of sedentary settlements around the artificial permanent water points some 32 to 51 y ago (Chapter 6). The effects of grazing on the structure of plant communities depend on the distance livestock travel from water points (Jeltsch et al. 1997) and temporal scale (Ward et al. 1998). Simulation data for the arid and semi-arid environments, southern Kalahari (Jeltsch et al. 1997) and northern Australia (Pickup 1994), showed that the effects of cattle grazing on vegetation can indeed extend beyond 7000 m from artificial water points. Thus beyond 7 000 m was farther away from water points than what this study

could possibly assess given the proximity of settlements in the study area. Historically livestock production has significant impact on the structure of plant communities in Namibia, even if current local-scale data suggest that the impact is confined to the areas near water points. Grass production in Namibia has decreased by approximately 50 % between 1939 and 1997 (Ward and Ngairorue 2000), while woody plants have increased in density over much of Namibia's rangelands over the past 40 to 50 y (De Klerk 2004).

However, a distance of more than 10 000 m between water points would potentially minimise the expansion of negative impacts on range resources, and ensure grazing reserves mid-way between settlements (Walker et al. 1987). Thus such distance may prevent starvation-induced mortality during droughts (Owen-Smith 1996). The 7 000 m distance applied by the Ministry of Agriculture, Water and Forestry in Namibia for spacing water points between pastoral settlements may intensify land degradation and increase drought vulnerability. In addition, the current uncontrolled fencing and subdivisions of communal rangelands by some pastoralists may confine livestock foraging activities, thereby causing excessive livestock pressure which may lead to potentially undesirable vegetation change.

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CHAPTER 3

**CATTLE DIET SELECTION DURING THE HOT-DRY SEASON IN A SEMI-ARID
REGION OF NAMIBIA**

ABSTRACT

The northern Kalahari Desert is dominated by *Terminalia sericea* savanna woodland and a sparse herbaceous layer. Range ecologists regard *Terminalia sericea* as a major encroaching species and that such encroachment represents a cost to cattle production. In contrast, pastoralists regard this woody species as an important component of cattle diet, particularly during the hot-dry season or during drought. In this study, free-ranging cattle were observed during the peak of the pre-rain flushing period of deciduous plants during the hot-dry seasons of 2001 and 2002. Diet preference was evaluated by taking into account the proportion of diet consumed in relation to its availability on the range. Diet preference was compared to diet quality. Cattle spent 71% of time feeding on browse during the hot-dry season. *Terminalia sericea*, *Bauhinia petersiana* and *Philenoptera nelsii* contributed 74.5% to browse consumption. *Philenoptera nelsii* was the most preferred browse. Generally, cattle preferred browse with high crude protein and phosphorus content but avoided browse with high fibre content. This study confirmed the long-term observations by local pastoralists that woody species contribute significantly to cattle diet during the hot-dry season in the northern Kalahari. We recommend that rehabilitation of encroached rangelands should take into account the role of browse in semi-arid environments.

Keywords: browse preference, diet quality, foraging behaviour, anti-herbivory, northern Kalahari

INTRODUCTION

In arid and semi-arid environments, the availability of quality diet for herbivores is largely seasonal (Owen-Smith 1994, Woodward and Coppock 1995). The variable rainfall in such environments determines primary production and patchiness of plant forage resources (Ellis and Swift 1988, Illius and O'Connor 1999, Ndlovu *et al.* 2000). In good years, forage resources are abundant and herbivores can be highly selective of dietary items (Hendricks *et al.* 2002). However, forage resources decline in diversity, abundance and quality during dry seasons and during droughts, thereby limiting diet choice (Wilson 1969, Le Houérou 1980). Hence, during the dry season and during drought, herbivores may expand their diet to include less palatable species (Owen-Smith 1994).

In most of Namibia's communal rangelands, grass cover is almost completely removed during dry seasons and drought years (Ward *et al.* 1998), leaving cattle with no choice but to shift to browsing or feeding on leaf litter (Alfeus Kauta, Otjinene Farmers Association – pers. comm. June 2001). Evergreens, pre-rain flushing deciduous trees and shrubs, and leaf litter are key resources that show little interannual variation (Frost 1985) and thus provide steady forage to cattle during the dry spells until sufficient herbage is produced in the wet season (Le Houérou 1980, Illius and O'Connor 1999). Bush encroachment in the current study area further diminishes the opportunities for herbage production (Bester 1998/1999) but provides a potentially abundant browse to herbivore (Chapter 6). Browsing impact on woody plants in African savannas indicates that browse can be a significant part of the total diet for large herbivores (Bergström 1992).

Browse species generally have high protein and energy content (Bergström 1992, Woodward and Coppock 1995) relative to grasses (Moleele 1998, Le Houérou 1986). However, browse does not always provide the best forage during dry seasons, particularly for herbivores traditionally thought to be grass-dependent such as cattle and sheep, because many woody species contain both physical and chemical anti-herbivory traits that constrain herbivore accessibility to dietary tissues or which reduce the

digestibility of dietary tissues. Physical traits such as high fibre content render biting, chewing and digestibility costly to herbivores (Woodward and Coppock 1995, Watson and Owen-Smith 2000, Shipley and Yanish 2001). Spinescence may increase with herbivory (Rohner and Ward 1997) and thereby reduce herbivore bite size and bite rate (Cooper and Owen-Smith 1986, Wilson and Kerley 2003). Other physical traits such as canopy height and leaf distribution also reduce accessibility or increase energy expenditure during foraging (Bergström 1992, Shipley and Yanish 2001).

Among the many chemical anti-herbivory traits, condensed tannins appear to be the most important in influencing diet selection in browsers, especially for those that do not secrete tannin-binding proline-rich salivary protein (McArthur *et al.* 1993, Aerts *et al.* 1999). Once ingested, condensed tannins forms complexes with protein that result in the precipitation of protein through faecal and urine excretion (Kaitho *et al.* 1998, Aerts *et al.* 1999). Browse often contains enough tannin to reduce protein digestibility by up to 50% (Beck and Reed 2001). As a result, high levels of condensed tannins decrease the acceptability and nutritional value of browse (Furstenburg and Van Hoven 1994, Aerts *et al.* 1999, Shipley and Yanish 2001).

Natural rangelands often consist of mosaic patches of a variety of vegetation differing in quality, accessibility and acceptability to foraging herbivores. Experience and the ability of the herbivore to remember the locality of preferred patches are important to the herbivore to minimise energy on selective foraging (De Vries and Daleboudt 1994, Illius *et al.* 1999). In terms of diet composition, principal dietary plants are those consumed in the greatest quantities (Hendricks *et al.* 2002), while preferred diet is one that is proportionately more frequently consumed than is available on the range (Chesson 1983). Deciduous trees in southern African savannas may become more palatable during pre-rain flush than later in the growing season (Owen-Smith 1994, Augustine and McNaughton 1998). Thus, herbivores may shift their diet and spend more time foraging on the new leaves of deciduous trees to maximise energy intake (Owen-Smith 1994).

Cattle consume browse mostly during the hot-dry season in the northern Kalahari (Chapter 6). The absence of grass combined with the increasingly available pre-rain flush during the latter half of the hot-dry season, increase browse consumption (Chapter 6). Of the 65 pastoralist households interviewed (pastoralists, pers. comm.), 94%, 52% and 46% ranked *T. sericea*, *Combretum collinum* and *Philenoptera nelsii* as the principal browse species consumed during the hot-dry season. These deciduous plants were among the first to flush before the beginning of the wet season, and hence may experience heavy browsing pressure.

We wished to determine the contribution of woody plants, in particular *Terminalia sericea*, to cattle diet during the hot-dry season. We selected *T. sericea* for two reasons: 1) the perceived problem associated with this species in beef production systems as an encroacher species, and 2) the local pastoralists consider it as a principal browse species for cattle during the hot-dry season. Our predictions were: 1) If *T. sericea* constitutes a principal browse for cattle during the hot-dry season, then it should be consumed in larger quantities than grass; 2) if cattle prefer to feed on *T. sericea*, then they should feed more on *T. sericea* relative to its abundance; and 3) that the preference of woody species correlates with the quality of foliage.

MATERIALS AND METHODS

Study Area

The study was conducted in a semi-arid region of Namibia with highly variable rainfall. The coefficient of variation of the annual rainfall varies between 30 – 50% of the long-term mean rainfall (Mendelsohn *et al.* 2002). The long-term rainfall ranges from 250 - 400 mm per annum (Dealie *et al.* 1993). The long-term mean annual rainfall recorded at the nearest weather station in Gobabis (about 180 km), over the period of 1897 to 1985 was 370.9 mm, with 14% falling during September to November, referred to as the hot-dry season. The highest rains occur from January to March (62%) (Namibia Meteorological Service, 2002). During the period of this study, 261 mm rainfall was received for the period October 2001 to March 2002.

The general study area consists of a large undulating landscape covered with sand and sand dunes with limestone outcrops at places, traversed by low-lying interdune depressions (*omiramba* in OtjiHerero) (Köhler 1959). The sandy landscapes have low levels of phosphorus and nitrogen contents (De Pauw *et al.* 1998/1999). Altitude ranges from 1200 - 1450 m above sea level. The study sites were located between the *Omuramba ua Pukiro* and *Omuramba ua Pata* (also known as *Eiseb Omuramba*) in the Otjinene communal area in the 21° S 19° E coordinates of eastern Namibia. The size of the Otjinene communal lands is about 1 283 000 ha (Adams and Werner 1990).

The vegetation type of the area is classified as the northern Kalahari broadleaved woodlands (Mendelsohn *et al.* 2002), characterised by dense stands of edible bush covering the dunes. *Baphia obovata* (Papilionoideae), *Croton gratisimus* (Euphorbiaceae), *Combretum apiculatum* (Combretaceae), *Terminalia sericea* (Combretaceae) and *Philenoptera nelsii* (Papilionoideae), and shrubs such as *Bauhinia petersiana* (Caesalpinioideae) and *Grewia species* (Tiliaceae) are the most important. In the dune valleys, *Acacia species* (Mimosoideae) such as *A. erioloba*, *A. mellifera* occur together with

Boscia albitrunca (Capparaceae) (Rawlinson 1994). *Terminalia sericea* is considered an encroaching bush species in the northern Kalahari (Bester 1998/1999, Mendelsohn *et al.* 2002, De Klerk 2004).

We selected sites on a relatively homogenous landscape. Thus, livestock impact on vegetation should be radial around water points, but with decreasing impact farther away (Tables 2.3 – 2.5). Cattle production is the main form of land use in the study area. Sheep and goats are rarely kept in the study area (Directorate of Veterinary Services, various years).

Data Collection

Browse consumption and preference

We observed the same herds of cattle during the first 3 weeks of the commencement of pre-rain flushing of deciduous trees during October for the years 2001 and 2002. Cattle were watered in the morning and spent most of the midday hours resting in kraals, and observed in the late afternoon between 17h00 and 19h00. Observations were carried out at one site, using two herds of about 40 and 60 cattle from two different households. The two herds ranged freely and utilized the same general rangeland. During the years 2001 and 2002, the cattle were not supplemented with commercially-available phosphorus, molasses and dry veld concentrates or salts, but relied solely on the range. We quantified the total time the animals spent foraging, and ignored behavioural activities such as walking, urinating and resting. Foraging time was subdivided into browsing and grazing to test the prediction that cattle in the semi-arid northern Kalahari mostly browse rather than grazing during the hot-dry season. The prediction that cattle mostly feed on and prefer *T. sericea* during the hot-dry season was also tested, using the procedure outlined below.

We initially used the 'site-based acceptability' measure which provides an estimate of the likelihood of browsing when a plant is encountered by a herbivore. According to Owen-Smith and Cooper, (1987a),

this method provided a classification of woody species into favoured, intermediate and neglected categories in a South African savanna. When tested under the current field conditions, we encountered difficulties with the method because the cattle were too wild to determine the distances at which plants were available to the focal animal; and the high density of woody plants made the assessment of plants available for browsing time consuming such that we could not keep up with the moving animals.

We simplified the 'site-based acceptability' method (Owen-Smith and Cooper 1987a) by recording the foraging activity of an adult lactating cow into a pocket tape recorder during an hour of observation, noting the time spent per feeding bite and the type of plant the animal fed on. We consistently observed adult cows to avoid differences that may exist in intake rate because food intake is influenced by body weight or sex (Illius and Gordon 1987). The lactating cows were selected at random from a foraging herd at about 2000 – 4000 m away from the water points, without repeatedly observing the same cow during the same year (the cows were easy to distinguish visually and were known individually to the observers). Grazing was recorded as a unit, comprising of the total time for grass species consumed. However, for browsing, feeding time was recorded separately for the various browse species consumed. Based on these recordings, we calculated the total foraging time and, for the browse, the relative abundance of each individual browse species in the diet (Equation 1). This equation makes the assumption that the contribution of a particular food item to the herbivore's dry matter consumption is directly proportional to the time herbivores spend consuming that particular item. Significant linear relationships between food intake and feeding time in herbivores have been reported (Berteaux *et al.* 1998). However, this relationship may not be consistent where accessibility to dietary items is reduced by, for instance, spinescence (Wilson and Kerley 2003). The majority of browse species in the study area did not bear spines (field observation).

$$r_i = \frac{\text{Browsing time spent on species } i}{\text{Total browsing time}} \times 100 \quad \text{Equation 1,}$$

where r_i is the relative abundance of the i th browse species in the diet.

In addition, we estimated the relative abundance of each browse species in the cattle home ranges, by placing three 50 m x 10 m plots in the localities where much of the foraging took place. Most woody species were within the cattle browsing height, which was estimated at about 200 cm for adult cows. Species diversity did not differ much between the plots. Ten plots with a mean species richness of 11 ± 1.9 SD were sampled. All browse species within the plots were counted and their relative abundances (P_i) on the home range were calculated using the formula below (Equation 2):

$$P_i = \frac{\text{Density of browse species } i}{\text{Density of browse species on range}} \times 100 \quad \text{Equation 2,}$$

where P_i is the relative abundance of the i th browse species on the range.

A number of diet selection indices exist, of which the Ivlev electivity index (E_i), (Ivlev 1961) is the most widely used (Krebs 1989). This index uses both r_i and P_i to estimate herbivore diet preference (Equation 3).

$$E_i = (r_i - P_i) / (r_i + P_i) \quad \text{Equation 3,}$$

Where E_i is the Ivlev electivity, r_i and P_i as defined in equations 1 and 2.

The Ivlev index has, however, a major shortcoming in that it is not independent of prey density, which seriously limits its usefulness in diet selection (Chesson 1983). In our initial analyses, this index favoured rare species on the range even if they were only browsed once. Therefore, we used the standardised forage ratio (S_i) as suggested by Chesson (1983), which is independent of prey availability (Equation 4), where r_i and P_i are defined as in equations 1 and 2, and n is the number of i th r_i/P_i observations in the system.

$$S_i = \frac{\left(\frac{r_i}{P_i} \right)}{\left(\frac{\sum_{n=1}^n r_n}{P_n} \right)} \quad \text{Equation 4,}$$

where S_i is the standardised forage ratio, while r_i and P_i are as defined in equations 1 and 2.

Browse Quality

This section tests the hypothesis that diet preference correlates with foliage quality. Foliage of 12 species browsed at least twice during October 2001/2002 were collected with eight sample replicates and placed in an air-draft oven at 65 °C for 48 h within 2 hours of collection. Samples were ground to pass through a 1 mm sieve in a “Micro Mill” and analysed for crude protein (CP), phosphorus (P), acid detergent fibre (ADF), neutral detergent fibre (NDF) and acid detergent lignin (ADL). Acid detergent fibre, NDF and ADL were determined using the detergent method (Goering and Van Soest 1970). Crude protein was analysed according to the AOAC methods (AOAC 1984). Phosphorus analysis followed the molybdovanate method (AOAC 1984). Samples for condensed tannin analysis were further sieved through a 0.4 mm sieve. Condensed tannin in leaf samples was measured using a standard acid-butanol protocol (Waterman and Mole 1994). The proanthocyanidin method with modification by Hagerman (1995) was applied to measure condensed tannin extracted with methanol. Two replicates were prepared and read by the spectrophotometer. Condensed tannin concentrations are expressed in quebracho equivalents (quebracho is used as a standard – Hagerman and Butler 1989). Quebracho for use in the standard was obtained from A. Hagerman (Miami University, Oxford, Ohio, USA).

Statistical Analysis

Feeding on browse or grass was expressed as a percentage of total feeding time. A Student’s t-test was applied (on the untransformed data) to compare the difference in time spent on browsing versus grazing. Chi-square statistics were used to determine significant differences between the levels of consumption

among browsed species. The forage ratio index was determined and browse species were plotted in decreasing order of preference. A forage ratio approaching unity indicates a highly sought-after dietary species while values closer to zero indicates avoided species (Chesson 1983). Condensed tannin content, ADF, NDF, ADL, CP and P in the foliage of browse species was analysed by a one-way factorial ANOVA. Acid detergent lignin and phosphorus data were transformed with the log and arcsine transformation to achieve a normal distribution. Statistical analyses were followed up by a multiple comparisons of means using Scheffe *post hoc* test. Means are represented \pm 1 standard error, unless otherwise stated. Furthermore, forage ratio and plant chemical composition were analysed in a backward step-wise multiple regression model, regressing forage ratio against the chemical compositions (nutrients and secondary compounds) of key forage species to determine which substances influenced diet selection. A P-value of ≤ 0.05 was used to include factors in the diet selection model.

RESULTS

Consumption and composition of forage

The cows were observed for a total of 17h 30 min during October of 2001 and 2002. Adult cows spent 71% of their feeding time browsing and 29% grazing during a total of 9h 17 min of actual foraging. This difference was highly significant ($t = 3.32$, $P = 0.01$, $df = 32$). As would be expected, all woody species were not consumed in equal amounts (Table 3.1). Contrary to the perception of the majority of pastoralists, *Terminalia sericea* (19.4%) was not the only main browse species that constituted cattle diet during the hot-dry season, but also *Bauhinia petersiana* (27.9%) and *Philenoptera nelsii* (27.2%). Cattle spent significantly more time browsing these three species than would be expected among all the browse species ($\chi^2 = 15255.6$, $P < 0.05$, $df = 7$).

Browse Preference

When we considered browse abundance, it became obvious that cattle preferred *P. nelsii* (forage ratio (S_i) = 0.54) above all other species, including *B. petersiana* which was consumed in greater quantities (Table 3.1). Thus, cattle actively sought to forage on *P. nelsii* despite its rarity on the range. *Grewia flava* and *Combretum psidioides* were the second- and third-most preferred plants with S_i = 0.13 and 0.12 respectively. *Terminalia sericea*, *Grewia flavescens* and *Bauhinia petersiana* were intermediate in the range of preferred browse and highly avoided plants. *Ochna pulchra* was the most avoided browse (S_i = 0.004).

A total of 13 woody species was browsed during the field observations. Thus, in addition to the nine species mentioned in Table 3.1, the following species were also browsed: *Rhigozum brevispinosa*, *Boscia albitrunca*, *Ozoroa paniculosa*, and *Commiphora africana*. We excluded these species from the forage ratio analysis because they were browsed once and for less than 50s during the 17h 30 min of observations, but included the majority in the diet quality analysis (Table 3.2). *Rhigozum brevispinosa*, *O. pulchra*, *O. paniculosa* and *B. albitrunca* each made up 0.14% of the species on the range, while *C. africana* constituted 3.7% of the species encountered on the range.

Table 3.1. Cattle diet composition of woody vegetation that was browsed at least twice and for more than 50s during two consecutive hot-dry seasons.

Species	Diet composition (%)	Relative abundance (P_i)	Forage ratio (S_i)
<i>Bauhinia petersiana</i>	27.9	24.49	0.044
<i>Philenoptera nelsii</i>	27.2	1.94	0.544
<i>Terminalia sericea</i>	19.4	13.68	0.055
<i>Combretum collinum</i>	9.3	12.75	0.028
<i>Grewia flava</i>	7.8	2.28	0.133
<i>Grewia flavescens</i>	4.4	3.21	0.053
<i>Combretum psidioides</i>	3.4	1.10	0.120
<i>Mundulea sericea</i>	0.4	0.93	0.018
<i>Ochna pulchra</i>	0.3	3.38	0.004

Browse quality

Condensed tannins

Cattle browsed on species with a wide range of condensed tannin concentrations (Figure 3.1). The concentration of condensed tannins differed significantly among the dietary species ($F = 115.053$, $P < 0.0001$, $df = 11, 168$). *Bauhinia petersiana*, *O. pulchra* and *G. flava* had the highest condensed tannin concentrations. There were no significant differences in tannin contents among these three species ($P > 0.05$).

Acid detergent fibre (ADF)

Acid detergent fibre content differed significantly among the browse species ($F = 56.09$, $P < 0.001$, $df = 11, 84$). Browse species revealed a gradient in the levels of ADF, with *O. pulchra* having the highest content, while *C. africana* and *B. albitrunca* contained the least amount of ADF (Table 3.2).

Combretum collinum, *G. flava*, *T. sericea* and *P. nelsii* had the second highest ADF contents with no significant differences among them ($P > 0.05$). *Terminalia sericea* and *P. nelsii* did not differ from the group with third highest ADF content (*M. sericea*, *O. paniculosa*, *B. petersiana*, *G. flavescens* and *C. psidioides*); together these species constituted the intermediate range of ADF levels. *Commiphora africana* and *B. albitrunca* had the lowest content, which differed significantly from all other species ($P < 0.05$), except for *C. psidioides*.

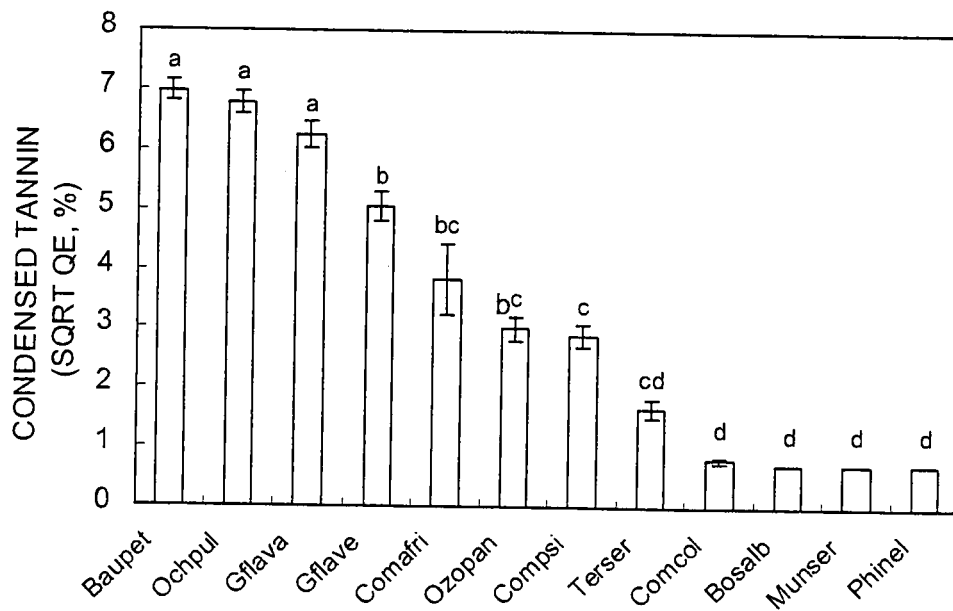


Figure 3.1. Condensed tannin concentrations (% Quebracho equivalents) of 12 browse species. Error bars denote 1 * S.E., and the different letters indicate significant differences among means ($p < 0.05$) in Scheffe *post hoc* tests. (Baupet = *Bauhinia petersiana*, Ochpul = *Ochna pulchra*, Gflava = *Grewia flava*, Gflave = *Grewia flavescens*, Comafri = *Commiphora africana*, Ozopan = *Ozoroa paniculosa*, Compsi = *Combretum psidioides*, Terser = *Terminalia sericea*, Comcol = *Combretum collinum*, Bosalb = *Boscia albitrunca*, Munser = *Mundulea sericea*, Phinel = *Philenoptera nelsii*).

Table 3.2: Mean \pm SE fibre, crude protein and phosphorus content (%) of 12 browse species. Means are represented with ± 1 * standard error, and the different letters indicate significant differences among means ($P < 0.05$) in Scheffe *post hoc* tests.

	ADF (%)	NDF (%)	ADL (log %)	CP (%)	P (arcsine %)
<i>M. sericea</i>	34.3 \pm 0.44 ^c	46.8 \pm 0.77 ^{bc}	1.1 \pm 0.02 ^{bc}	25.4 \pm 0.40 ^b	0.14 \pm 0.003 ^a
<i>G. flavescens</i>	30.6 \pm 0.85 ^c	45 \pm 0.88 ^{bc}	1.2 \pm 0.02 ^{bc}	23 \pm 0.49 ^{bc}	0.13 \pm 0.006 ^{ab}
<i>B. petersiana</i>	31.2 \pm 0.97 ^c	41.7 \pm 1.16 ^c	1.2 \pm 0.02 ^b	21.3 \pm 0.66 ^c	0.12 \pm 0.003 ^{ab}
<i>O. paniculosa</i>	32.1 \pm 1.53 ^c	49 \pm 2.01 ^{bc}	1.2 \pm 0.03 ^{bc}	16.4 \pm 0.83 ^d	0.11 \pm 0.008 ^{ab}
<i>C. psidioides</i>	29.3 \pm 0.56 ^{cd}	38 \pm 0.42 ^{cd}	1 \pm 0.01 ^c	18.2 \pm 0.36 ^{cd}	0.11 \pm 0.003 ^{ab}
<i>P. nelsii</i>	35.2 \pm 0.77 ^{bc}	48 \pm 1.41 ^{bc}	0.96 \pm 0.02 ^c	29.4 \pm 1.08 ^a	0.11 \pm 0.009 ^{ab}
<i>B. albitrunca</i>	22 \pm 0.63 ^d	32 \pm 0.72 ^{cd}	1.1 \pm 0.01 ^{bc}	27.4 \pm 0.75 ^{ab}	0.09 \pm 0.006 ^b
<i>C. collinum</i>	42.9 \pm 1.14 ^b	54.1 \pm 1.12 ^b	1.1 \pm 0.03 ^{bc}	14.4 \pm 0.15 ^{de}	0.09 \pm 0.002 ^{bc}
<i>G. flava</i>	40.6 \pm 1.05 ^b	53 \pm 0.83 ^b	1.3 \pm 0.01 ^{ab}	18 \pm 0.61 ^{cd}	0.08 \pm 0.005 ^{bc}
<i>C. africana</i>	22.5 \pm 2.79 ^d	31 \pm 3.99 ^d	1.1 \pm 0.08 ^{bc}	15 \pm 0.51 ^{de}	0.07 \pm 0.005 ^{bc}
<i>T. sericea</i>	38.9 \pm 0.77 ^{bc}	48.8 \pm 0.23 ^{bc}	1.3 \pm 0.01 ^{ab}	9.4 \pm 0.06 ^c	0.06 \pm 0.000 ^c
<i>O. pulchra</i>	53.6 \pm 0.57 ^a	68.3 \pm 0.61 ^a	1.5 \pm 0.0 ^a	11.4 \pm 0.24 ^c	0.06 \pm 0.004 ^c

Neutral detergent fibre (NDF)

Browse species differed in NDF content ($F = 44.78$, $P < 0.001$, $df = 11, 84$). Comparisons of NDF content (Table 3.2) among species resembled those of ADF. *Ochna pulchra* had the highest NDF levels, while *C. africana*, *B. albitrunca* and *C. psidioides* had the lowest NDF contents, although the latter two species did not differ significantly from most species.

Acid detergent lignin (ADL)

Ochna pulchra, *G. flava* and *T. sericea* had the highest ADL content, with no significant differences among them ($P > 0.05$). However, *G. flava* and *T. sericea* did not differ significantly ($P > 0.05$) from most of the remaining species (*B. petersiana*, *G. flavescens*, *O. paniculosa*, *C. collinum*, *M. sericea*, *C. africana* and *B. albitrunca*), except for *C. psidioides* and *P. nelsii* (Table 3.2).

Crude protein (CP)

CP content differed among the browse species ($F = 116.6$, $P < 0.001$, $df = 11, 84$). *Philenoptera nelsii* and *B. albitrunca* had the highest crude protein (Table 3.2). However, *B. albitrunca* did not differ significantly from *M. sericea* and *G. flavescens*. Most species overlapped in their CP content in the intermediate ranges of CP content. *Ochna pulchra* and *T. sericea* had the lowest CP, although they did not differ significantly from *C. collinum* and *C. africana*.

Phosphorus

Phosphorus content differed among the browse species ($F = 25.79$, $P < 0.001$, $df = 11, 84$). *Mundulea sericea*, *G. flavescens*, *B. petersiana*, *O. paniculosa*, *C. psidioides* and *P. nelsii* had similar levels of phosphorus ($P > 0.05$) (Table 3.2). *Ochna pulchra* and *T. sericea* were among the species with the lowest phosphorus, although they did not differ significantly from *C. africana*, *G. flava* and *C. collinum*.

Model for diet selection

The saturated model for diet selection was non-significant ($F = 8.77$, $P = 0.1059$, $df = 6, 2$). However,

the final solution was highly significant ($F = 25.43$, $P = 0.0019$, $df = 3,5$), indicating that 93.9% ($R^2 = 0.9385$) of the variation in diet selection could be accounted for by variation in CP, P and ADL. The multiple regression model describing this relationship is:

$$\text{Forage ratio} = 0.522 + 1.55 \times \text{CP} - 1.6 \times \text{P} - 0.60 \times \text{ADL}.$$

DISCUSSION

Browse consumption and composition

Our results demonstrate that under the conditions of low grass availability that prevailed during the study period the cattle consumed more browse than grasses during the hot-dry season. This result confirms pastoralists' impressions that cattle do relatively more browsing than grazing during the hot-dry season in the northern Kalahari. The reduced availability of grass due to continuous grazing in Namibian communal areas (Ward *et al.* 1998), is presumably the main reason why cattle shift to browsing during the hot-dry season (A. Kauta, personal communication, 2001). These results add to the growing literature on the role of woody vegetation in cattle diet in semi-arid and arid environments (Le Houérou 1980, Mangan 1988, Bergström 1992, Woodward and Coppock 1995, Scoones 1995, Moleele 1998, Illius and O'Connor 1999). Browse generally has higher protein content than grasses (Woodward and Coppock 1995, Moleele 1998, Lauchbaugh 2001), but often contains anti-herbivore substances (Kaitho *et al.* 1998, Beck and Reed 2001). In this study, cattle fed on a variety of browse, but with three species, *B. petersiana*, *P. nelsii* and *T. sericea*, accounting for 74.5% of dry matter intake. This is contrary to the observations by local farmers that *T. sericea* was the most consumed species.

Deciduous woody plants produce leaves of high quality during the dry season, particularly at the time of flushing (Papachristou and Nastis 1996, Augustine and McNaughton 1998, Ngwa *et al.* 2000). *Terminalia sericea* was more nutritious during the dry season than during the wet season. It experienced

a 50% and 23.4% decline in P and CP by the middle of the wet season (Katjiua and Ward, unpublished data). In contrast, condensed tannin concentrations increased as the season progressed (Chapter 4). This may be the reason why cattle mainly browsed on *T. sericea* during the hot-dry season after new leaf flush rather than during the wet season (Chapter 6). Furthermore, these results support previous work that leaf phenophase influences browse acceptability (Cooper *et al.* 1988, Owen-Smith 1994).

Browse chemistry and its influence on preference

Browse quality and availability influence the consumption pattern of herbivores (Langvatn and Hanley 1993, Shipley and Spalinger 1995, present study). Principal browse may not necessarily be the most preferred browse because herbivores may expand diet breadth to include less palatable species during periods of food scarcity (Owen-Smith 1993). Our study indicates that the combined high levels of ADF, NDF, ADL and condensed tannins may lower the preference ranking of browse species. Cattle avoided *O. pulchra*, which had consistently high levels of fibre and condensed tannins, while elsewhere in the study area cattle browsed heavily on the evergreen *B. albitrunca* (field observations), which contained low concentrations of fibre (Table 3.2) and condensed tannins (Figure 3.1). Evergreen trees store carbon reserves in their leaves; hence browsing removes carbon reserves which lowers the carbon:nutrient ratio and subsequently improves palatability of evergreens (see review by Stamp 2003). *Boscia albitrunca* had high levels of CP (Table 3.2). This demonstrates why *B. albitrunca* may constitute a key browse species in other arid and semi-arid environments (Owen-Smith 1993, Hendricks *et al.* 2002).

Furthermore, high concentrations of ADF and NDF on their own may not necessarily lead to low preference to herbivores. For example, *Philenoptera nelsii* had high levels of ADF and NDF, yet was most preferred by cattle. However, this species also had the highest CP levels, a high concentration of P, and negligible condensed tannins. These results demonstrate that browse preference is not directly determined by the absolute levels of nutrients and secondary compounds, but more likely by the ratio of nutrients to secondary compounds. This observation is consistent with the results of Cooper *et al.*

(1988).

Cattle browsed on a range of woody species of which the majority was avoided. They browsed much on what was mostly abundant, that is, on *B. petersiana* ($P_i = 24.49$) and *T. sericea* ($P_i = 13.68$), and also on what they preferred, that is, *P. nelsii* ($S_i = 0.54$). This is consistent with Illius *et al.*'s (2002) contention that diet optimisation, involving a trade-off between diet quality and quantity, offers a better explanation of herbivore foraging behaviour than quality or quantity alone. *Philenoptera nelsii* generally had a low abundance on the range (field observation) but relatively greater abundance in the foraging sites ($P_i = 1.94$), indicating that cattle also selected preferred foraging patches. Experience and ability of herbivores to remember patches of preferred browse help the herbivore to minimise energy spent on searching (De Vries and Daleboudt 1994, Edward *et al.* 1994, Illius *et al.* 1999). *Bauhinia petersiana*, *O. pulchra* and *G. flava* had the highest condensed tannin concentrations of all other species. These species were among the species with the lowest ADF and NDF content. They also had high contents of ADL, as well as the highest phosphorus content. However, despite being a poorer species (*B. petersiana*) than *G. flavescens* and *M. sericea* in terms of crude protein content, it was highly consumed. This may be attributed to its high relative abundance and availability during the study period (October). We found that diet selection was best explained by a multiple linear regression model. Thus, the combination of CP, P and ADL in specified proportions determined diet selection. Condensed tannins did not influence diet selection significantly, although condensed tannin is considered to be the most important chemical anti-herbivory substance influencing diet selection (McArthur *et al.* 1993, Aerts *et al.* 1999).

The relationship between browse preference and chemical anti-herbivory traits has not been clearly established (Bergeron and Jodoin 1987, McArthur *et al.* 1993, Illius *et al.* 1999). When forage resources are relatively abundant, large herbivores commonly browse on preferred species when encountered, while less preferred or avoided species are eaten seldom when encountered (Owen-Smith and Cooper 1987b). However, large herbivores expand the range of species consumed when diet quality declines

but in such a manner that both protein and digestible energy are maximised (Owen-Smith and Novellie 1982). When such resources are limited, herbivores spent longer periods browsing and consume bulky forage to compensate for the low diet quality (Owen-Smith 1994). Gradual intake of forages with high phenolic contents allows adaptation of microbial populations in the rumen, and thereby may prevent potential negative effects of phenolics on metabolism (Lowry *et al.* 1996). Furthermore, the effect of condensed tannins on forage digestibility may not necessarily be costly unless gut fill becomes a constraint as a result of ingestion of high fibre forages (Spalinger *et al.* 1986). This may explain why *B. petersiana* with very high condensed-tannin concentration, but low NDF and ADF content, was consumed in large volume.

Dry matter intake and, subsequently, the digestible energy that herbivores obtain from a diet influences their decision in terms of where, what diet and how long to feed on a particular diet item (Shipley and Spalinger 1995, Berteaux *et al.* 1998). Despite the costs involved in searching, recognition and selection of food items in spatially heterogeneous habitats, free-ranging herbivores select food items that maximise energy and nutrient intake (Gross *et al.* 1993, Nyamangara and Ndlovu 1995, Illius *et al.* 1999, Ngwa *et al.* 2000). Also, browsers select plants on the basis of trade-offs between the benefits derived from digestible dry matter as opposed to costs associated with anti-herbivory substances such as the phenolics in the browse (McArthur *et al.* 1993).

Implications for management

This study shows that cattle in the northern Kalahari are not able to obtain preferred high value items during the hot-dry season and need to trade-off dietary quality with quantity. Furthermore, the ratio of nutrient:secondary compounds, combined with availability of browse species appear to strongly influence foraging decisions. Herbivore experience with the various dietary items and their knowledge of the spatial and temporal distributions of preferred dietary items on the rangeland may considerably improve foraging decisions (Owen-Smith and Novellie 1982). Consequently, for optimal browse

management, a high diversity of browse species should be maintained on these arid rangelands to allow cattle the widest range of preferred high value items. Thus, management practices that confine cattle mobility and that minimise rangeland heterogeneity may constrain cattle foraging decisions and limit diet selection.

CONCLUSIONS

1. Cattle under the conditions of low grass availability consumed more browse than grasses during the hot-dry season in the northern Kalahari communal farming rangelands.
2. *Philenoptera nelsii* was the most preferred browse and, together with *Bauhinia petersiana* and *T. sericea*, constituted the principal browse species during the hot-dry season.
3. Browse quality, quantity and availability affected the consumption patterns of cattle. Cattle browsed a variety of woody plants in a manner that indicates that the availability of browse and the ratio of nutrient:secondary compounds were important in foraging decisions.
4. Management practices in the northern Kalahari should aim to maximise rangeland heterogeneity to facilitate broader diet selection by herbivores.

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CHAPTER 4

PHENOTYPICALLY-PLASTIC RESPONSES OF *TERMINALIA SERICEA* TO GRADED
FOLIAR DAMAGE UNDER DIFFERENT SOIL NUTRIENT CONDITIONS IN THE
NORTHERN KALAHARI, NAMIBIA

ABSTRACT

1. We investigated the independent and interactive effects of plant damage and soil nutrients on the growth (tolerance) traits and phytochemistry (resistance traits) of *T. sericea*, a deciduous tree in the Kalahari Desert that constitutes a significant component of cattle diet during the hot-dry season.
2. We established enclosures to determine the effects of cattle browsing and manual defoliation on the growth traits and phytochemistry of *T. sericea*.
3. High browsing pressure and complete defoliation resulted in reduced shoot length, cluster size and leaf size, and an increased number of branches. Fertilizer addition increased shoot length, reduced cluster size and leaf size but had no effect on the number of branches. Complete defoliation induced increased condensed tannin concentrations under natural soil conditions, while fertilizer addition reduced condensed tannin concentrations.
4. In contrast, the levels of condensed tannin in damaged plants with fertilizer addition were the same as the controls. Fiber content of trees on poor soils was high, but was low under improved soil fertility. Furthermore, foliar damage under natural soil conditions resulted in higher fiber contents than undamaged controls, while the levels of crude fiber and fiber fractions in damaged plants with fertilizer addition did not differ significantly from that of controls.
5. Tolerance of and resistance to herbivory have evolved as adaptations to low resource conditions, which constrain growth more than photosynthesis. Thus resistance to herbivory results from nutrient deficiency, while tolerance is manifested in the reallocation of reserves to regrowth upon tissue loss. The magnitude of compensatory responses of tolerance and resistance upon damage reflects the source/sink relationship along a resource gradient.

Key-words: Compensation, mammalian herbivory, resistance, resource availability, tolerance

INTRODUCTION

Mammalian herbivory has a significant impact on browse in climatically-variable environments in African savannas, particularly as a result of limited pre-rain browse available during the hot-dry season (Illius & O'Connor 1999). Resources available to plants determine their defensive strategies against herbivore damage in terms of the constitutive levels of defense and regrowth rate (Coley et al. 1985). Early growing-season herbivore damage is costly to the plant (Augustine & McNaughton 1998), more so in resource-poor environments (Heil et al. 2000; Heil et al. 2002), because it represents an immediate loss of carbon and nutrients, and the opportunity to assimilate more carbon through photosynthesis in future (Pearcy et al. 1987). Consequently, the plant is forced to re-allocate additional energy, carbon, nitrogen and other nutrients from other plant parts to construct new leaves (Scholes & Walker 1993; Augustine & McNaughton 1998). Allocation decisions prior to damage may influence tolerance traits (see reviewed by Stowe et al. 2000). Plants that store relatively a high proportion of resources in the below-ground structures are more tolerant of foliar damage (Hochwender et al. 2000). High below-ground biomass production may enable plants to acquire more nutrients for regrowth and seed production (Chapin & McNaughton 1989). Plants may also allocate resources to resistance traits such as defensive chemicals to deter herbivore attack (Furstenburg & Van Hoven 1994; Strauss & Agrawal 1999). Tolerance of herbivore damage may be expressed as a reduction in leaf size (Massei et al. 2000) and lowered above:below-ground biomass ratio (review by Stowe et al. 2000), which reduces the effect of herbivore damage on plant fitness (Simms 2000).

Selection for resistance and tolerance traits does not occur independently (Abrahamson & Weise 1997; Mauricio 2000). Plants may use both strategies but with varying degree of expression (Van der Meijden et al. 1988). These strategies are influenced by the degree (Young 1987; Rohner & Ward 1997; Ruiz et al. 2002) and frequency of herbivory (Du Toit et al. 1990), timing of herbivore attack (Underwood 1999) and resources available to the plant (Coley et al. 1985; Haukioja et al., 1998; Katjiua & Ward – Chapter 5 in press). Heavy and persistent herbivory imposes resource limitation on the plant (Augustine

& McNaughton 1998), thereby constraining plant growth and photosynthetic capacity (review by Koricheva et al. 1998). Therefore, under these conditions, plants preferentially shunt resources to growth processes over differentiation (Waring and Pitman 1985; Wilkens et al., 1996; see review by Stamp 2003). Consequently, heavy and frequent herbivory may increase the relative concentrations of nutrients versus carbon-based secondary metabolites in plant tissues (Du Toit et al. 1990). Moderate levels of herbivory in intermediate-resource environments may lead to overcompensation of resistance traits (Belsky 1986; Adler & Karban 1994). Some low levels of herbivory may lead to full compensation of resistance traits particularly if resources are abundant in the environment (Ferraro & Oosterheld 2002). Early-season herbivory may lead to elevated defence levels later in the season, and thus reduce herbivore attack (Karbon et al. 1999). Compensatory response describes a plant's reaction norm to herbivore damage (Simms 2000). Overcompensation occurs when the levels of tolerance and/or resistance traits of the treated plants are greater than the levels of tolerance and/or resistance traits of the control plants; full compensation occurs when the levels of tolerance and/or resistance traits of treated plants equal that of the controls; and undercompensation occurs when such levels of tolerance and/or resistance traits of treated plants are lower than that of the controls (Belsky 1986).

PHENOTYPICALLY-PLASTIC RESPONSES OF *T. SERICEA* TO HERBIVORY

The chief objective of this study was to determine the phenotypically-plastic responses of *T. sericea* to livestock herbivory. We chose to study *T. sericea* because it is an important dry-season browse species in the northern Kalahari (Chapter 3). The specific objectives were to investigate the: 1) effects of actual cattle browsing and manual defoliation on the foliage quality of *T. sericea* under field experimentation; and 2) responses of *T. sericea* to fertilization in terms of its growth, and production of condensed tannins, fiber contents and proteins. We predicted that: 1) foliar damage will enhance plant growth; 2) heavy foliage damage (under simulated and natural conditions) will reduce the allocation of resources to carbon-based defensive traits in nutrient-poor environments and therefore improve foliage quality; 3) fertilization will reduce the production of condensed tannins relative to proteins; and 4) *T. sericea* will

have a higher ability for compensatory growth (tolerance) to foliar damage under high-resource conditions than under low-resource conditions.

MATERIALS AND METHODS

GROWTH AND PHYTOCHEMICAL RESPONSES IN ENCLOSURES

We investigated the responses of *T. sericea* to actual cattle browsing and manual defoliation under natural and enriched soil conditions during a hot-dry season at Ombujanjama (21°00.421'S; 19°08.987'E). We established two 900 m² enclosures about 50 m apart in September 2001. The enclosures were covered predominantly by shrubby *T. sericea* with heights ranging from one to two meters. These were naturally grown trees on sandy nutrient-poor soils of the Kalahari. We intended to use a completely-crossed design with four levels of herbivory (control, low, high and complete) and three levels of fertilizer (control, low and high), but results from the two enclosures behaved differently. Subsequently we abandoned this design and treated each enclosure as a separate entity, analyzed accordingly and discuss trends in relation to a complementary nursery experiment (Chapter 5). Two large enclosures were constructed for the two main categories of plant damage, viz 'cattle browsing' and 'manual defoliation'. Each enclosure was subdivided into six smaller plots in which the cattle browsing received two levels of herbivory (low and high) and three levels of fertilizer treatment (control, low, high). Low treatment level consisted of a cow being introduced into a particular plot, while high herbivory constituted three cows. The manual defoliation enclosure received two levels of leaf damage (control, complete defoliation) and three levels of fertilizer treatment (control, low, high). In each subdivision (plot) 15 trees were sampled, which made a total of 90 trees in each enclosure.

We applied the initial plant damage treatments in mid-November 2001 when all trees had flushed. We introduced the low and high browsing treatment levels into the 'cattle browsing' enclosure in the

morning (06h00 – 08h00) and then in the afternoon (16h00-18h30) for three consecutive days in November 2001. On the fourth day all plots were sampled for condensed tannin analysis. For the ‘manual-defoliation’ enclosure, we defoliated three plots completely and analyzed samples for condensed tannin from each tree to represent the general leaf quality in the enclosures prior to the administration of complete defoliation treatment. The same plots were sampled again three weeks later when sufficient foliage had regrown to determine condensed tannin levels in the regrown foliage.

The fertilizer treatment was also applied in mid-November, but this could not have affected leaf quality at the time of the initial sampling three days later, because of the short period after the fertilizer application and the absence of rain had certainly made nutrient absorption impossible. Therefore the response of the plants to actual herbivory early in the growing season, took place under normal soil conditions. This could not be avoided, because if we waited for the rains to fall in order to administer the fertilizer and to wait for at least two weeks before the fertilizer could sufficiently be absorbed. Thus we would have missed assessing any response of *Terminalia sericea* to early-season herbivory. *Terminalia sericea* is usually heavily browsed early in the growing season before the wet season rains, when pasture is of poor quality and in low supply (Chapters 6; Chapter 3 in press).

We supplemented the experimental trees with NPK (2:3:2) to represent 10 g N/m² and 30 g N/m² for the low and high fertilizer treatment-levels. This allowed us to investigate the response of *T. sericea* to herbivory under control, low and high-resource conditions. The manually-defoliated plants slowly regained foliage during December 2001 and January 2002 mainly because the rains were poor and temporally scattered during this period. Total rainfall during December and January was 67 mm and 29 mm respectively. By the beginning of February, all plants had regained full foliage cover. At this time, we re-introduced lactating cows to the low and high herbivory plots for duration of about 16 h 30 min, starting at about 14h00 until 06h30 the following day. The cows were brought back because the initial herbivory may have not interacted with fertilizer application. Observation of plots after 16 h 30 min of herbivory showed that the plots with three cows were heavily browsed (particularly plots 3 and 4,

followed by plot-1. Among the low herbivory plots, plot-2 was the least browsed, followed by plots 6 and 5. After this assessment, leaf samples were collected. The defoliation plots were not pruned for the second time, but a handful of leaves was collected from both the experimental and control trees to determine the response of condensed tannin over the growing season upon previous leaf damage. Leaf samples were collected three times throughout the experiment (Table 4.1), i.e. the first set was collected in November prior to treatment applications. The second set represents the first post-treatment sampling which took place after three days of browsing for the 'cattle enclosure' and three weeks on the new regrowth from the 'defoliation enclosure'. The third set was collected after two months (February 2002) of regrowth.

Leaves for condensed tannin analysis were hand plucked from all around the trees within the browsing heights. Samples were placed in paper bags in the early morning hours to reduce variability in leaf chemistry due to diurnal rhythms and wilting (Furstenburg & Van Hoven 1994).

Table 4.1. Collection of leaf samples from the browsing and defoliation enclosures from a month after flushing (November 2001) to 3.5 months (14-15 February 2002) into the growing season.

	Browsing enclosure	Defoliation enclosure
Pre-treatment sampling	-	45 samples from treatment plots (3), 15 – 17 Nov. 2001
Post-treatment sampling: 1	After 3 days of browsing (4.5 h daily), 10 Dec. 2001	On 3 week-old regrowth, 8 – 10 Dec. 2001
Post-treatment sampling: 2	After 16 h 30 min of continues exposure to herbivores, 12 Feb. 2002	On 2 month-old regrowth, 10-12 Feb. 2002.

Samples were put in a cool box to keep them cool, but not frozen, for less than 4 h before drying them in an air-draft oven at 65 °C for 48 h. Growth traits (shoot length, leaf cluster size and number of branches) were recorded in February 2002 before leaves were collected for chemical analysis (described below). We collected regrown leaves and control-defoliated leaves of plants on the 'defoliation enclosure' to determine leaf size index. This would allow assessing the impact of high leaf damage on leaf size.

MEASUREMENT OF GROWTH TRAITS

Plant growth was measured in February 2002 when leaf growth had reached maturity. We took measurements from the apical shoot and from two randomly selected branches in the middle and lower ranges of the canopy. All measurements were recorded within a pre-set 50 cm length of branches to their apices. We measured the shoot length of current season growth from the base of the shoot to the apex. The total number of branches was counted systematically from a distance of 50 cm to the apices of the three branches. The leaves of *T. sericea* are produced in clusters. We recorded the number of leaves in nine clusters along the three branches from their apices. Pre-mature leaves were excluded if their blades were still rolled up. Leaf size index was expressed as leaf weight (g) which would be directly proportional to leaf area, obtained after photocopying leaves, cutting and weighing each 'leaf'.

ANALYTICAL PROCEDURES FOR SAMPLE ANALYSES

Samples were ground to pass through a 1 mm sieve in a micro-mill and analyzed for crude fiber (CF), acid detergent fiber (ADF), neutral detergent fiber (NDF), acid detergent lignin (ADL) and crude protein (CP). Acid detergent fiber, NDF and ADL were determined using the detergent method (Goering and Van Soest 1970). Crude protein and CF were analyzed according to the AOAC methods (AOAC 1984). Samples for condensed tannin analysis were further sieved through a 0.4 mm sieve. Condensed tannin in leaf samples was measured using a standard acid-butanol protocol (Waterman and

Mole 1994). The proanthocyanidin method with modification by Hagerman (1995) was applied to measure condensed tannin extracted with methanol. Two replicates were prepared and read by the spectrophotometer. Condensed tannin concentrations are expressed in quebracho equivalents (quebracho is used as a standard – Hagerman and Butler 1982). Quebracho used in the standard was obtained from A. Hagerman (Miami University, Oxford, Ohio, USA).

STATISTICAL ANALYSES

Analysis of cattle browsing and manual defoliation enclosures were split because the two enclosures differed greatly in the manner they affected the results. As a result of this split, the cattle enclosure remained with three low and high browsing plots. The defoliation enclosure had three completely defoliated plots and control defoliation plots. Analyses proceeded as follow:

Growth responses were analyzed in a three-way factorial ANOVA with fertilizer, shoot position and browsing as treatment factors in the case of the cattle enclosure. In contrast, defoliation was used as the plant damage treatment instead of browsing for the defoliation enclosure. These analyses were performed on log-transformed data of shoot length, number of branches and leaf cluster size. Additionally leaf size was analyzed for completely defoliated trees versus their controls across the fertilizer treatment.

Condensed tannin was analyzed in a two-way factorial ANOVA on arcsine transformed data with fertilizer and browsing as treatment effects for the cattle enclosure, while defoliation treatment was substituted for browsing treatment in the defoliation enclosure. Sampling for condensed tannin analyses did not take shoot position into account. Furthermore, the levels of condensed tannin were recorded over the growing season on the defoliation enclosure, and analyzed in a repeated measure ANOVA with fertilizer as a fixed factor and period as the repeated factor, using log transformed data.

Crude fiber, fiber fractions and crude protein in both cattle and defoliation enclosures were analyzed in a two-factorial ANOVA with fertilizer and browsing as the main effects for the cattle enclosure, but with defoliation treatment instead for browsing for the defoliation enclosure. Data were transformed where necessary to achieve a normal distribution. Where appropriate, analyses were followed by a multiple comparisons of means using a Scheffe *post hoc* test. Means are represented \pm 1 standard error, unless otherwise stated.

RESULTS

GROWTH RESPONSES TO CATTLE BROWSING AND FERTILIZATION

Shoot length. The vertical distribution of shoots in the tree canopy influenced shoot elongation ($df = 2,252, F = 9.63, P < 0.0001$), shown by the analysis of log-transformed data. The apical shoots had the highest mean growth 20.34 ± 0.476 cm, followed by shoots in the middle ranges of the canopy (18.42 ± 0.522 cm) then shoots in the lower part of the canopy (17.10 ± 0.601 cm). The interaction effect of browsing and shoot spatial distribution was also significant ($df = 2,252, F = 3.17, P = 0.0438$). High cattle browsing greatly reduced apical shoot growth such that no differences existed in shoot length across the canopy heights. The apical shoots were significantly longer than shoots in the lower part of the canopy exposed to low browsing pressure ($P < 0.05$). Fertilizer addition did not affect shoot elongation ($P = 0.6808$).

Number of branches. Fertilizer addition affected branch production significantly ($df = 2,252, F = 4.57; P = 0.0113$), shown by the analysis of log-transformed data. High levels of fertilizer addition significantly increased the production of branches when compared to control fertilizer treatment level (Scheffe *post hoc* test, $P < 0.05$). The effect of low fertilizer addition was moderate as it did not differ from either the control or high treatment levels ($P > 0.05$). Fertilizer addition interacted with cattle

browsing ($df=2,252$, $F=9.38$, $P=0.0001$). High browsing pressure increased the number of branches significantly compared to low browsing pressure under control fertilizer treatment ($P < 0.05$). In contrast, low browsing pressure increased the number of branches significantly under high fertilizer treatment ($P < 0.05$) (Table 4.2). The vertical distribution of shoots in the tree canopy affected the number of branches for a given shoot length ($df=2,252$; $F=5.18$, $P=0.0063$). Shoots in the lower part of the canopy produced fewer branches (1.400 ± 0.0157). These did not differ from branches (1.428 ± 0.0145) produced in the middle ranges of the canopy ($P > 0.5$), but differed significantly from the apical branch (1.474 ± 0.0210), $P < 0.05$). Apical shoots produced more branches, but not significantly different from those in the middle ranges ($P > 0.05$).

Leaf cluster size. Cattle browsing affected leaf cluster size significantly ($df=1,2412$, $F=41.10$, $P < 0.0001$), shown by the analysis of log-transformed data. Mean cluster size under high browsing (0.985 ± 0.0031) was 2.84 % less than under low browsing pressure (1.013 ± 0.0033). Fertilizer addition also affected cluster size significantly ($df=2,2412$, $F=55.6$, $P < 0.0001$). Both the low and high levels of fertilizer treatment reduced cluster size significantly ($P < 0.05$), and to a similar extent. Thus no significant differences existed between the effects of low and high fertilizer treatment levels ($P > 0.05$), but only with respect to the control fertilizer treatment level (Fig. 4.1). The interaction of browsing x fertilizer was significant ($df=2,2412$, $F=3.9$, $P < 0.05$). Fertilizer addition under low browsing pressure reduced cluster size significantly ($P < 0.05$).

Table 4.2. Interaction effect of cattle browsing and fertilizer treatments on the number of branches.

Letters indicate 5% significant differences between treatment levels. Data were log-transformed.

Browsing treatment	Fertilizer treatment		
	Control	Low	High
Low	1.360±0.0195 a	1.429±0.0213 a	1.528±0.0266 b
High	1.455±0.0262 c	1.412±0.0238 ac	1.421±0.0249 ac

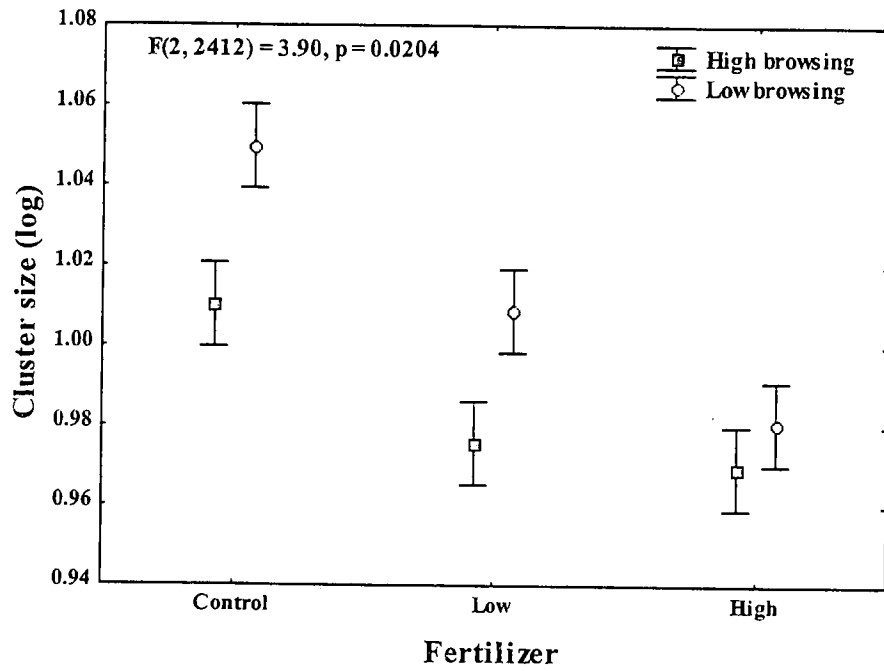


Fig. 4.1. Interaction effect of cattle browsing and fertilizer treatments on the number of leaves per leaf cluster. Error bars denote 95% confidence limits.

GROWTH RESPONSES TO MANUAL DEFOLIATION AND FERTILIZATION

Shoot length. Complete defoliation reduced shoot length significantly ($df = 1,252$, $F = 11.05$, $P = 0.001$). Mean shoot length was 436.9 ± 17.86 cm under complete defoliation and 513.4 ± 17.40 cm on the control trees. Fertilizer addition increased shoot length significantly ($df = 2,252$, $F = 13.23$, $P < 0.0001$). Shoots grew with 35.5% and 18.1% longer under the high and low fertilizer treatment levels than under control fertilizer treatment level. The interaction effect of defoliation x fertilizer was significant ($df = 2,252$, $F = 6.33$, $P = 0.00208$) (Table 4.3). Fertilizer did not affect shoot length of control defoliation trees ($P > 0.05$), but high fertilizer resulted in full compensatory response following complete defoliation. Shoot length undercompensated significantly under low fertilizer addition ($P < 0.05$). The spatial distribution of shoots affected shoot elongation ($df = 2,252$, $F = 8.18$, $P = 0.0004$). Apical shoots grew longer than shoots lower in the canopy ($P < 0.05$).

Number of branches. Complete defoliation affected the number of branches significantly ($F = 4.18$; d.f. = 1,252; $P = 0.0419$), shown by the analysis of log-transformed data. Mean number of branches was 1.66 ± 0.016 under complete defoliation and 1.61 ± 0.014 on the control trees. Fertilizer addition did not affect the number of branches ($P = 0.4787$). The spatial distribution of shoots in the canopy affected the number of branches ($df = 2,252$, $F = 3.42$, $P = 0.03416$). Apical shoots had more branches than shoots lower in the canopy ($P < 0.05$). The mean number of branches of the apical shoots was 1.67 ± 0.020 , and was significantly higher than those in the middle (1.63 ± 0.017) and lower part (1.60 ± 0.017) of the canopy. No differences existed in the number of branches between the middle and lower shoots in the canopy ($P > 0.05$).

Table 4.3. Interaction effect of complete defoliation and fertilizer treatments on the shoot length (cm).

Letters indicate 5% significant differences between treatment levels.

Defoliation treatment	Fertilizer treatment		
	Control	Low	High
Control	472.0±32.23 a	503.1±27.24 a	565.1±29.72 a
Complete	461.6±28.91 a	311.1±29.29 b	537.8±2483 a

Leaf cluster size. Complete defoliation significantly affected leaf cluster size ($df = 1, 2398, F = 106.2, P < 0.0001$), shown by the analysis of log-transformed data. Mean cluster size under complete defoliation (0.98 ± 0.003) was 4.17 % less than under control defoliation treatment (1.019 ± 0.003). Fertilizer treatment also significantly reduced cluster size ($df = 2, 2398, F = 3.7, P = 0.0246$). The defoliation x fertilizer interaction was significant ($df = 2, 2398, F = 13.4, P < 0.0001$). Low and high levels of fertilizer significantly reduced cluster size of control defoliation trees ($P < 0.05$) (Fig. 4.2), however the mean cluster size between the low and high fertilizer treatment levels did not differ ($P > 0.05$). High fertilizer treatment level increased cluster size significantly in comparison with the control and low fertilizer treatment levels ($P < 0.05$) when trees were exposed to complete defoliation (Fig. 4.2).

Leaf size index. The individual effects of defoliation and fertilizer treatments on leaf size were significant ($df = 1, 2860, F = 6.65, P = 0.0099$; $df = 2, 2860, F = 32.16, P < 0.0001$), shown by the analysis of Johnson (g) transformation. The interaction effect of defoliation and fertilizer on leaf size was also significant ($df = 2, 2860, F = 14.54, P < 0.0001$). Completely defoliated trees fully compensated for leaf size when growing under natural soil condition (Fig. 4.3). Furthermore, leaf size did not differ between control and completely defoliated trees when exposed to the high fertilizer treatment ($P > 0.05$). The low fertilizer treatment did not reduce the leaf size of control defoliation trees (Fig. 4.3).

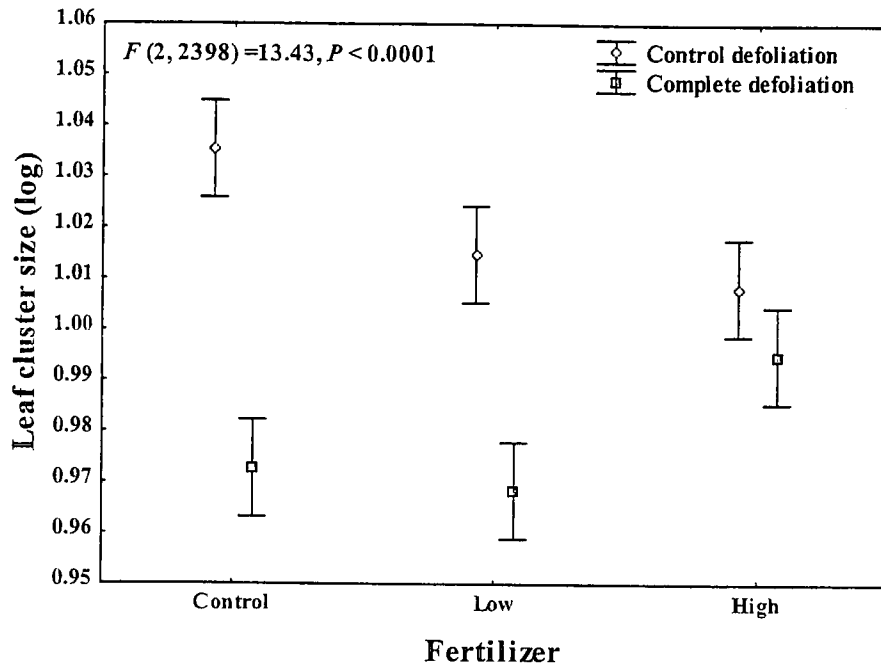


Fig. 4.2. Interaction effect of complete defoliation and fertilizer treatments on leaf cluster size. Error bars denote 95% confidence limits.

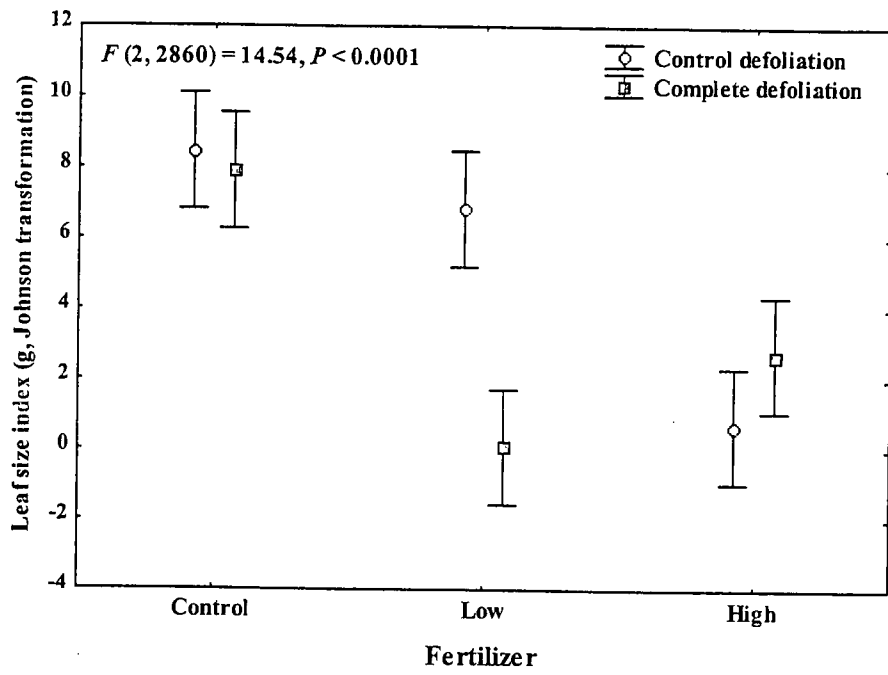


Fig. 4.3. Interaction effect of defoliation and fertilizer treatments on leaf size. Error bars denote 95 % confidence limits.

PHYTOCHEMICAL RESPONSE TO DAMAGE AND FERTILIZATION

Condensed tannin in the cattle enclosure

We tested the response of condensed tannin to cattle browsing under natural and improved soil conditions. Low and high cattle browsing did not have a differential effect on condensed tannin concentration ($df = 1,84, F = 1.63, P = 0.205$), shown by the analysis of arcsine transformed data. The individual effect of fertilizer treatment was significant ($df = 2,84, F = 5.93, P = 0.0039$). The production of condensed tannin was negatively affected by the low fertilizer treatment level ($P < 0.05$). The interaction effect of cattle browsing x fertilizer treatments was significant ($df = 2,84, F = 5.16, P = 0.0077$). Low and high fertilizer treatment levels reduced the production of condensed tannins by 64.1 % and 61.4 % respectively under conditions of low cattle browsing, but had no effect under high cattle browsing (Fig. 4.4).

Condensed tannin in the manual-defoliation enclosure

The effect of defoliation on condensed tannin was non-significant ($df = 1,84, F = 0.66, P = 0.4172$), although defoliation interacted significantly with the fertilizer treatment ($df = 2,84, F = 15.75, P < 0.0001$) – analyzed on arcsine transformed data. Complete defoliation caused overcompensation of condensed tannin concentrations under control fertilizer (Fig. 4.5). Fertilizer addition reduced the production of condensed tannin in previously defoliated trees ($P < 0.05$), but did not significantly affect the concentrations of condensed tannins under control defoliation treatment level ($P > 0.05$).

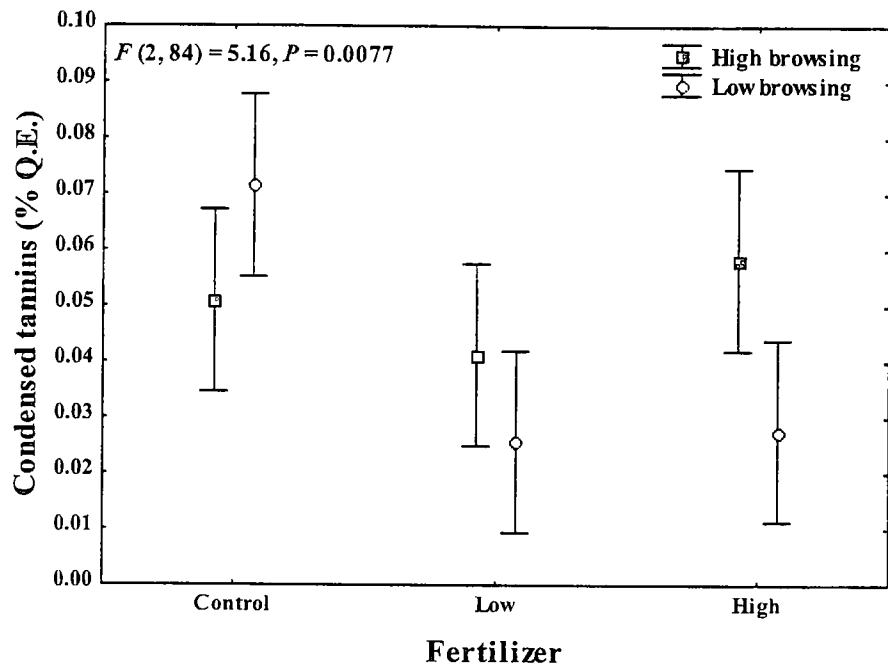


Fig. 4.4. Interaction effect of browsing and fertilizer on condensed tannin. Error bars denote 95 % confidence limits.

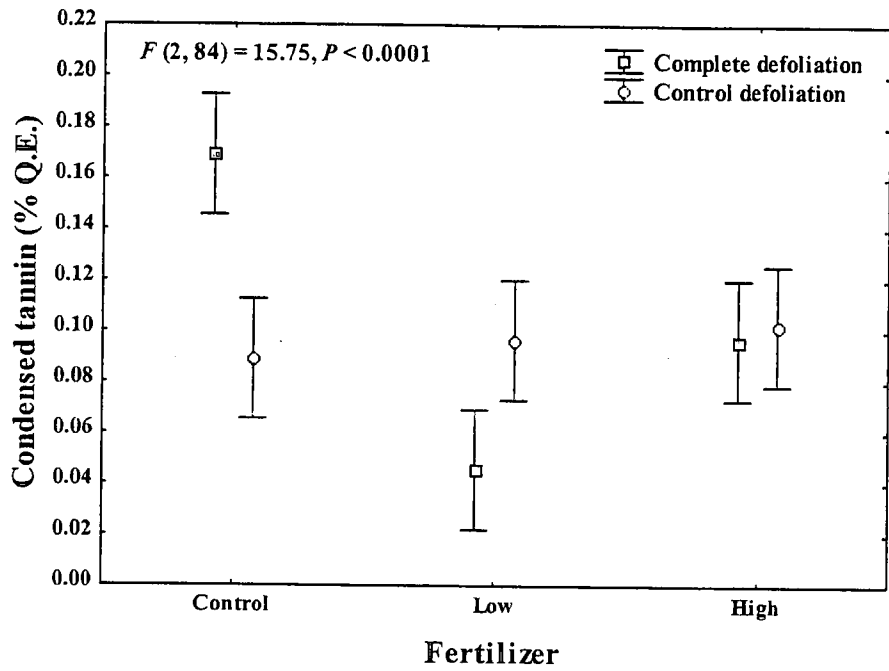


Fig. 4.5. Interaction effect of defoliation and fertilizer on condensed tannin. Error bars denote 95 % confidence limits.

Condensed tannin concentration over the growing season

The results of repeated measures analysis of variance showed that the main effects of fertilizer ($df = 2, 42, F = 28.12, P < 0.0001$) and period of sampling ($df = 4, 84, F = 142.14, P < 0.0001$), as well as their interaction effect ($df = 4, 84, F = 21,35, P < 0.0001$) affected condensed tannin concentrations of previously completely-defoliated trees significantly. This was demonstrated by the analysis of arcsine transformed data. Among the defoliated trees, only those administered with high levels of fertilizer showed a significant decline in the concentrations of condensed tannin from a mean pre-defoliation concentration of 0.046 ± 0.006 % Q.E. to 0.011 ± 0.002 % Q.E. three weeks after defoliation ($P < 0.05$) (Fig. 4.6). Thereafter, condensed tannin concentrations increased significantly ($P < 0.05$) as the season progressed. As discussed above (also Fig. 4.5), tannin concentrations of previously completely-defoliated under high fertilizer treatment did not differ from that of the control defoliation trees by the middle of the growing season (February).

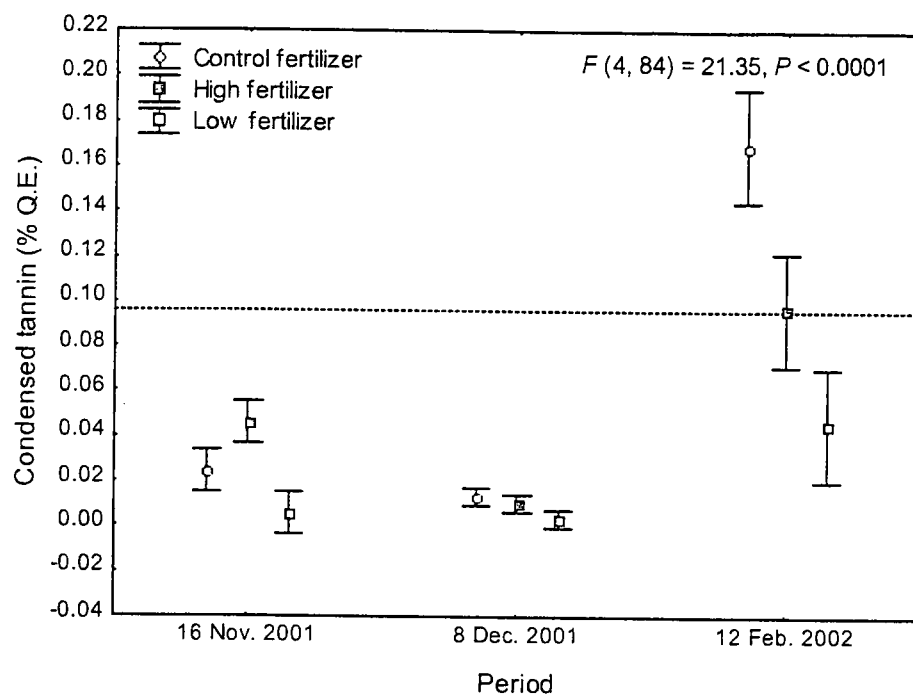


Fig. 4.6. Interaction effect of period and fertilizer on the production of condensed tannins in previously complete-defoliated trees. The dotted line represent the concentration of condensed tannin in the non-defoliated trees during mid-growing season. The error bars show the 95% confidence intervals.

CRUDE FIBER, FIBER FRACTIONS AND CRUDE PROTEIN IN CATTLE ENCLOSURES

Crude fiber: Fertilizer addition reduced the crude fiber content of browsed trees significantly ($df = 1,83$, $F = 5.14$, $P = 0.0078$), but no significant differences existed between the low and high fertilizer treatment levels ($P > 0.05$). Thus, trees exposed to the control-fertilizer treatment level had significantly higher content of crude fiber than those treated with fertilizer ($P < 0.05$). No significant differences existed in crude fiber content between the effects of low and high cattle browsing ($P = 0.6964$), but browsing interacted significantly with fertilizer treatment ($df = 2,83$, $F = 5.14$, $P = 0.0192$). High fertilizer addition reduced crude fiber when trees were heavily browsed (Table 4.4).

Acid detergent fiber: Fertilizer addition reduced ADF content of browsed trees significantly ($df = 2,83$, $F = 7.31$, $P = 0.001$). No significant differences existed between the effect of low and high fertilizer treatment levels ($P > 0.05$). Low and high cattle browsing did not have a differential effect on ADF content ($P = 0.313$). The interaction effect of browsing x fertilizer was significant ($df = 2,83$, $F = 15.34$, $P < 0.0001$). High browsing increased ADF production under natural soil conditions, but the addition of fertilizer moderated the effects of high browsing, resulting in no differential effect when compared to low browsing pressure (Table 4.4).

Neutral detergent fiber: Fertilizer addition reduced NDF content of browsed trees significantly ($df = 2,83$, $F = 10.80$, $P < 0.0001$). The low and high fertilizer treatment levels reduced NDF content to a similar level ($P > 0.05$). No significant differences existed in NDF content between the effects of low and high cattle browsing ($P = 0.121$), but browsing interacted significantly with fertilizer treatment ($df = 2,83$, $F = 3.30$, $P = 0.042$). Thus the effect of browsing was influenced by the level of fertilizer enrichment. Browsed trees growing under natural soil conditions had generally higher NDF content than those on fertilized soils ($P < 0.05$) (Table 4.4).

Table 4.4. Interaction effect of browsing and fertilizer treatments on crude fiber (CF, %), acid detergent fiber (ADF, %), neutral detergent fiber (NDF, %) and acid detergent lignin (ADL, %). Letters indicate significant difference between treatment effects across each fiber constituent.

	Browsing treatment	Fertilizer treatment		
		Control	Low	High
CF	Low	16.51±0.189 ab	15.82±0.257 ab	16.70±0.168 ab
	High	16.83±0.283 a	16.09±0.232 ab	15.89±0.171 b
ADF	Low	31.86±0.409 a	32.60±0.737 a	32.92±0.520 a
	High	35.93±0.568 b	31.03±0.429 a	31.81±0.623 a
NDF	Low	47.12±0.683 ab	45.35±0.939 b	44.45±0.724 b
	High	49.09±0.781 a	44.08±0.519 b	46.65±0.810 ab
ADL	Low	15.36±0.420 ab	15.41±0.486 ab	16.74±0.459 ab
	High	16.74±0.459 a	13.62±0.382 b	15.14±0.456 ab

Acid detergent lignin: Fertilizer addition affected ADL content of browsed trees significantly ($df = 2,83$, $F = 5.62$, $P = 0.005$). ADL declined significantly under low fertilizer treatment ($P < 0.05$), while the effect of high fertilizer addition was moderate. No significant differences existed in ADL content between the effects of low and high cattle browsing ($P = 0.665$), but browsing interacted significantly with fertilizer treatment ($df = 2,83$, $F = 5.96$, $P = 0.004$). The effect of fertilizer was contingent on the degree of browsing. Fertilizer addition only had a significant effect on ADL when browsing was high (Table 4.4). High cattle browsing increased ADL content under natural soil condition, but reduced ADL content under low fertilizer treatment when compared to the effect of low browsing.

Crude Protein: The effect of cattle browsing on crude protein was influenced by soil fertility. This was demonstrated by the significant interaction effect of browsing x fertilizer on crude protein ($df = 2,84$, $F = 16.00$, $P < 0.0001$). Crude protein increased following high browsing under natural soil conditions, and remained at this elevated level across the soil fertility gradient (Fig. 4.7). The highest crude protein content was produced following low browsing pressure under enriched soil fertility.

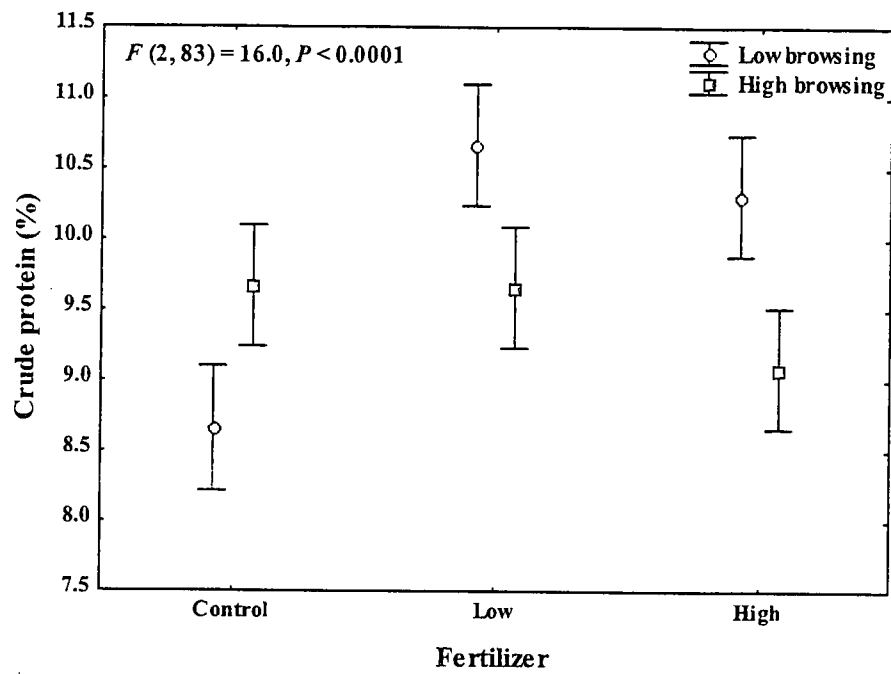


Fig. 4.7. Interaction effect of browsing and fertilizer treatments on crude protein. Error bars denote 95% confidence limits.

CRUDE FIBER, FIBER FRACTIONS AND CRUDE PROTEIN IN MANUAL-DEFOLIATION ENCLOSURES

Crude fiber: The main effects of defoliation and fertilizer on crude fiber were significant ($P < 0.05$), as well as their interaction effect ($df = 2,84$, $F = 3.50$, $P = 0.0348$). Complete defoliation increased crude fiber in the control fertilizer treatment, while fertilizer addition maintained crude fiber at the levels of control-defoliation treatment. Thus fertilizer addition negated the effect of defoliation or promoted full compensation of crude fiber content (Table 4.5).

Acid detergent fiber: The main effects of defoliation and fertilizer on ADF were non-significant ($P > 0.05$), but their interaction effect was significant ($df = 2,84$, $F = 8.6$, $P = 0.0004$). Trees fully compensated for ADF content under control and high fertilizer addition following complete defoliation (Table 4.5).

Acid detergent lignin: The main effects of defoliation and fertilizer on ADL were significant ($P < 0.05$), as well as their interaction effect ($df = 2,84$, $F = 8.96$, $P = 0.0003$). Acid detergent lignin content of previously completely-defoliated trees did not respond to fertilizer addition, but ADL content of control defoliation trees was elevated when treated with low fertilizer (Table 4.5).

Neutral detergent fiber: Defoliation did not affect NDF significantly ($P = 0.10998$), but the effect of fertilizer treatment was significant ($df = 2,84$, $F = 5.6$, $P = 0.0053$). Low fertilizer addition increased NDF significantly by 2.3 % ($P < 0.05$), while high fertilizer addition resulted in full compensation of NDF content (6.63 ± 0.032 %), and did not differ from that under low fertilizer treatment (6.73 ± 0.030 %).

Table 4.5. Interaction effect of defoliation and fertilizer treatments on crude fiber (CF, %), acid detergent fiber (ADF, log %) and acid detergent lignin (ADL, sqrt %). Letters indicate significant difference between treatment effects across each fiber constituent.

	Defoliation treatment	Fertilizer treatment		
		Control	Low	High
CF	Control	17.61±0.191 b	17.40±0.275 b	17.51±0.235 b
	Complete	18.76±0.225 a	17.26±0.290 b	17.92±0.244 ab
ADF	Control	1.53±0.009 ab	1.55±0.008 a	1.53±0.006 ab
	Complete	1.55±0.015 a	1.51±0.005 b	1.54±0.006 ab
ADL	Control	3.83±0.064 b	4.15±0.078 a	3.81±0.043 b
	Complete	3.82±0.056 b	3.79±0.040 b	3.90±0.049 ab

Crude protein: Defoliation did not affect crude protein content significantly ($P = 0.4751$), but fertilizer addition increased crude protein content significantly ($df = 2,84$, $F = 14.28$, $P < 0.0001$). Both the low and high fertilizer enrichment levels had similar effects on crude protein, that is 3.22 ± 0.017 and 3.18 ± 0.015 %, respectively, compared to 3.07 ± 0.029 %, for the control fertilizer treatment.

DISCUSSION

This study supports the Resource Availability Hypothesis (Coley et al. 1985), i.e. as the maximal growth rate increases along an increasing resource gradient, the constitutive level of defence decreases (Coley et al. 1985). However, it does not support the assumption that high constitutive defence levels are maintained in low resource environments to prevent tissue loss from herbivory (Strauss & Agrawal 1999), but rather that the high levels of constitutive defences are a direct consequence of constrained growth. The strategy of plants in the low resource environments to deter rather than to tolerate herbivores (Strauss & Agrawal 1999) is also not supported by this study because tolerance and resistance traits occurred concurrently in *T. sericea*. This is consistent with the findings that selection for these traits does not occur independently (Abrahamson & Weise 1997; Tiffin & Rausher 1999). We found that the degree to which tolerance and resistance traits were expressed in *T. sericea* was resource-dependent, consistently with Van der Meijden et al. (1988) and Mauricio (2000). In another study, Katjiua and Ward (Chapter 5 in press) showed that *T. sericea* often allocated more investments to tolerance and resistance traits under low resource conditions than under high resource conditions.

Improved resource availability can increase sink strength as actively-growing meristems are strong photosynthetic sinks (review by Herms & Mattson 1992). Strong meristematic activity requires copious supplies of water and nutrients for cell division and expansion (review by Herms & Mattson 1992). Once growth is optimized, sink strength declines and some allocations of photosynthetic products seem to be directed to secondary metabolism and storage in uncorrelated proportions. Allocations to resistance and tolerance traits in *T. sericea* were largely uncorrelated under high resource conditions (Katjiua & Ward - Chapter 5 in press).

It appears that along an increasing resource gradient, tolerant plants have to adjust allocation patterns, from overcompensating growth traits, through full compensation to undercompensating growth traits in high resource environments. Thus, it may be true that at some increasing level of resource availability,

tolerant plants will switch from compensating for damage to growing faster (Hochwender et al. 2000). Fast-growing plants in high resource environments have insufficient prior investments for tolerance and thus undercompensate for damage (Hochwender et al. 2000). Investment in underground structures provides plants with the ability to compensate for above-ground tissue loss by reallocating reserves to replace the lost tissues (Strauss & Agrawal 1999; Hochwender et al. 2000). The results of this study suggest that compensatory responses of tolerance and resistance traits upon damage result from the high accumulation of photosynthates in excess of constrained growth requirement under low resource conditions. Thus, compensatory ability reflects the degree to which growth in the low resource environments is constrained and, subsequently, the amount of photosynthates shunted into storage and secondary metabolites. Furthermore, compensatory ability reveals the adaptability of plants to environmental stress in their struggle to maintain fitness, and is thus not a reflection of how herbivory benefits plants, as was previously suggested for grasses (see review by Belsky 1986).

GROWTH RESPONSES

Shoot length. High cattle browsing and complete manual defoliation reduced shoot length. Cattle in the enclosures had a greater negative effect on the apical shoot than complete defoliation. This may be because cattle browsing damaged shoots, whereas complete defoliation removed leaves only.

Number of branches. Complete defoliation increased the number of branches significantly (2.69 % more than control trees). High cattle browsing increased the number of branches, but only when compared to low browsing under low nutrient conditions. In contrast, low browsing pressure increased the number of branches under high soil nutrients compared to those produced under high browsing pressure. The removal of apical dominance increases the development of additional branches (Rost et al. 1984). The greater number of branches following herbivore damage may result in higher overall leaf production, even if damage reduced leaf and cluster size in the low resource environment.

Cluster size. This study showed that leaf production is resource dependent. *Terminalia sericea* produced more leaves per cluster under poor soil condition. This may be so to maximize the conversion of limited resources into photosynthates. In contrast, fewer leaves were produced with soil nutrient improvement. This suggests that the reduced number of leaves were efficient enough to convert the high soil nutrients into photosynthates. Heavy browsing and complete defoliation reduced cluster size, but improved soil nutrient status negated the negative effects of complete defoliation and high browsing pressure on cluster size.

Leaf size index. Our results showed that not only is leaf production dependent on available resources and herbivore damage, but so is leaf size. Leaf damage under natural soil conditions had no effect on leaf size. Plants in low resource environments have a greater capacity to compensate for damage (review by Stowe et al. 2000). However, complete defoliation reduced leaf size under low fertilizer addition, whereas the low fertilizer addition itself had no effect on leaf size. In contrast, high fertilizer addition and complete defoliation reduced leaf size equally.

PHYTOCHEMICAL RESPONSE TO LEAF DAMAGE AND FERTILIZER

Condensed tannin response to cattle browsing. *Terminalia sericea* constitute a key cattle diet in the Kalahari early in the growing season (Chapter 3 in press). While early-season browsing may induce defences, we found no evidence for increased defences as a result of cattle herbivory across a soil nutrient gradient. Karban et al. (1999) postulated that early-season browsing will only induce defences if it is a good predictor of future herbivory. In contrast, completely-defoliated trees growing under natural soil conditions induced increased defences despite late season browsing being rare in this species (Chapter 6). Our results showed that the concentration of condensed tannins increases as the season progresses, and this may minimise herbivore attack or the effect of herbivore damage. Katjiua and Ward (Chapter 6) reported that cattle, the most abundant herbivore in the current study area, do not browse on *T. sericea* later in the growing season. Insect outbreaks were rare and did not occur during

the three years of this study.

The addition of fertilizer reduces the production of condensed tannins in a variety of plant species (Mutikainen et al. 2000; Kouki & Manetas 2002). In a seedling experiment, Katjiua and Ward (Chapter 5 in press) found reduced foliar condensed tannin concentrations in *T. sericea* seedlings, but increased growth of the seedlings when fertilizer was supplemented. Condensed tannin and protein synthesis (growth) are produced in the same shikimic acid pathway in which they share a common precursor, phenylalanine (Haukioja et al. 1998). Therefore, a strong biochemical basis for a trade-off between the synthesis of phenolics and proteins is expected (Muzika & Pregitzer 1992). In this study, fertilizer addition reduced condensed tannin concentrations of lightly browsed trees, but had no effect on the condensed tannin of heavily-browsed trees (Fig. 4.4). This suggests that heavy herbivore damage on *T. sericea* counteracted the negative effect of fertilizer on condensed tannin production, resulting in full compensation of condensed tannin. This is consistent with the response of condensed tannin to complete defoliation under high fertilizer supplementation (see below).

Condensed tannin response to manual defoliation. Repeated early-season defoliation can remove the energy that has just been translocated from roots to leaves. The roots would have to use whatever reserve available to issue new leaves (Larcher 1995). Thus, repeated defoliation depletes the plants' energy reserves (Du Toit et al. 1990; Augustine & McNaughton 1998). Our results showed that repeated early-season defoliation induces foliar condensed tannin by 89.9% in nutrient-poor environments. This is because limited soil nutrients and / or depleted internal plant reserves may constrain growth more than photosynthesis and, as a result, photosynthates in excess of plant growth requirements are shunted into carbon-based secondary compounds such as lignin and condensed tannin (review by Herms & Mattson 1992).

Our results also showed that when moderate fertilizer was supplemented to completely defoliated trees, trees produced lower concentrations of condensed tannins than those treated with control defoliation

and control fertilizer treatment levels. This suggests that moderate fertilizer may have increased the propensity of plants to grow to the extent that photosynthetic capacity became limiting, and, hence, limited photosynthates were invested in condensed tannin. High fertilizer supplementation to the completely-defoliated trees resulted in full compensation of condensed tannin (Fig. 4.5). We postulate that high fertilizer accelerates demand for growth to the extent that growth reaches an asymptote and this would allow photosynthetic biomass to expand and to match growth requirement. When photosynthetic rate matches growth requirements, *T. sericea* invest in constitutive defence-levels while maintaining a healthy growth. Consistent with this postulate, completely-defoliated *T. sericea* fully compensated for condensed tannin production under the high fertilizer treatment level.

The control defoliation treatment yielded trees with equivalent concentrations of condensed tannin across different levels of fertilizer treatment (Fig. 4.5). This demonstrated that even if the short-term response of *T. sericea* to fertilizer enrichment is to reduce the production of condensed tannin, condensed tannin concentration increases as the season progresses and reaches the level of controls possibly only if the trees remain excluded from defoliation during the late growth season. If damage to the plant is withdrawn during the growing season, the plant will engage itself in a process to normalize its internal chemical balance to the level of controls (Larcher 1995; Underwood 1999).

Our results suggest that the effects of fertilizer and defoliation on condensed tannin are complex and dependent on the temporal scale. Foliar damage under natural soil conditions promoted overcompensation while fertilizer addition reduced condensed tannin concentrations. However, the interaction effect of foliar damage and fertilizer treatments promoted full compensation.

Crude fiber, fiber fractions and crude protein responses to browsing and manual defoliation. Our results showed that resource allocation to phytochemical substances and (perhaps) the ability of *T. sericea* to restore its internal resource balance over the growing season, is influenced by the interactive effects of soil fertility and (the degree of) plant damage.

Terminalia sericea overcompensated for crude fiber content under natural soil nutrient condition when damaged, but fully compensated for crude fiber content when soil fertility was improved. High cattle browsing, in particular, also increased ADF content of trees growing under natural soil fertility (Table 4.4), but trees maintained ADF contents similar to that of low browsing pressure when fertilizer was added. Thus fertilizer ameliorated the effects of high browsing on ADF content. Similarly, high fertilizer addition resulted in full compensation of ADF content following complete defoliation (Table 4.5). We found no plausible reason why low-fertilizer addition increased ADL contents of control-defoliated trees. Our results revealed that fertilizer addition had no significant effects on fiber (ADF and ADL) content when trees were lightly browsed, but that it ameliorated the effects of high browsing on fiber (ADF and ADL) contents.

Browsing improved crude protein content. Similar results of elevated nutritional value of plants following high levels of herbivory were reported in the current study area (Chapters 3 & 4), and elsewhere in the African savanna systems (Du Toit et al. 1990; Augustine & McNaughton 1998; Ward & Young 2002). The improvement of soil nutrients did not further increase the crude protein content of heavily-browsed trees, but that of lightly browsed trees. Our results suggest that soil enrichment does not directly translate into higher crude protein content of *T. sericea* when subjected to heavy early-season damage, but that it only enables the plant to fully compensate for protein content. However the crude protein content of *T. sericea* on fertilized soils was generally higher than on unfertilized soils.

CONCLUSION

Herbivore damage had significant effects on the growth and the chemical composition of *T. sericea*, but such effects depended on the available soil nutrients, the degree of damage, and the height distribution of plant parts in the canopy. Plants in low resource environments had higher contents of anti-nutritive substances such as condensed tannin and fiber fractions, while improved soil conditions increased plant quality for herbivores. Furthermore, herbivore damage elevated crude protein content in the low resource environment. Foliar damage under natural soil conditions promoted overcompensation of tolerance and resistance traits, while the interaction effect of foliar damage and improved soil conditions promoted full compensatory responses. Additionally, the compensatory ability of *T. sericea* ensured that the negative effects of early-season damage did not endure for the entire growing season.

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CHAPTER 5

**THE RESISTANCE AND TOLERANCE OF *Terminalia sericea* TREES TO SIMULATED
HERBIVORE DAMAGE UNDER DIFFERENT SOIL NUTRIENT AND MOISTURE
CONDITIONS**

ABSTRACT

Resource availability, degree of herbivore damage, genetic variability and their interactions influence the allocation of investment by plants to resistance and tolerance traits. We evaluated the independent and interactive effects of soil nutrients and moisture, and simulated the effects of herbivore damage on condensed tannins (resistance) and growth / regrowth (tolerance) traits of *Terminalia sericea*, a deciduous tree in the Kalahari desert that constitutes a major component of livestock diet. We used a completely-crossed randomized-block design experiment to examine the effects of nutrients, water availability and herbivore damage on regrowth and resistance traits of *T. sericea* seedlings. Plant height, number of branches, inter-node length, leaf area, leaf mass for each seedling, combined weight of stems and twigs, and root mass were recorded. Condensed tannin concentrations (a measure of defensive investment) were 22.5% and 21.5% higher under low nutrients and low soil moisture than under high nutrient and high water treatment levels. Tannin concentrations did not differ significantly between control and experimental seedlings two months after simulated herbivore damage. Tannin concentrations correlated more strongly with growth traits under low nutrient conditions than under high nutrient conditions. No trade-offs were detected among individual growth traits, nor between growth traits and condensed tannins. *Terminalia sericea* appeared to invest more in both resistance and regrowth traits when grown under low nutrient conditions. Investment in the resistance trait (condensed tannin) under high-nutrient conditions was minimal and, to a lesser degree, correlated with plant growth. These results indicate that *T. sericea* displays both resistance and tolerance strategies and that the degree to which each is expressed is resource dependent.

Key Words—Fertilization, defoliation, herbivory, condensed tannins, compensation, trade-offs, plant defences, resistance.

INTRODUCTION

Plants are subjected to a wide variety of stress factors that affect both their development and survival (Kozłowski et al., 1991; Larcher, 1995). On the African savanna, where low nutrient availability and water scarcity are commonplace, herbivory by mammals is also a key factor which may cause significant deviations from conditions of optimal plant life (Scholes, 1990; Du Toit, 1995). In response to these limitations, plants have evolved tolerance and resistance strategies to deal with stress (Meijden et al., 1988; Mauricio, 2000; Van der Pijl, 2000). Tolerance is the ability of plants to maintain fitness after herbivory in the presence of potentially fitness-reducing stress (Van der Meijden et al., 1988; Mauricio, 2000; Pijl, 2000; Simms, 2000). A tolerant genotype minimizes declines in fitness by increasing photosynthetic rate, regrowth capacity and seed production (Belsky, 1986; Tiffin, 2000). Some tolerant plants grow faster to escape herbivores (Milewski et al., 1991; Palo et al., 1993). Resistance traits such as thorns and chemical substances presumably reduce plant acceptability to herbivores (Cooper and Owen-Smith, 1985; Bennisson and Paterson, 1993; Scholes and Walker, 1993; Furstenburg and Van Hoven, 1994) and, thus, the amount of damage that a plant suffers is reduced. Defensive chemical production is linked to nutritional deficiency in plants (Lundberg and Åström, 1990). Defensive chemicals, such as condensed tannins may bind with proteins in the herbivore diet and thereby reduce digestibility of proteins (Kumar and Singh, 1984; Mangan, 1988; Ngwa et al., 2000; Beck and Reed, 2001). Increased thorniness and thorn length have also been reported in some heavily-browsed tree species (Young, 1987; Milewski et al., 1991; Rohner and Ward, 1997).

Plant defensive strategies are influenced by the availability of resources to the plant (Coley et al., 1985; Bryant et al., 1992). According to the resource availability hypothesis for plant defence (Coley et al., 1985), the optimal strategy in resource-poor environments may be to deter herbivores (Strauss and Agrawal, 1999), because the cost of replacing lost tissues is presumably high (Percy et al., 1987). In contrast, in high-resource environments, plants can recoup lost nutrients quickly and regrow with little cost (Bryant et al., 1983; Meyer, 2000). In low-resource environments, plants often allocate more

resources to roots than shoots (Dyer et al., 1991). This investment in underground structures may provide plants with the ability to compensate for aboveground tissue loss by re-allocating reserves to replace the lost tissues (Van der Meijden et al., 1988; Strauss and Agrawal, 1999; Hochwender et al., 2000). Compensatory ability often contributes more to plant fitness when damaged in low-resource environments, but less to plant fitness in high-resource environments (Hochwender et al., 2000).

Any effect on carbon:nutrient ratio, be it herbivory, changes in soil nutrient condition, water availability or exposure to light can cause a change in the total defence level (see review by Stamp, 2003). When a plant experiences herbivory, a temporary nutrient deficiency is experienced by the plant (Luxmore, 1991; Augustine and McNaughton, 1998), which may limit growth more than photosynthesis. Therefore, carbon in excess of growth demand may be shunted into storage and production of resistance traits (see review by Koricheva et al., 1998), while storage may aid tolerance (regrowth) ability (Stowe et al., 2000). Furthermore, excess carbon may increase the production of carbon-based defences under conditions of low resources, but at little cost to plant fitness (Tuomi, 1992; Adler and Karban, 1994; Rohner and Ward, 1997; Ruiz et al., 2002). This situation may lead to higher production of induced carbon-based secondary metabolites following herbivore damage (Adler and Karban, 1994).

Allocation of carbons to defence is thought to proceed in two ways (Tuomi, 1992): The first allocation (P_1) is the proportion of carbon that is in direct competition with growth requirements, whereas the second proportion (P_2) consists of carbon surplus beyond growth demand. The latter is assumed to have no cost to growth. Stamp (2003) regarded P_1 as a fixed allocation that provides the active defence investments, and P_2 is a flexible allocation that is determined by factors that constrain growth, such as low nutrient availability and herbivory, but that maintain or promote photosynthesis (Bryant et al., 1983; Tuomi et al., 1988; Tuomi, 1992).

Mammalian Herbivory on Terminalia sericea Trees in the Kalahari Desert. Terminalia sericea (Combretaceae) is a deciduous woody plant dominating the deep sandy soils of the Kalahari desert of

southern Africa. The plant is a major contributor of browse for both domestic cattle and goats during the hot-dry season under heavy grazing systems (Chapter 3, in press). In contrast, *Terminalia sericea* has been reported to possess some defensive chemicals, which may be the reason for its low preference among ungulates (Cooper and Owen-Smith, 1985). This apparent contradiction is resolved by taking into account the fact that browse consumption often depends on both the diversity and abundance of browse species (Chapter 3, in press), whereas browse preference is often associated with browse quality and relative abundance (Cooper and Owen-Smith, 1985; Chapter 3, in press). We presumed that browsing pressure on *T. sericea* would elicit carbon-based chemical defences, given the high light conditions, and poor soil nitrogen and phosphorus concentrations of the Kalahari desert (Mendelsohn et al., 2002). Thus, we reasoned that *T. sericea* would have poor regrowth capacity upon damage because allocations to carbon-based chemical defences may present an opportunity cost to regrowth capacity (Van der Meijden et al., 1988; Pilson, 2000).

The potential interactions of foliar damage, nutrient availability and soil moisture content provide an opportunity to examine the effects of herbivore damage on the recovery and leaf quality of *T. sericea*. We investigated the effects of simulated herbivory on the resistance and tolerance traits of *T. sericea* in a fully crossed randomized-block design experiment with 12 factor-level combinations (three levels of herbivory, two levels of fertilizer addition and two levels of water treatment) across plants derived from five mother plants.

We made the following predictions regarding the levels of condensed tannin (resistance trait): 1) Under conditions of high resource availability (i.e. water and nutrients), plants will reduce the synthesis of condensed tannin but increase growth rate; 2) Foliar damage to seedlings growing on poor soil nutrients will induce greater levels of condensed tannin than on nutrient-rich soils; 3) Low water and nutrient availability will result in increased condensed tannin at no cost to plant growth. We also predicted the following regarding tolerance traits: 1) Compensation for herbivory is resource dependent, that is, compensatory ability will be enhanced under low-resource environments and reduced under high soil

.. nutrient conditions; 2) Tolerance of herbivory is complex and involves trade-offs between tolerance traits that are likely to be expressed under low resource conditions; and 3) The seedling siblings (i.e. from the same mother plants) with high levels of resistance traits will have low levels of tolerance traits and *vice versa*.

MATERIALS AND METHODS

We investigated condensed tannin levels (resistance trait) of *Terminalia sericea* and its tolerance for partial simulated herbivory among seedlings taken from five mother plants under varying levels of nutrient and water availability in a nursery experiment at the Forestry Research Station in Okahandja, Namibia. Seedlings were raised from seeds collected from 13 individual trees (mother plants) in their natural environment and sown at the end of winter (August 2001) in sterilized river sand. Germination rates and establishment varied considerably among mother plants. Seedlings from five mother plants with the highest establishment were transplanted and grown in 10 l polythene bags with a surface area of about 0.047 m². Each bag was inoculated with 100-cm³ soil collected under *T. sericea* trees in the field to allow for growth of soil mycorrhizae. Seedlings were grown under nursery conditions for 12 months, hardened for one month under reduced solar radiation and then for two weeks under full radiation. At this stage, all seedlings were watered to field capacity three times per week. The two weeks of hardening was necessary because simultaneous exposure to direct radiation and supplementation of fertilizer resulted in the death of seedlings in the pilot phase. Thus, experimental treatments commenced after two weeks of hardening the plants to direct solar radiation (3rd week of January 2003) on 15.5 month old seedlings and were terminated 3.5 months later.

We used a completely-crossed randomized-block design experiment with two levels of water treatment (low and high), two levels of fertilizer treatment (control and fertilizer addition) and three levels of herbivory (control, low and high). For details of treatment levels, see below. This constituted 12 treatment-level combinations across the five mother plants with four replicates in each treatment-level

combination. Thus, a total of 240 seedlings were used.

For the water treatment, plants were watered once a week (Monday) for the low water level, and three times per week for the high water level. A commercially available fertilizer (N:P:K 2:3:2) was used for the fertilizer treatment. We applied approximately four g of the fertilizer fortnightly over a period of three months (Feb-Apr), which is considered an intermediate level of fertilization. This frequency of application did not only allow for the initial hardening but also prevented excessive leaching of the nutrients from the sandy soil. The intermediate amount that was applied (30 g/m^2), corresponded with those applied by Tilman (1988) and on field plantations in South Africa (J.M.T. Theron, personal communication). Simulated herbivory was applied one month after the application of water and fertilizer treatments. For the low herbivory level, one out of three (33%) leaves was damaged and later removed by hand within an hour of damage while two out of three (66%) leaves were damaged and also removed in the case of high simulated herbivory. The apical shoot was left intact, as some plants had poor growth and the removal of the apical shoot could have had detrimental effects on further growth. Thus, manual defoliation started just below the apical shoot.

The experiment was terminated at the end of April 2003, one month before winter and senescence. Several plant growth parameters, viz. height, leaf area (length and width), number of branches and internode length, were sampled. Twigs and stems (above-ground biomass), roots (below-ground biomass) and leaves were oven dried at $65 \text{ }^\circ\text{C}$ for 48 hr to obtain dry mass. Whole leaves were counted before drying. Plant height was measured twice, before the experiment started and at the end of the experiment.

Condensed tannin in leaf samples was measured using a standard acid-butanol protocol (Waterman and Mole, 1994). This method with modification by Hagerman (1995) was applied to extract condensed tannin with 50 % methanol. The extract was added to the acid-butanol reagent and heated at $95 \text{ }^\circ\text{C}$ in a boiling bath for 1 hr, then cooled and absorbance read at 550 nm. Two replicates were used. Condensed tannin concentrations are expressed in quebracho equivalents (% Q.E), (quebracho is used as a standard

– Hagerman and Butler, 1989). Quebracho tannin is the only readily available condensed tannin. Purified quebracho standard prepared from a single lot of the crude commercial mixture is recommended for use in tannin analysis to minimize differences that may exist among materials provided by even a single supplier (Hagerman and Butler 1989). Quebracho used as the standard was obtained from A. Hagerman.

To protect comparison-wise error (see e.g. Zar 1984), we performed an overall comparison of the seven dependent variables using multivariate analysis of variance (MANOVA), with water, herbivory, fertilizer and their interactions as fixed factors, and mother plants as random factors. The dependent variables used were: tannin concentration, leaf area per unit final height, leaf mass per unit final height, change in height during the experiment (per unit initial height), aboveground:belowground mass, internode length per unit final height, and number of branches per unit final height. Leaf area, leaf mass, internode length and number of branches were standardized by dividing by final plant height because of strong positive correlations between these variables and final height. Subsequent to the detection of significant effects, post hoc univariate analysis (ANOVA) tests were performed. These effects were analysed in a mixed-model randomized block-design ANOVA (error terms as for model III ANOVA), using Statistica v. 6, GLM procedure. Where appropriate, analyses were followed by a multiple comparisons of means using a Scheffe *post hoc* test. Means are represented ± 1 standard error, unless otherwise stated. Pearson product-moment correlations were used to determine trade-offs between resistance and tolerance traits and between the various tolerance traits investigated.

RESULTS

The MANOVA results revealed a significant overall multivariate effect for water ($df = 7, 218, F = 10.55, P < 0.001$), herbivory ($df = 14, 436, F = 1.953, P = 0.020$) and fertilizer ($df = 7, 218, F = 27.496, P < 0.001$) (Table 5.1). There were significant interaction effects for water x herbivory ($df = 14, 436, F = 2.14, P = 0.009$) and herbivory x fertilizer ($df = 14, 436, F = 1.96, P = 0.019$). The interaction effects of water x fertilizer and water x herbivory x fertilizer were non-significant. The effect of mother plant was significant ($df = 28, 787.4, F = 13.633, P < 0.001$).

Resistance Trait and Growth

Fertilizer addition reduced production of condensed tannin ($df = 1, 224, F = 26.91, P < 0.001$).

Mean \pm SE condensed tannin in the low resource environment was 22.86 ± 1.229 (% Q.E.)

compared to 17.73 ± 0.741 (% Q.E.) on fertilized soils. Thus, tannin levels declined by 22.5 %

when fertilizer was added. In contrast, fertilizer positively significantly affected all growth traits ($P < 0.005$), with the exception of inter-node length.

The mean growth of fertilized seedlings was higher than those grown on the control-fertilizer soils (Table 5.2). The biggest difference in parameters was in seedling height. Seedlings treated with fertilizer grew 165% taller. Similarly, fertilized seedlings yielded a greater number of branches (48.2 %), above:below-ground biomass ratio (31.3 %), number of branches:height ratio (29 %), leaf area (15 %) and leaf mass (14 %) than control seedlings.

We predicted that leaf damage on seedlings growing in low-resource environments would induce greater levels of condensed tannin to avoid future damage (resistance prediction 2). This was not the case. Although condensed tannin concentration was higher in the low resource environment, simulated herbivory did not induce higher tannin concentration in the low resource environment ($df = 2, 224, F = 2.77, P = 0.065$). The interaction of herbivory and fertilizer was also not significant

($df = 2, 224, F = 0.05; P = 0.9526$). That is, resource availability did not influence the response of condensed tannin concentration to simulated herbivory.

Water level affected tannin concentration significantly ($df = 1, 224, F = 24.84, P < 0.001$). Tannin concentration was 21.7 % higher in the low water treatment (22.76 ± 1.092 Q.E. %) than in the high water treatment (17.82 ± 0.935 Q.E. %).

Table 5.1. Multivariate Analysis of Variance (MANOVA) of nursery experiment. Dependent variables used in this analysis were: Tannin concentration, Leaf area per unit final height, Leaf mass per unit final height, Change in height during experiment (per unit initial height), Above:Below mass, Internode length per unit final height, and No. branches per unit final height. Leaf area, leaf mass, internode length and no. of branches were standardized by dividing by final plant height because of strong positive correlations between these variables and final height

Factor	Wilks λ	F	Effect df	Error df	P
Water	0.747	10.545	7	218	<0.0001
Herbivory	0.885	1.953	14	436	0.020
Fertilizer	0.531	27.496	7	218	<0.0001
Water X Herbivory	0.875	2.144	14	436	0.009
Water X Fertilizer	0.978	0.693	7	218	0.678
Herbivory X Fertilizer	0.885	1.964	14	436	0.019
Water X Herbivory X Fertilizer	0.924	1.254	14	436	0.233
Mother Plant	0.240	13.633	28	787.4	<0.0001

Table 5.2. Significant ($P < 0.05$) effects of fertilizer treatment on seedling growth (mean \pm SE)

Growth parameter	Fertilizer treatment	
	Control	Fertilizer addition
Plant height (cm)	17.5 \pm 6.49	46.8 \pm 7.70
Leaf area (mm ²)	913.1 \pm 31.38	1053.6 \pm 27.09
Leaf mass (g)	0.05 \pm 0.000	0.06 \pm 0.002
Branches:height ratio	0.01 \pm 0.000	0.02 \pm 0.001
Number of branches	5.1 \pm 0.23	7.5 \pm 0.26
Above:below-ground biomass ratio	0.2 \pm 0.01	0.3 \pm 0.01

Trade-Offs between Resistance and Growth Traits

We considered trade-offs in seedlings grown in low resource conditions (low water and control fertilizer, i.e. LW-CF treatment combination) and in high resource conditions (high water and fertilizer addition treatment, i.e. HW-IF combination). Condensed tannins in the low-resource environments (LW-CF) correlated positively with the majority of growth traits but negatively with the number of branches:height ratio ($r = -0.376$, $P = 0.003$) (Table 5.3). The correlations of condensed tannin with leaf area, leaf mass, seedling height, number of branches and inter-node length were significant ($P < 0.05$) and positive, while above:below-ground biomass ratio did not correlate significantly ($P > 0.05$) with tannin concentration. The positive correlations between condensed tannin synthesis and the majority of growth traits is consistent with resistance prediction 3, which predicted that tannin would accumulate at no cost to plant growth in the low-resource environment.

Results showed a similar trend in the high-resource environment (HW-IF treatment combination) (Table 5.3). Most correlations were significant ($P < 0.05$) and positive, except for a negative correlation involving the number of branches:height ratio. The correlations were generally weaker in the high-resource environments, than in the low-resource environment.

Table 5.3. Correlations of condensed tannin concentrations (%Q.E.) with seedling growth traits, grown under low and high resource environments

Growth traits Tannin		Leaf area (mm ²)	Leaf dry mass (g)	Height (cm)	No. of Branches	Inter-node length (cm)	No. of Branches:height	Above:below-ground biomass
Low resource environment (LW-CF)	<i>r</i> =	0.70	0.80	0.44	0.43	0.73	-0.38	-0.10
	<i>P</i> =	0.0001	0.0001	0.0001	0.001	0.0001	0.003	0.450
High resource environment (HW-IF)	<i>r</i> =	0.66	0.51	0.37	0.39	0.56	-0.35	0.37
	<i>P</i> =	0.0001	0.0001	0.004	0.002	0.0001	0.006	0.004

Tolerance Traits

We predicted that compensatory ability of previously herbivore-damaged seedlings is resource-dependent (tolerance prediction 1). However, there was no significant interaction effect of herbivory x water x fertilizer treatments for: seedling height ($df = 2, 224, F = 0.61, P = 0.545$), number of branches:height ratio ($df = 2, 224, F = 0.77, P = 0.465$), above:below-ground biomass ratio ($df = 2, 224, F = 2.23, P = 0.110$), inter-node length ($df = 2, 224, F = 1.36, P = 0.259$) and the number of branches ($df = 2, 224, F = 1.92, P = 0.149$). Thus, no differences existed in the (re-) growth rate of these traits among seedlings exposed to control herbivory, low herbivory and high herbivory.

Leaf regrowth capacity, was resource-dependent. Herbivory reduced leaf area ($df = 2, 57, F = 5.79, P = 0.005$) and leaf mass ($df = 2, 57, F = 8.89, P < 0.001$) significantly when grown under conditions of low water and fertilizer addition levels. Both leaf area (Figure 5.1) and leaf mass (Figure 5.2) under-compensated (i.e. size upon regrowth was less than the original) equally under the low and high levels of herbivory treatment.

The interaction effect of herbivory x water on the number of branches was significant ($df = 2, 224, F = 4.35, P = 0.0140$). Both low and high simulated herbivory reduced the number of branches produced when seedlings were exposed to the high water treatment-level (Figure 5.3). The results also indicate that the reduced branches produced under herbivory in the high water treatment-level did not differ from those produced in the low water treatment-level, irrespective of the degree of herbivory.

Trade-Offs among Growth Traits

Resource conditions affected trade-offs among tolerance traits (Tables 5.4 & 5.5). Under high stress conditions (LW-HH-CF), leaf mass correlated negatively with above:below-ground biomass ratio ($r = -0.471, p = 0.036$) and the number of branches:height ratio ($r = -0.491, P = 0.028$) (Table 5.4). No trade-offs were detected under the least stressful conditions (HW-CH-IF) (Table 5.5). There were stronger correlations under the high stress conditions (Table 5.4) than in the least stressful conditions (Table

5.5).

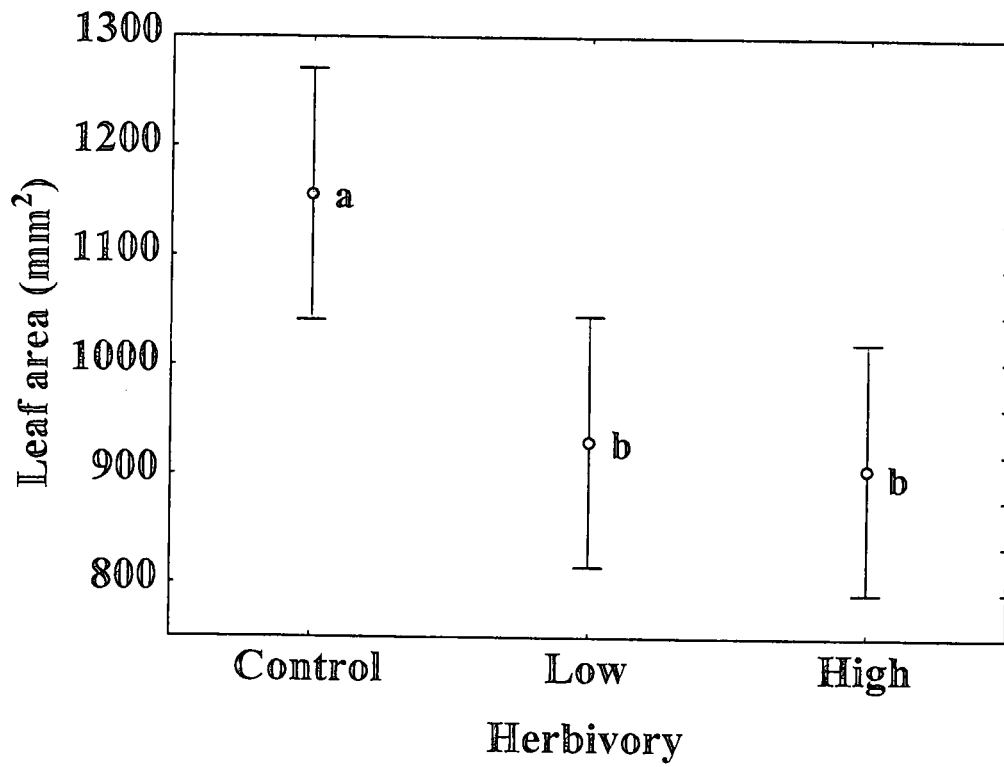


Fig. 5.1. Effect of simulated herbivory on leaf area. Error bars denote 95 % confidence limits, and the different letters indicate significant mean differences at $P < 0.05$

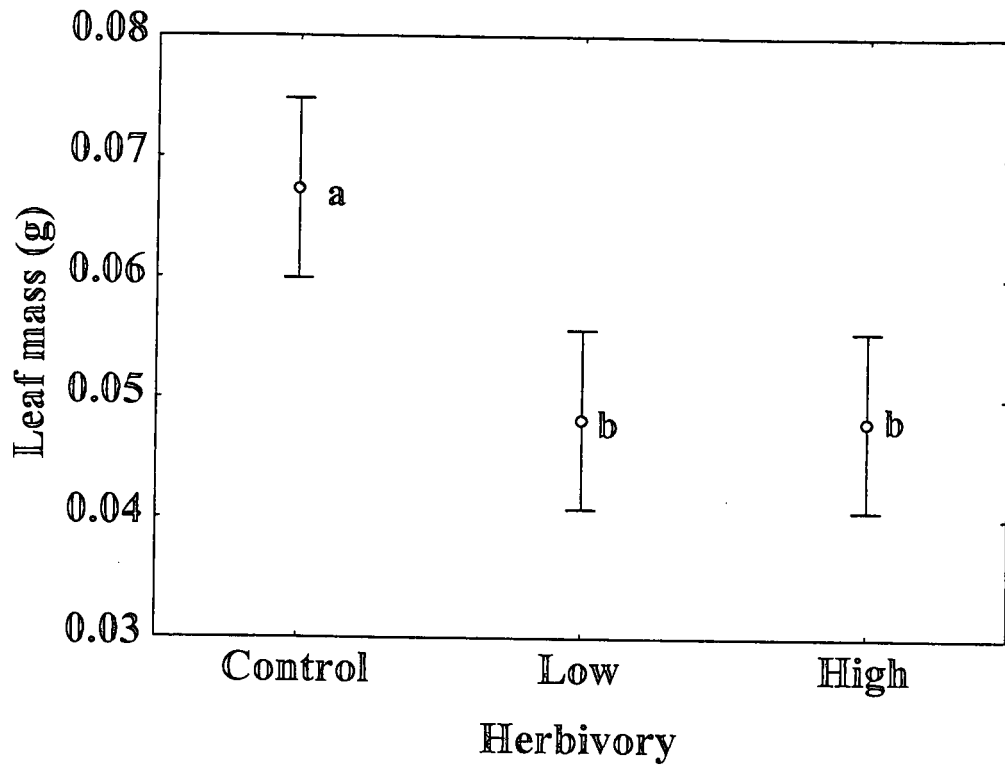


Fig. 5.2. Effect of simulated herbivory on leaf dry mass. Error bars denote 95 % confidence limits, and the different letters indicate significant mean differences at $P < 0.05$

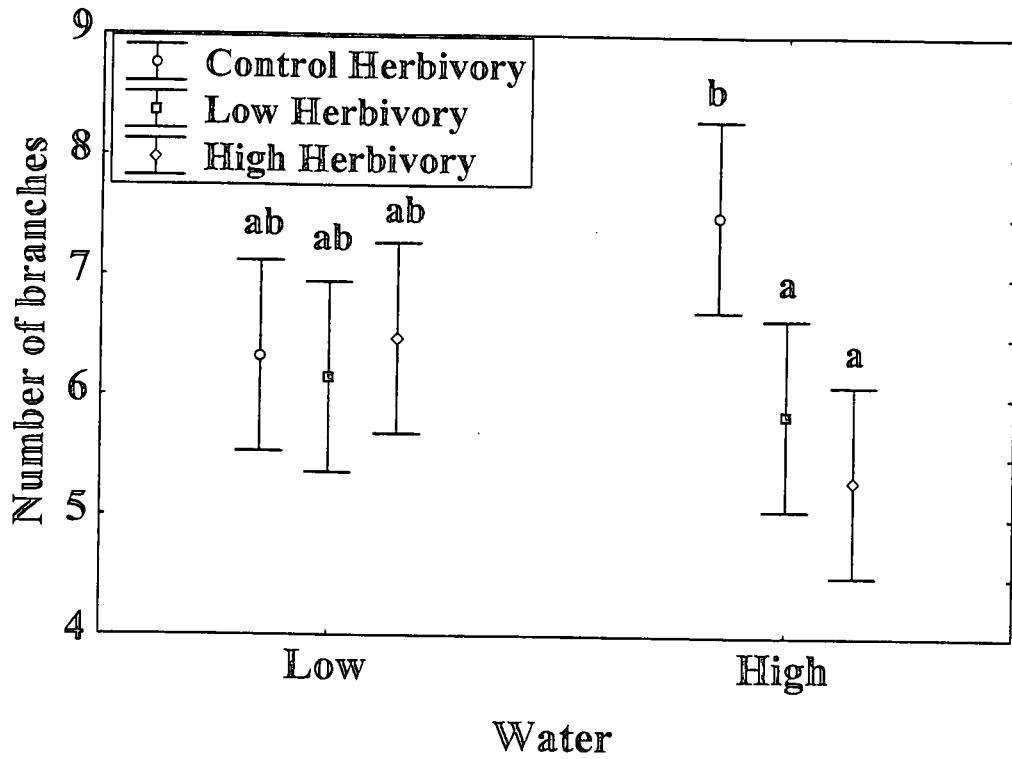


Fig. 5.3. Effect of simulated herbivory on the number of branches produced when seedlings were treated with high water levels. Error bars denote 95% confidence limits, and the different letters indicate significant mean differences at $P < 0.05$

Negative correlations among growth traits were detected in the intermediate range of stress conditions. For example, leaf area correlated negatively with branches:height ratio under HW-HH-IF ($r = -0.59, P = 0.006$), LW-LH-IF ($r = -0.51, P = 0.021$) and even under LW-CH-CF ($r = -0.51, p = 0.023$). Leaf mass correlated negatively with branches:height ratio under LW-CH-CF ($r = -0.56, P = 0.010$) and LW-LH-IF ($r = -0.46, P = 0.040$).

Mother-Plant Resistance and Tolerance Traits

Tannin concentrations differed significantly among mother-plants ($df = 4, 180, F = 89.281, P < 0.001$). Differences in allocation to condensed tannins (resistance trait) among mother-plants corresponded linearly with investments into growth traits such as: leaf area ($r = 0.91, P = 0.03$), leaf mass ($r = 0.94, P = 0.02$), height ($r = 0.93, P = 0.02$) and inter-node length ($r = 0.97, P = 0.006$). These results contradicted tolerance prediction 3. Tannin synthesis was not significantly correlated with above:below-ground biomass production ($r = -0.27, P = 0.657$).

Table 5.4. Correlations between growth traits of seedlings exposed to high stress conditions (LW-HH-CF), using Bonferroni-adjusted values of α to control the comparison-wise error (Type I error) for A large number of correlations. α was only considered significant if $p < 0.0024^*$. Correlations involving height and the number of branches *versus* the number of branches:height were not reported because they were autocorrelated

	Leaf area	Leaf mass	Height	Branches	Internode length	Branches:height
Leaf mass	$r = 0.81,$ $p < 0001^*$					
Height	$r = 0.53,$ $p < 0.0001^*$	$r = 0.49,$ $p = 0.001^*$				
Number of branches	$r = 0.58,$ $p < 0.0001^*$	$r = 0.36,$ $p = 0.006$	$r = 0.46,$ $p = 0.0019^*$			
Internode length	$r = 0.85,$ $p < 0.0001^*$	$r = 0.76,$ $p < 0.0001^*$	$r = 0.51,$ $p = 0.0011^*$	$r = 0.37,$ $p = 0.005$		
Branches:height	$r = -0.29,$ $p = 0.011$	$r = -0.49,$ $p = 0.001^*$	-	-	$r = -0.51,$ $p = 0.001^*$	
Above:below	$r = -.28,$ $p = 0.011$	$r = -0.47,$ $p = 0.002^*$	$r = -0.10,$ $p = 0.032$	$r = -0.06,$ $p = 0.038$	$r = -0.28,$ $p = 0.011$	$r = 0.33,$ $p = 0.007$

Table 5.5. Correlations between growth traits in seedlings exposed to low stress conditions (HW-CH-IF), using Bonferroni-adjusted values of α to control the comparison-wise error (Type I error) for A large numeric correlations. α was only considered significant if p values < 0.0024*. Correlations involving the number of branches and height *versus* the number of branches:height were not reported because they were autocorrelated.

	Leaf area	Leaf mass	Height	Branches	Internode length	Branches:height
Leaf mass	$r = 0.60,$ $p = 0.0002^*$					
Height	$r = 0.17,$ $p = 0.023$	$r = 0.26,$ $p = 0.013$				
Number of branches	$r = 0.48,$ $p = 0.002^*$	$r = 0.19,$ $p = 0.020$	$r = 0.30,$ $p = 0.009$			
Internode length	$r = 0.58,$ $p = 0.0004^*$	$r = 0.68,$ $p < 0.0001^*$	$r = 0.26$ $p = 0.013$	$r = 0.45,$ $p = 0.0002^*$		
Branches:height	$r = 0.11,$ $p = 0.031$	$r = -0.32,$ $p = 0.008$	-	-	$r = -0.42,$ $p = 0.003$	
Above:below	$r = 0.21,$ $p = 0.018$	$r = -0.03,$ $p = 0.044$	$r = 0.43,$ $p = 0.003$	$r = 0.70,$ $p < 0.0001^*$	$r = 0.43,$ $p = 0.003$	$r = -0.10,$ $p = 0.032$

DISCUSSION

Resource Gradients

Seedlings in the resource-poor environments had 22.5% higher condensed tannin concentrations than those seedlings grown in high-resource environments. Consistent with this result, other studies have shown that plants growing in resource-poor environments maintain a high resistance level against herbivore damage (Coley et al., 1985; Gebauer et al., 1998; Osier and Lindroth, 2001). High levels of resistance traits in resource-poor environments are maintained because the cost of replacing lost tissues is presumably high (Coley et al., 1985; Pearcy et al., 1987). Hence, the strategy of such plants is to deter rather than to tolerate herbivores (Strauss and Agrawal, 1999). Nutrient-poor soils combined with drought conditions constrain growth more than photosynthesis, and, subsequently, assimilates in excess of growth requirements are shunted into defence (Herms and Mattson, 1992) and storage (see review by Koricheva et al., 1998). In this study, seedlings under limited soil-moisture synthesized higher (21.7 %) concentrations of condensed tannins than those seedlings in the high soil-moisture environment. Such effects of drought conditions have been reported elsewhere (Kouki and Manetas, 2002). The current study showed that droughts and poor soil-nutrients affect condensed tannin synthesis in a similar manner.

Fertilizer addition to poor soils seem to reduce the ratio of carbon:nutrients available to defence, thereby reducing potential resistance (Lavola and Julkunen-Tiito, 1994; Folgarait and Davidson, 1995; Hartley et al., 1995; Ruohomäti et al., 1996; Kouki and Manetas, 2002), but promoting greater plant growth relative to investments into defence (Bryant et al., 1983; Ruohomäti et al., 1996; Mutikainen et al., 2000). In high-resource environments, plants presumably suffer lower costs of herbivory and thus require little allocation into resistance traits against tissue damage (Bryant et al., 1983; Meyer, 2000). Along an environmental resource gradient, tolerant plants seem to be faced with the dilemma whether to grow faster or to compensate for damage (Hochwender et al., 2000). In this study, fertilizer addition increased seedling leaf area, leaf dry mass, height, number of branches, number of branches:height ratio

and above:below ground biomass ratio, rather than enhancing compensatory responses upon damage. Nutrient limitation constrained the growth of *T. sericea* seedlings.

Inducible Resistance

The effects of herbivory or its interactions with either fertilizer or water treatments did not influence the synthesis of condensed tannins in seedlings. The high concentrations of condensed tannins in low-resource environments may have been sufficient to deter future herbivore damage or to minimize the effect of damage and thus perhaps did not warrant further increases. The concentration of condensed tannin needed to deter large mammalian herbivores remains poorly understood (Cooper and Owen-Smith, 1985). Under natural conditions, cattle consumed *Bauhinia petersiana* in large amounts in the northern Kalahari despite higher tannin concentrations (mean \pm SD, 48.6 ± 9.87 Q.E. %) than *T. sericea*, although cattle generally avoided dietary items with high tannin concentrations (Chapter 3, in press). Cooper and Owen-Smith (1985) suggested that tannin:nutrient ratio may be a more appropriate measure of the role of tannin as a deterrent against herbivores. High tannin:nutrient ratio reduces forage acceptability (Robbins et al., 1987; Bryant et al., 1989; Du Toit et al., 1990). Katjiua and Ward (Chapter 3, in press) concluded that inclusive of high tannin levels, the sum total of anti-quality substances relative to nutrient contents, and the quantity of available forage determine herbivore consumption patterns.

Expression of resistance traits in previously browsed species may take time to reach levels above the controls (Larcher, 1995; Ruohomäti et al., 1996). Initially, browsed plants may show a decline in allocation to resistance traits (stress reaction), followed by mobilisation of resources for resistance traits which, depending on the severity and persistence of stress, may recover and exceed the levels of the controls (= overcompensation of resistance), or may revert back to levels similar to that of control plants (= full compensation) if stress was light and of short duration (Underwood, 1999), or if sufficient time is allowed without further herbivore damage over the growing season (Chapter 4). Severe and persistent herbivore damage may, however, reduce tannin concentrations to levels lower than that of

control seedlings (= undercompensation) due to reduced resources (see review by Bergelson and Purrington, 1996).

A number of studies in the African savanna have found that tannin content decreased with herbivory (Du Toit et al., 1990; Ward and Young, 2002; Chapter 4). Ward and Young (2002) found that *Crematogaster nigriceps*, a herbivorous ant that eats the axillary shoots of its host trees, reduced the number of leaves per branch and resulted in a decrease in tannin production. Additionally, shoots subjected to low herbivory contained higher concentrations of tannins than shoots subjected to high herbivory. Du Toit et al. (1990) found that heavily-browsed *Acacia nigrescens* had significantly lower condensed tannin concentrations than those excluded from herbivory. Frequently-browsed *Grewia flava* plants had 24.3 % lower condensed tannin concentrations than infrequently-browsed specimens in the northern Kalahari (Chapter 4). Increased number of bites and browse consumption upon heightened herbivore damage were also reported in African savannas (see review by Bergström et al., 2000). Plants may decrease tannin production depending on the part of the plant that is consumed. Du Toit et al. (1990) and Ward (in prep.) found that *Acacia* species decrease tannin production when the apical shoot is browsed and increase tannin production when other shoots are browsed. Tannin production may thus serve to protect the apical shoot – production therefore declines when this shoot is removed.

Under resource-poor conditions, developing leaves may represent a strong sink for assimilates, such that allocation to defence is constrained (Herms and Mattson, 1992; Furstenburg and Van Hoven, 1994; Wilkens et al. 1996; Augustine and McNaughton, 1998). Studies elsewhere concluded that carbohydrate demand incurred during rapid leaf regrowth after herbivore damage caused substrate limitation for carbon-based secondary metabolite synthesis (Bryant et al., 1983; Danell and Huss-Danell, 1985). Hence, under low-resource conditions, increased herbivore damage causes a reduction in defence investments (= resistance) (see review by Bergelson and Purrington, 1996). However, our results were not consistent with these studies. This may be because the high simulated herbivory was not frequent enough to deplete plant reserves needed for condensed tannin production.

Early-season damage may lead to the decay of induced potential resistance in the absence of herbivory as the season progresses or when herbivore damage is spaced over a long interval (Underwood, 1999), but may also increase potential resistance to herbivores later in the season or in subsequent years (Bryant et al., 1991; Karban, 1993), only if past and current herbivory is a reliable predictor of future risk of herbivory, and when herbivory reduces plant fitness (Karbon et al., 1999).

Resistance versus Growth Trade-Offs

The total amount of condensed tannin in the seedlings of *T. sericea* accumulates as the growing season progresses (Katjiua and Ward, in prep.). This study showed no indication of trade-offs between investments into tannin synthesis and the majority of growth traits (leaf area, leaf dry mass, height and inter-node length) in the low-resource environments. These results contradicted resistance prediction 3. The negative correlation between condensed tannin content and the number of branches:height ratio in the low-resource environment was also detected in the high-resource environment. Thus, resource availability alone could not explain this negative correlation.

Growth traits such as leaf area, inter-node length and above:below-ground biomass ratio correlated positively with condensed tannin concentration. A comparison of these results (Table 5.3) suggests that investments into resistance traits may be more closely coupled with growth traits in low-resource environments than in high-resource environments. The cost of allocation to resistance traits is expected to be more evident when plants are grown under stressful conditions (Bazzaz et al., 1987; Herms and Mattson, 1992). It appears that our plants under low-resource conditions had limited investment budgets available for growth and resistance traits and that investment partitioning between growth and resistance traits could approximate unity with greater resource limitation. Thus, our results yielded no evidence of cost implications for allocations to resistance and tolerance traits. This is consistent with results reported by Ward and Young (2002) on *Acacia drepanolobium* in north-central Kenya.

Plant defences are assumed to be costly (Adler and Karban, 1994; Strauss and Agrawal, 1999), yet empirical results have not consistently detected trade-offs between tolerance and resistance traits (see review by Bergelson and Purrington, 1996; Mauricio, 2000; Ward and Young 2002). The absence of trade-offs among defence traits has been attributed to a lack of rigorous experimentation and misinterpretation of plant defence hypotheses (see review by Stamp, 2003) and limited control of the genetic background of plants under investigation (see review by Bergelson and Purrington, 1996). Trade-offs may also not be revealed by simple pairwise correlations of resistance and growth traits because ecological costs may involve complex correlations among multiple traits (Houle, 1991; Pilson, 2000). Mauricio et al. (1997) and Tiffin and Rausher (1999) concluded that tolerance and resistance traits could coexist in a species, but that the scales of both intrinsic and extrinsic factors that a plant experiences may determine the ratio in which tolerance and resistance traits are expressed (Mauricio, 2000).

Tolerance Compensatory Responses

There was no significant interaction effect of water x herbivory x fertilizer treatment on seedling height, branches:height ratio, above:below-ground biomass ratio, inter-node length and number of branches. The lack of a difference in the regrowth rates of the above growth traits between the control, low and high simulated herbivory implies that either herbivory had little or no effect on these traits or that growth capacity was fully compensated. In contrast, leaf compensatory ability was resource-dependent. Leaf area and leaf dry mass under-compensated for growth when grown on the low water and intermediate fertilizer treatments. However, both leaf area and leaf dry mass fully compensated for growth in low-resource environments (=control fertilizer treatment). Hochwender et al. (2000) argued that because compensatory growth and reproduction is more prevalent in low-resource environments it contributes greatly to the survival and reproduction of plants in these environments.

In this study, a 31.3 % lower above:below-ground biomass ratio was found in seedlings grown on the low-resource environment than in the high-resource environment. Prior investments into storage

structures in the low-resource environments are reallocated to sites where new growth is required and thereby enhancing compensatory regrowth (Strauss and Agrawal, 1999; Hochwender et al., 2000). In high-resource environments, compensatory ability is limited or may even be absent, because investments into storage structures is presumably limited by high growth rates. Indeed, plants invest more in above-ground growth than in below-ground structures when growing in high-resource environments (Bryant et al., 1983; Kouki and Manetas, 2002). High above-ground growth rates allow plants to escape herbivory usually by growing too tall for mammalian herbivores; (Palo et al., 1993), and thereby ensure survival and reproductive output.

Herbivory did not affect the number of branches, possibly because the apical shoots were not damaged during experimentation. There was a significant water x herbivory interaction effect on the number of branches. Seedlings exposed to low and high herbivory treatments produced fewer branches when given the high water treatment. This is consistent with tolerance prediction 1 that compensatory ability is resource dependent. Among all growth traits investigated, leaf area and leaf dry mass were most sensitive to herbivore damage.

Trade-Offs among Tolerance Traits

Allocations among growth traits in high-resource environments seem to be flexible and less coupled to the competing demands of the different growth traits (Table 5.5), than in the low-resource environments (Table 5.4). In general, our results indicate that: 1) resource conditions, internal or external to the plant, resulting from variability in soil moisture, herbivory and soil-nutrients determine the proportional allocation of investments among competing growth traits; 2) partitioning of investment appears to be more strongly correlated among competing growth traits in the low-resource environments than in the high resource environments; and 3) leaf area and leaf mass are the most sensitive traits to allocation shifts in *T. sericea*.

Mother-Plant Resistance and Tolerance

The concentrations of condensed tannin (=resistance trait) differed in the same way as the regrowth capacity (=tolerance traits) among the five mother-plants. That is, plants with high vigor invested heavily in both resistance and tolerance traits, while weak plants invested equally poorly in resistance and tolerance traits. Thus, there was a positive genetic correlation between the levels of resistance and tolerance traits among *T. sericea* mother-plants.

CONCLUSIONS

Conditions of low water availability and poor soil fertility increased the production of condensed tannins in *T. sericea*. Simulated effects of herbivory did not induce potential resistance, irrespective of environmental resource conditions. High soil fertility enhanced the growth and regrowth capacity of *T. sericea*, while soil nutrients and moisture content determined the allocation of photosynthates to the production of condensed tannin and growth or regrowth among the *T. sericea* plants. Seedlings in low-resource environments allocated proportionally more photosynthates to the production of condensed tannins per unit of growth than in high-resource environments.

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CHAPTER 6

**PASTORAL PRODUCTION AND BUSH ENCROACHMENT: A BENEFICIAL
COMBINATION IN A SEMI-ARID REGION OF NAMIBIA**

ABSTRACT

Pastoral production around artificial water points in semi-arid environments affects the structure and composition of plant communities. In the Kalahari desert of southwestern Africa, bush encroachment is often perceived as the major form of vegetation change related to pastoral production around water points. We investigated traditional OvaHerero pastoralists' perceptions of the extent of vegetation change in a communal ranching area on the edge of the Kalahari desert, Namibia since the establishment of artificial water points there, and related this to ecological data on vegetation change. We determined the utility of woody vegetation to pastoralists' livelihoods in terms of provision of construction material and fuel wood. Furthermore, we quantified local knowledge of cattle browse consumption and correlated it with field data from concurrent work in the study area. We also assessed the purposes for which major livestock types were used. Our results showed that: 1) the current level of bush encroachment was perceived to be beneficial for pastoral production, 2) pastoral knowledge of bush encroachment and browse consumption was consistent with concurrently-collected field data in the study area, and 3) although pastoralists raised cattle, goats and sheep, cattle played a significant primary role in the production of milk and milk products for consumption, and generation of cash income, while sheep and goats were primarily kept for meat consumption. This result contrasts with historical studies that portray cattle primarily as a symbol of social status among the OvaHerero pastoralists, thus demonstrating that the traditional role of cattle in this society has diminished over the years. The integration of local knowledge and practices of range management with scientific methods of range assessment and management can enhance local-level adaptive range resource management.

Keywords: rural livelihoods; water points; vegetation change; fodder trees; traditional ecological knowledge; Herero; Kalahari

INTRODUCTION

Semi-arid grazing systems are renowned for their high resource variability in space and time (see e.g. Ellis & Swift 1988; Vetter 2003; Ward et al. 2004). The combination of infrequent droughts and continuous grazing may impose intense grazing pressure on forage resources (Illius & O'Connor 1999). Subsequently, heavy grazing decreases the occurrence of palatable and mostly perennial grasses. The dominance of annual forage biomass on the rangeland increases the variability of primary production and limits the amount of standing forage biomass that can be transferred between years, thereby increasing drought vulnerability (Illius & O'Connor 1999). This is because the productivity of annual plants is tightly coupled to the volume and frequency of rainfall events (Ellis & Swift 1988). The proliferation of woody plants in many semi-arid savanna ecosystems further limits grass biomass production (Moleele et al. 2002).

In the semi-arid parts of Namibia in southwestern Africa, rangeland productivity has declined precipitously over the last century (Ward & Ngairorue 2000). Most notable is the 50% decline in grass biomass per unit annual rainfall from the biomass reported by Walter (1939), in spite of a lack of change in rainfall in the interim (Ward & Ngairorue 2000). Such changes have occurred in tandem with large-scale increases in woody plant density (known as bush encroachment) (De Klerk 2004). Bush encroachment is responsible for massive losses in productivity of the savanna environment because the trees are not usually consumed by cattle and sheep. The impenetrable nature of encroaching tree species, especially the thorny *Acacia* species, may render large areas inaccessible to large mammalian herbivores (Rohner & Ward 1997), thus reducing their productivity.

Vegetation change around artificial water points

Abel & Blaikie (1989) defined land degradation as 'an effectively permanent decline in the rate at which land yields livestock products under a given systems of management'. This definition was

derived from experiences and findings from rangelands in Botswana and Zimbabwe. Dougill & Cox (1995) argued that land degradation is seldom an issue unless vegetation change is accompanied by soil degradation.

Van Rooyen et al. (1994) and Perkins and Thomas (1993) have argued that vegetation change in the Kalahari is restricted to limited radii around water points, which expand and contract in response to rainfall, but that there was no progressive outward expansion of the piospheres over time. In contrast, Jeltsch et al. (1997), applying a grid-based simulation model, demonstrated that piosphere zones expanded outwards at a rate correlated with grazing pressure, and that piosphere development is limited by rainfall in the relatively low rainfall areas of the southern Kalahari. Consistent with this, piosphere development around permanent water points utilized by native OvaHerero pastoralists was less defined in the more arid zones than in the semi-arid zone of Namibia (Ward et al. 1998).

Bush encroachment in the Kalahari desert

The northern Kalahari desert of Namibia is used primarily for pastoral production by the native OvaHerero people and is considered particularly vulnerable to land degradation (Aharoni & Ward 1997), owing to high livestock densities. Large-scale changes in the vegetation of this region have been ascribed to heavy grazing by livestock over the last century (Aharoni & Ward 1997). Bush encroachment in the northern Kalahari desert region of Namibia is often perceived as the most important form of vegetation change (Bester & Reed 1997; De Klerk 2004).

The OvaHerero pastoralists

The OvaHerero are traditional cattle pastoralists like the Maasai of Kenya, Borana of southern Ethiopia and the Fulani of West Africa. They are more animal-dependent than any other group in Namibia such as the Ovambo, Kwangali and Masubia who, besides keeping cattle, also cultivate crops. Pastoralists in

arid- and semi-arid environments have used transhumance to exploit ephemeral water and forage resources in heterogeneous landscapes (Behnke & Scoones 1993; Scoones 1995). In Namibia, the OvaHerero used to migrate within a region of relatively permanent residence such as Okaoko and between such regions to exploit spatially and temporally variable resources (Fig. 6.1).

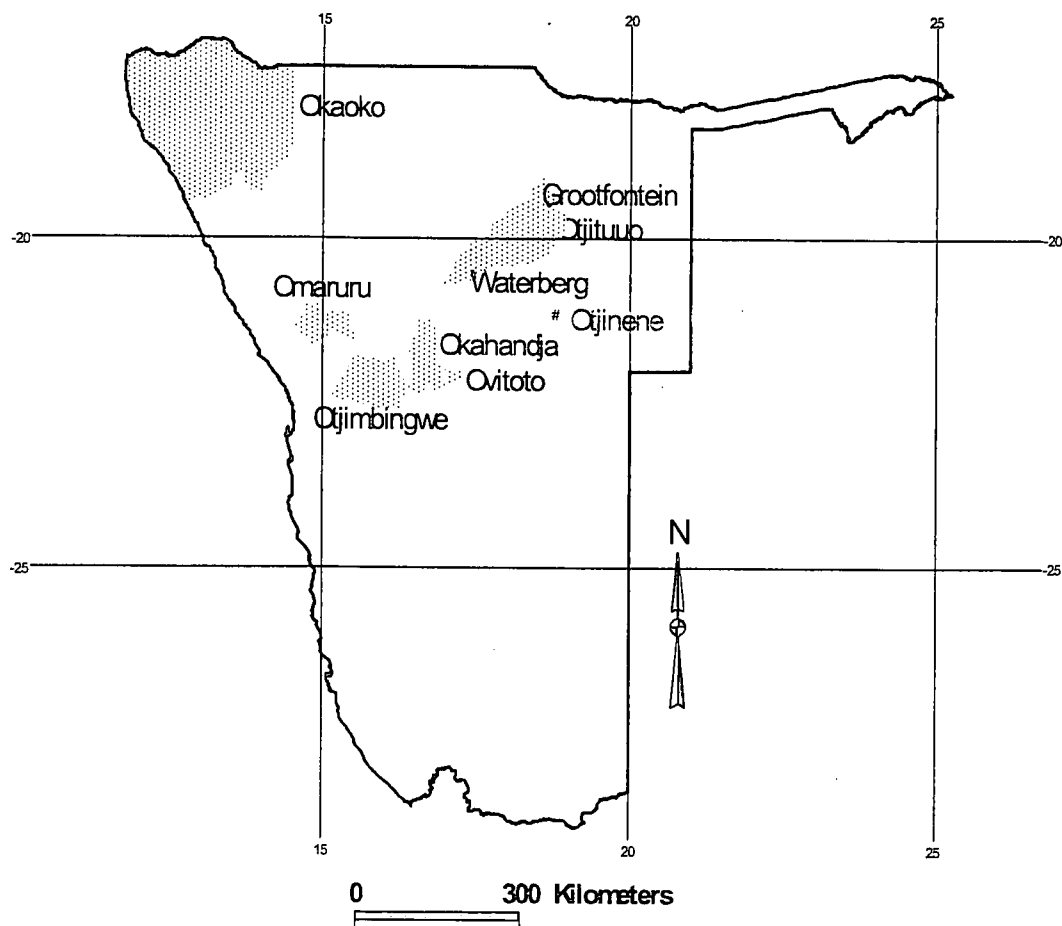


Figure 6.1. Major livestock production areas used by the OvaHerero prior to German colonial rule and land alienation. The OvaHerero used to migrate with their livestock within and between the shaded areas in search of spatially- and temporally-variable forage resources.

Transhumance allows for grazing ecosystems to recover after heavy grazing (Behnke & Scoones 1993). Following the genocide of the OvaHerero by the German colonial government in 1904 – 1907, the OvaHerero were increasingly confined to identified reserves. This process of confinement of the OvaHerero was continued by the South African colonial administration after the First World War under the mandate of the League of Nations, while much of central Namibia was allocated to white settler farmers (Köhler 1959; Gewalt 1999). In the native reserves, livestock production was confined to a few perennial water points (cattle must drink every other day). Hence, the sedentarization of the OvaHerero pastoralists around these water points since the early 1920s has intensified rangeland use.

A conventional view of communal pastoralism is that each pastoralist is concerned with increasing her/his own herd size and, thus, little or no management is in place to protect the commonage. This pursuit of self-interest and lack of coordinated effort among pastoralists to manage the commons may lead to what is generally known as the “tragedy of the commons” (Hardin 1968). We note that this notion has been heavily criticised, mainly for failing to make a distinction between common-pool resources characterized by open access regime and common-property resources where resources are owned in common or where a strong sense of ownership exists and is characterized by coordinated access regimes (Ostrom 1990; Kipuri 1993). Thus, village inhabitants have joint-usage of resources in the latter system (Ostrom 1990) and village membership enables right of access to use the common-pool resources (Lawry 1990). African pastoral lands are largely governed by coordinated access institutional regimes, and not by means of open access regimes as previously thought (Lawry 1990).

The high livestock numbers in communal pastoral regimes have been regarded as an optimal strategy to ensure flow of livestock benefits in otherwise very unpredictable and variable environments (Abel 1993). However, this has often been regarded as injudicious overstocking by pastoralists and disregard for carrying capacity (Sebina & Düvel 1998). In contrast, the infrequent and unpredictable droughts are now believed to largely maintain livestock numbers below the ecological carrying capacity (Ellis & Swift 1988; Burke 2004); thus, livestock numbers remain uncoupled to primary productivity for much

of the time (Ward & Ngairorue 2000; Ward et al. 2000). Rainfall is the key determinant of plant biomass production rather than livestock numbers (Ellis & Swift 1988; Abel 1993). Recent reviews propose opportunistic stocking rates, whereby livestock numbers should be increased during good years to exploit the available forage resources, but decreased during years of low rainfall to reduce heavy grazing and to ensure animal productivity (Burke 2004; Ward et al. 2004). This may be counter-intuitive to traditional pastoralists, whose multiple uses of livestock may not require that animals be in good condition all year around. Furthermore, there may be limits to a variable stocking strategy because breeding herds must be maintained through the dry periods so that sufficient breeding cows are available for the subsequent wet period. This may be unrealistic because communal pastoralists, such as the OvaHerero, may be unable to afford to buy in animals immediately after a drought.

We wished to examine how the OvaHerero pastoralists in the Otjinene constituency (Namibia)(Fig. 6.1) perceived changes in the structure and composition of vegetation, and how these perceptions matched the realities of current status of vegetation change (cf. Ward et al. 2000). We also determined livestock browse consumption during the year, and specifically compared hot-dry season browse consumption with local knowledge about cattle browse consumption during the same period. Land degradation is frequently a slow and a long-term process, which makes early detection difficult. This creates a lag in adaptations to changes in environmental quality (Behnke & Abel 1996). Problems of perception and adaptation to changes in environmental quality are acute where land degradation occurs in inherently variable environments (Ward et al. 2000). Therefore, long-term residence and subsequent transfer of acquired pastoral-ecological knowledge to younger pastoralists has the potential to allow for the evolution of local management strategies to reverse or reduce land degradation. We also sought to determine how rangeland resources contribute to pastoralist livelihoods because pastoralists use these resources in multiple ways, including among others, firewood for cooking and heating, timber for construction of cattle pens and houses, and as livestock feed. In particular, we wished to ascertain whether the recognized changes in vegetation had affected the ways in which the pastoralists used their resources and whether this limited their livelihoods. Thus, pastoralists may perceive changes as

beneficial or costly depending on the utility of such change.

METHODS

Site Description

The general study area consisted of an undulating landscape covered with sand-dunes, and with limestone outcrops at places, traversed by low-lying interdunal depressions (pl.: *omiramba* in the local OtjiHerero language) (Köhler 1959). The sandy soils have low levels of phosphorus and nitrogen (Mendelsohn et al. 2002). Altitude ranges from 1200 – 1450 m above sea-level. The study sites were located between the Epukiro Omuramba and the Eiseb Omuramba in the Otjinene constituency in eastern Namibia (S21° E19°). The long-term rainfall ranges from 300 – 400 mm per annum (Mendelsohn et al. 2002).

Four villages were selected to represent the constituency in terms of land use, local culture, vegetation, landscape and rainfall, and were all within 45 km radius of each other. Oukango and Erindi Otjirarua were the oldest settlements of the sites (Table 6.1). These sites used to have ephemeral water bodies, which allowed for seasonal grazing. Erindi Otjirarua was used for wet season grazing from as early as the late 1920s until the 1950s (Köhler, 1959). According to one of the first residents of Oukango, Mr. Naftalie Mukungu, the village borehole was sunk at the end of 1951. The borehole at Erindi Otjirarua was drilled in 1960 (Mr. Alfeus Kauta, pers. comm. 2002). The boreholes at the other sites, Okatjana and Ombujonjama wells were drilled at the end of 1969 to cater for the translocation of the OvaHerero people from Tses, near Keetmanshoop, in the southern part of Namibia in accordance with the Odendaal Plan to place native peoples on reserves fostered by the apartheid policies of the South African government that controlled Namibia at that time (Mendelsohn et al. 2002). Prior to this resettlement, only a few Khoi San hunter-gatherer families roamed the area (Village elder, Chief Ben Hembapu, pers.

comm. 2002).

The inhabitants of the area

The OvaHerero pastoralists were resettled in the northern Kalahari in 1923 after the proclamation of Epukiro reserve in the same year, which currently consists of Epukiro and Otjinene constituencies. By the end of 1925, 303 adults and 286 children had been moved from the current commercial farms such as Kehoro, Okazeva, Okajombo and other places around Gobabis area and also from Orumbo (a former concentration camp of OvaHerero prisoners of war during the aftermath of the OvaHerero-German war in Windhoek (Köhler, 1959). Livestock numbers increased as more people were resettled in the reserve and, by 1955, when the reserve was divided into two administrative areas, the distribution of livestock in Otjinene and Epukiro areas was as follows: 12 471 cattle, 213 sheep and 2 694 goats; and 11 523 cattle, 90 sheep and 1 198 goats respectively. At this stage, there were 1 295 inhabitants, residing in 15 villages in Otjinene area (Köhler, 1959). These figures increased over the years, and by 2004 there were about 72 620 cattle, 6 875 sheep and 12 125 goats in Otjinene constituency alone (J.J. Ndjarakana, local state veterinary officer, pers. comm. 2005). The populations of other livestock in the Otjinene area are currently: horses (1 365), donkeys (1 234) and mules (19) (J.J. Ndjarakana, pers. comm.). The human population has also increased to 14 932 by the year 2001 (National Planning Commission 2001 census), residing in 125 villages (Abraham Katjiukua, Agricultural extension officer, pers. comm. 2002). This increase in human population is largely due to immigration into the area; population projection for 2001 based on 1955 population and a local population growth rate of 3 % per annum (Namibian national average growth rate) = 5045 people.

Table 6.1. Location, date in which water points were drilled and livestock numbers at the selected sites

Settlement	Geographical coordinates	Borehole drilled (year)	Cattle no. (2002)	Goats no. (2002)	Sheep no. (2002)
Oukango	S21°16.509'; E19°04.904'	1951	561	237	73
Erindi Otjirarua	S21°12.714'; E19°13.871'	1960	916	356	135
Okatjana	S21°02.402'; E19°04.958'	1970	480	202	31
Ombujanjama	S21°00.421'; E19°08.987'	1970	734	157	48

Livestock production is constrained by the availability of surface and groundwater resources. There are currently about 130 operating boreholes in the Otjinene constituency (A. Katjiukua, pers. comm. 2002). Livestock sales started in 1954 with two to three sales per annum during the first few years. Currently, about 24 cattle sales are held and a few small stock auctions take place intermittently in the constituency during the course of the year (A. Kauta – pers. comm. 2002).

Sampling and Survey Approach

Members of 48 out of a total of 65 households in the area were interviewed. The remaining 17 households were absent at the time of the interviews. At least two members of each household participated in the semi-structured interviews (Appendix A). Surveys addressed households irrespective of their social standing and addressed issues pertaining to: 1) household demography, 2) household livestock types and uses, 3) observed long-term vegetation change, 4) utilisation of range resources and livestock browse consumption, and the 5) perception of pastoralists towards vegetation change, particularly with regard to plant composition and woody species proliferation. Additional unstructured interviews were carried out with five knowledgeable informants recommended by the local farmers' association. These were: Messrs: A. Kauta (pastoralist and marketing officer of the Otjinene Farmers' Association), Chief B. Hembapu (pastoralist and village head of Okatjana), N. Mukungu (pastoralist and senior resident of Oukango) and S. Tjahere (pastoralist). The purpose of the study was to: 1)

ascertain the objectives of raising livestock, 2) test the prediction that local farmers have knowledge of vegetation change and browse utilization, 3) determine the main woody plants that support the livelihoods of farmers, and 4) test the prediction that the farmers perceived bush encroachment as a beneficial outcome of vegetation change in the northern Kalahari vegetation type.

Data analyses

We analyzed the data using descriptive statistics and tested significant differences with χ^2 statistics. Means are represented ± 1 standard deviation unless otherwise stated. Reasons for livestock uses were first categorized into three categories of decreasing priority based on a pre-selected list of uses. The pre-selected list was representative of livestock uses among the pastoralists and was derived after consultations with the key informants. In addition to the χ^2 analysis, we used cluster analysis for the analysis of differences and similarities in the respondents' purpose of cattle raising, encompassing: meat consumption, milk consumption, cultural uses, gifts to children, social status, cattle as estate goods and for generating cash income. The cluster analysis was performed on these seven variables representing major cattle uses with 45 cases representing the respondents who owned cattle. A cluster analysis was performed using UPGMA (Unweighted Pair Group Means with Arithmetic Averages) based on a Euclidean distance matrix. Pearson product-moment correlations were also used to determine the relationships between local knowledge of cattle browse consumption and actual field-based browse consumption data obtained from a concurrent study (Chapter 3, in press).

RESULTS

Demography

The pastoralists lived in permanent villages of about 17 ± 3 homesteads, of which each homestead comprised one household. This was comparable to average 15 ± 7 households ($n = 44$) previously sampled across the entire constituency (Ministry of Agriculture, Water and Forestry, unpublished data). Members per household were 16 ± 14 persons. Thus, approximately 272 persons resided in each village. The majority of households were male-headed (77 %, $n = 37$). The age of female household heads was much higher (69 ± 18) than that of their male counterparts (49 ± 17). The pastoralists had been living in these villages for about 29 ± 11 years, while 7 ± 3 homesteads (of the 17 ± 3 SD homesteads) existed in these villages since the first 5 y of water point establishment. Thus, about 41 % of homesteads in the villages were among the first to settle in what used to be virgin lands, except for Erindi Otjirarua and Oukango, which were occasionally used as wet season grazing areas. Hence, residents should have sufficient knowledge of the dynamics of local range resources.

The newer villages, Okatjana and Ombujanjama, had retained the largest percentage of households (50 and 66 % respectively) that originally settled in these villages from 1969 to 1974. Oukango, whose borehole was drilled in 1951, had retained only 29 % of the first households that settled during the first five years of its formal establishment as a village with a permanent water point. Only 20 % of the households at Erindi Otjirarua continued to inhabit the village since they settled from 1960 to 1964.

Reasons for raising livestock

The majority of pastoralists raised cattle primarily to obtain milk and its derivatives (sour milk, butter milk and fat) (93 % respondents) and as a means to generate cash income (82 % of respondents) (Table 6.2). These two uses were significant under the priority-category 1 ($\chi^2 = 117.8, P < 0.05, n = 45$). Under the 2nd priority-category, three uses featured significantly, namely: maintaining a cultural identity (35 %), achieving good social standing (33 %) and giving children cattle as gifts to motivate them to become pastoralists (31 %) ($\chi^2 = 27.5, p < 0.05$). Under the 3rd priority-category, cattle were mainly kept to be part of the estate after one's death (64 %), for meat consumption (51 %), as gifts for children (47 %), and also to maintain a cultural identity (40 %). The pastoralists showed significant preferences for these categories ($\chi^2 = 46.3, P < 0.05, n = 45$).

The cluster analysis showed that the keeping of cattle for meat consumption clustered separately from all other uses. Cash and milk clustered distinctly while, perhaps unsurprisingly, keeping cattle for estate and gift purposes and status and culture formed 2 distinct clusters (Fig. 6.2). The results of the cluster analysis were comparable with the χ^2 analysis with minor deviations. The cluster analysis showed three major distinct groupings (cash+milk; estate+gift and status+culture; meat) (Fig. 6.2).

Table 6.2. Livestock uses categorized by 48 respondents into three priority groups in decreasing order of importance. The asterisks (*) indicate those uses that were significantly highly rated (relative to other uses in each priority category).

Livestock	Priority 1	Priority 2	Priority 3
Cattle	*Milk – 93%	*Culture – 35%	*Estate – 64%
	*Cash income – 82%	*Social status – 33%	*Meat – 51%
	Culture – 20%	*Gifts – 31%	*Gifts – 47%
	Social status – 16%	Cash income – 16%	*Culture – 40%
	Gifts – 11%	Meat – 9%	Social status – 29%
	Estate – 4%	Milk – 4%	Cash income – 2%
		Estate – 4%	Milk – 2%
Sheep	*Meat – 69%	Meat – 30%	*Estate – 69%
	*Cash income – 46%	Culture – 30%	*Gift – 61.5%
	*Culture – 30%	Social status – 23%	*Social status – 46%
	Social status – 7.7%	Cash income – 23%	Culture – 23%
	Gifts – 0%	Gift – 15%	Cash income – 23%
	Estate – 0%	Estate – 15%	
Goats	*Meat – 77%	*Meat – 21%	*Culture – 68%
	*Cash income – 62%	*Cash income – 21%	*Social status– 59%
	*Milk – 29%	*Gift – 12%	*Estate – 53%
	Gift – 9%	Milk – 9%	*Gift – 41%
	Inherit – 0%	Social status– 7%	Milk – 12%
	Culture– 0%	Culture – 3%	Cash income – 9%
	Social status– 0%	Estate – 0%	Meat – 0%

Thirteen pastoralists raised sheep for meat consumption (69 % of the respondents), for generating cash income when sold to individuals or at organised public auctions (46 % respondents), and also for cultural practices and rituals (31 % respondents) (see Table 6.2). These uses yielded significantly higher scores than among other uses considered under the first priority-category ($\chi^2 = 20$, $df = 5$, $P < 0.05$). Priority category two showed non-significant differentiation of uses ($\chi^2 = 1.33$, $df = 5$, $P = 0.97$).

However, uses of sheep for attaining a high social status, serving as gifts and providing for estate goods were significantly highlighted as key uses under the third category of uses ($\chi^2 = 12.17$, $df = 5$, $P = 0.04$).

Goats were primarily raised for meat consumption (77 %, $n = 34$), generating cash income (62 %) and, to a lesser extent, for milk consumption (29 %) (see Table 6.2). These uses were significantly heterogeneous ($\chi^2 = 83$, $df = 6$, $P < 0.05$). Under the second category, generating cash income and meat consumption were equally important and together with the usage for gifts were significantly scored than would be expected ($\chi^2 = 13.33$, $df = 6$, $P = 0.04$). Cultural usage (68 %), social status (59 %), estate (53 %) and gifts to children (41 %) were significantly differentiated under the third priority category ($\chi^2 = 44$, $df = 6$, $P < 0.05$). The respondents who had donkeys ($n = 19$ households) and horses ($n = 29$ households) kept these animals solely for the purpose of draught power and tracking stray livestock. Thus, no second and third priority-categories were identified.

Livestock types and distribution among households

Cattle population was far larger than all other livestock populations. The 48 households had a mean \pm SD of 51 ± 60.5 herd of cattle, 19 ± 24.5 goats, 8 ± 20.4 sheep, 3 ± 3.5 horses and 1 ± 1.96 donkeys. The distribution of livestock among the households was skewed. Three households did not own cattle, 14 did not own goats, 35 did not own sheep, 17 did not own horses and 29 did not own donkeys. The majority of households (60 % and 94 %) owned fewer than 40 cattle and goats, respectively. The majority of households who owned sheep (94 % of 13 households) possessed 30 or fewer sheep. The disparity in cattle holding from 0 – 350 was much wider among households than for goats (range: 0 – 129) and sheep (0 – 125), horses (0 – 15) and donkeys (0 – 7).

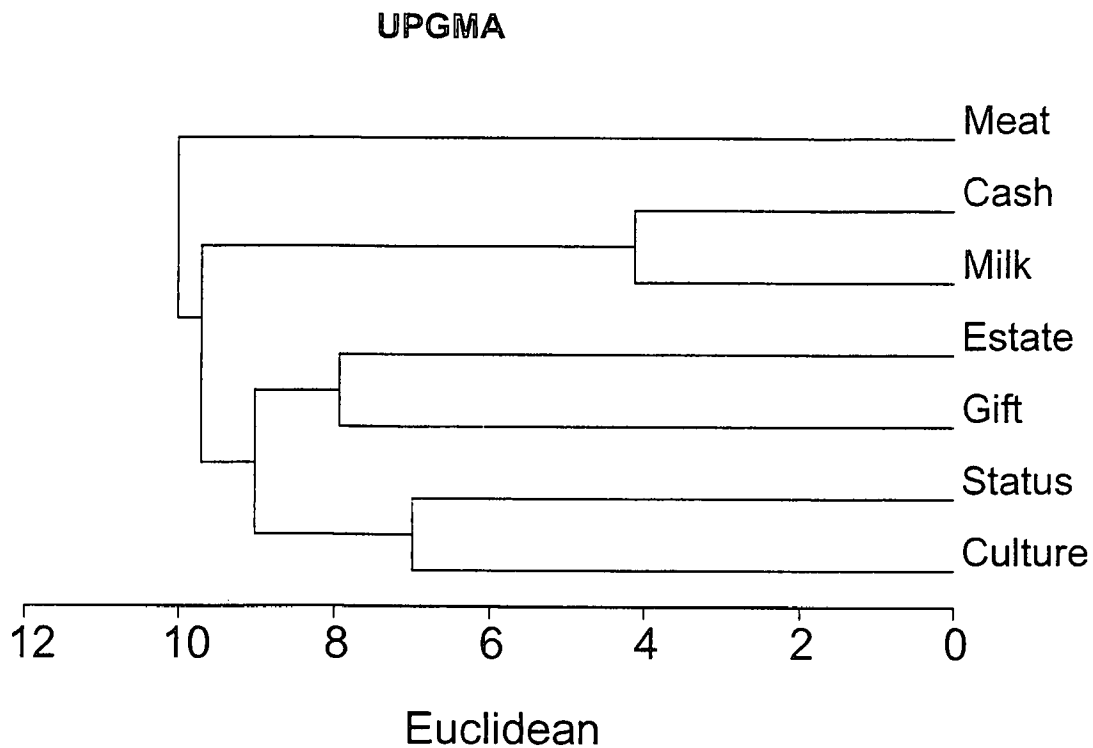


Figure 6.2. Cluster analysis of cattle-ranching priorities for ovaHerero pastoralists. The cluster method used was UPGMA (Unweighted Pair Group Means with Arithmetic Averages) based on a Euclidean distance matrix.

Cattle sales

Two types of livestock sales (auction and permit sales) took place in the constituency. Auctions involve multiple buyers (bidders) and multiple sellers, while a permit sale involves a single buyer and multiple sellers at unit prices announced in advance for specified sex and live-mass of the animals. We obtained data for 12 sales (July to December 2003), consisting of 11 auction sales and one permit sale. A total of 5 324 cattle (4 909 at auctions, and 415 at the permit sale) were sold, while 467 cattle were withdrawn from the auctions. The fate of the withdrawn animals varied; some were sold to private individuals who offered higher prices, re-sold at future auctions when sellers were not happy with prevailing prices or

transported to Meatco (a meat company) some 280 km away where animals were likely to fetch higher profits if transport cost was minimized. Monthly cattle sales were 810 ± 182 during the latter half of 2003 (Table 6.3; cattle sold over a six month period). Sales of male animals exceeded that of female animals (Table 6.3; cattle sold over a six month period). The disparity between male and female sales decreased towards the calving season (December) (Table 6.3).

For both sexes, weaners (six to eight months-old calves recently weaned) and young adults with an average live-mass of 126 and 225 kg dominated the sales, more so for the male animals (Table 6.4). These components of stock sales made the most significant contribution to the sales (males: $\chi^2 = 4785.39$, $P < 0.05$, $df = 10$; female: $\chi^2 = 1837.999$, $P < 0.05$, $df = 9$). Only a few adult males (oxen and bulls) were available for sales. Farmers kept their female animals longer on the range and only sold as a last resort, resulting in a higher proportion of older female animals (heifers and cows of > 301 kg) sold compared to their male counterparts (Table 6.4). Annual cattle sales were estimated between 11 000 and 12 000 animals of the about 72 620 cattle in the Otjinene constituency (A. Kauta, pers. comm.). This gives an annual off-take between 15.3 % and 16.5 %. We estimate annual sales at 10 648 based on the half-yearly sales ($5\,324 \times 2 = 10\,648$).

Table 6.3. Monthly cattle sales from July to December 2003. Figures between brackets indicate male or female animal sales as a percentage of the total over the stated period. Mixed sales are undifferentiated animals sold at a permit sale.

Month	Male animals	Female animals	Mixed sales	Totals
July	751 (68.3 %)	348 (31.7 %)		1099
August	470 (65.4 %)	249 (34.6 %)		719
September	467 (53.2 %)	411 (46.8 %)		878
October	439 (54.6 %)	365 (45.4 %)		804
November	274 (50.1 %)	273 (49.9 %)		547
December	192 (48.6 %)	203 (51.4 %)	415	395 (+ 415)
Total	2593 (58.4 %)	1849 (41.6 %)		4442 (4857 for all sales)
Mean	432	306		810 (for all sales)
SD	193.4	82.0		182.0 (for all sales)

Table 6.4. Cattle sales from July to December 2003 indicating weight category, mean weight (kg) for each weight category, number of animals sold and unit price per kg of live-mass. (Average exchange rate was US\$ 1 : N\$ 6.50 during the period under study). The asterisks (*) show the live-mass classes that made significant contribution to sales.

Live-mass class (kg)	Male animals				Female animals			
	Mean weight (kg)	Number of animals sold	Mean N\$/kg	Unit price (N\$)	Mean weight (kg)	Number of animals sold	Mean N\$/kg	Unit price
≤ 100	90.3	61	5.85	530	86.2	18	5.02	432
101 – 150	126.5	880*	6.79	862	125.6	291*	6.12	778
151 – 200	176.4	971*	7.11	1253	177.6	572*	6.53	1159
201 – 250	222	380*	6.74	1499	225.7	365*	6.12	1380
251 – 300	275.6	142	6.18	1700	277.3	167	5.51	1530
301 – 350	323.3	32	5.52	1786	327.9	127	4.57	1494
351 – 400	372.6	27	5.28	1968	377.6	125	4.62	1746
401 – 450	416.3	32	4.84	2012	423.5	110	4.84	2047
451 – 500	489	16	4.50	2200	473.5	54	4.94	2338
501 – 550	517.3	28	5.08	2630	533	9	5.67	3016
551 – 600	570.4	15	3.81	2169	-			
601 – 650	620	3	4.32	2683	-			
651 – 700	657.3	3	4.03	2647	-			
701 – 750	-				-			
751 – 800	757.3	3	4.56	3450	-			

Vegetation composition and bush encroachment

A significant number of respondents (81 %, $n = 48$) indicated that the composition of woody and herbaceous vegetation had changed significantly since they settled in the villages ($\chi^2 = 45.5$, $df = 2$, $P < 0.05$). When asked where bush encroachment had occurred, a significant 79 % of the respondents said that it has occurred over the whole rangeland ($\chi^2 = 4.5$, $df = 2$, $P < 0.05$), while 23 % said that most encroachment was within 1000 m from water points, a few said it occurred far away (8 %) and some (15 %) were not certain. The majority of respondents (80 %) regarded *Acacia mellifera*, *Terminalia sericea*, *A. erioloba* and *Combretum collinum* as contributing significantly to bush encroachment in the study area ($\chi^2 = 60.4$, $df = 8$, $P < 0.05$), (Table 6.5). According to 90 % of the respondents, the herbaceous *Sida cordifolia* has increased in density within the village centre (the area between the centrally-located water point and the surrounding homesteads - generally within 600 m of the water points).

Despite forming thickets, *A. mellifera* was the most preferred firewood species (96 % of respondents), followed by *A. reficiens* (40 %), *T. sericea* (38 %) and *Combretum collinum* (31 %) among nine firewood species (Table 6.5). These four species were used significantly more than others for firewood ($\chi^2 = 107.2$, $df = 8$, $P < 0.05$). *Acacia erioloba* and *T. sericea* were mainly used in the construction of livestock pens, as poles and droppers for fences, respectively ($\chi^2 = 63.6$, $df = 3$, $P < 0.05$). In addition, *T. sericea* was almost the only tree used in the construction of houses ($\chi^2 = 103$, $df = 3$, $P < 0.05$).

Browse consumption

The availability of pre-rain flush of deciduous vegetation during the hot-dry season plays a more critical role in the survival of livestock in the study area than during any other time of the year (83 % respondents, $\chi^2 = 88.5$, $df = 3$, $P < 0.05$). Pastoralists highlighted 13 species browsed by cattle during

the hot-dry season. Ten of these species were incorporated into the χ^2 analysis, while three (*Mundulea sericea* and *Rhus tenuinervis* and *Rhigozum brevispinosum*) were excluded because of their very low frequency. *Terminalia sericea* (94 % respondents), *Combretum collinum* (52 %) and *P. nelsii* (46 %) obtained significantly higher scores than the remaining seven species ($\chi^2 = 87.3$, $df = 9$, $P < 0.05$) (Table 6.5). A correlation of previously-obtained data for the actual time cattle spent consuming a particular species (Chapter 3 in press) and pastoralists' ranking of browse species contribution to cattle diet was highly significant (Spearman rank correlation, $r = 0.70$, $P < 0.05$, $n = 13$).

The timing of pre-rain flushing is determined by the amount of rain received during the preceding rainy season (S. Tjahere & A. Kauta, pers. comm.). If good rains fell, then flushing may be initiated as early as during late September. However, poor rains would often delay flushing. Pre-rain flushing started during the third week of October during the two years of field observations (2001 and 2002). During winter (June-August), key respondents (A. Kauta, S. Tjahere & N. Mukungu pers. comm.) indicated that cattle feed on leaf litter of *A. mellifera*, pods of *A. erioloba* and *A. hebeclada*.

Table 6.5. Woody plants identified by respondents (n = 48) as contributing to bush encroachment, firewood and hot-dry season browse. The asterisks (*) indicate those species that were considered to contribute significantly to bush encroachment, firewood and browse consumption ($P < 0.05$). The numbers in the table represent percentages of respondents (%).

Woody species	Encroaching species	Firewood species	Browsing species
<i>Acacia ataxacantha</i>	2	-	-
<i>A. erioloba</i>	40*	15	29
<i>A. fleckii</i>	6	19	-
<i>A. hebaclada</i>	23	2	29
<i>A. mellifera</i>	56*	96*	6
<i>A. reficiens</i>	8	40	-
<i>Bauhinia petersiana</i>	-	-	27
<i>Boscia albitrunca</i>	-	-	17
<i>Burkea africana</i>	-	-	-
<i>Combretum collinum</i>	29*	31	52*
<i>Commiphora africana</i>	-	-	4
<i>Dichrostachys cinerea</i>	4	4	-
<i>Grewia flava</i>	4	-	31
<i>Philenoptera nelsii</i>	-	17	46*
<i>Terminalia sericea</i>	42*	38	94*

Perceptions of woody proliferation

Pastoralists perceived bush encroachment as a positive outcome of vegetation change (60 % of the respondents ($\chi^2 = 34.2$, $df = 3$, $P < 0.05$)). Of the 35 respondents, 80 % indicated that bush proliferation provided an opportunity for reliable forage resources for livestock during the hot-dry season and drought years ($\chi^2 = 312.6$, $df = 1$, $P < 0.05$). A few pastoralists (14 %) stated that the abundant trees also provided shelter for livestock and wildlife in addition to materials for construction and fuel wood. Thus, current levels of bush encroachment were regarded as beneficial in terms of pastoral production and human wood consumption. In contrast, 58% of those respondents who stated that bush encroachment was detrimental highlighted the impenetrability of thickets as the main problem rather than lowered grass production (42 %), although this difference was not significant ($\chi^2 = 5.47$, $df = 2$, $P = 6$).

DISCUSSION

Livestock production in variable environments

Pastoralists on African drylands have long been accused of keeping too many livestock beyond the ecological carrying capacity (Abel 1993; Lusigi & Buursink 1994), thus causing land degradation due to heavy grazing and soil trampling (Harrison & Shackleton 1999). However, some studies have shown that livestock numbers remain below the nominal carrying capacity on African drylands for much of the time, because of recurrent droughts (Ellis & Swift 1988; Burke 2004). Following the latter view, livestock numbers are not coupled to plant biomass production; rather rainfall was the critical factor determining plant productivity and livestock populations (Ellis & Swift 1988). In contrast, Illius & O'Connor (1999) argued that although plant biomass was determined by rainfall pattern, livestock may exert pressure on plants in certain key habitats, even at low stock densities, simply because insufficient rainfall may produce plant biomass that is too low to support available livestock biomass. Consistent with this, Desta & Coppock (2002) argued that grazing alters vegetation and that density-dependent factors influence cattle populations. Hence, they indicated that a dynamic carrying capacity does exist in arid and semi-arid pastoral systems. Cattle-plant biomass coupling under frequent forage scarcity reduces the ability of key resources, such as perennial grass and browse species, to continue providing a steady flow of forage resources (Illius & O'Connor 1999). The reduced stability and regenerative vigor of key resources increases the variability of interannual forage production and reduces the amount of standing biomass that could reach the foregoing growing season (Illius & O'Connor 1999). This leads to greater variability in forage production and a mismatch between livestock density and plant biomass, and consequently increases herd instability (Desta & Coppock 2002). Hence, livestock experience intermittent deaths. Westoby et al. (1989) proposed an opportunistic stocking rate in semi-arid rangelands based on (expected) annual biomass as a function of rainfall variability. This is problematic to maintain in highly variable environments because tracking stocking densities to match forage

production increases the vulnerability of subsistence pastoralists to droughts (Abel 1993). Therefore, further destocking urged by development partners in Africa can only be successful if the productive potential of the herd can be re-established more rapidly after droughts than is possible from depleted resources (Illius et al. 1998). Thus, high costs associated with restocking in Namibia will continue to keep subsistence pastoralists away from destocking policies. It was recently demonstrated that destocking policies for subsistence pastoralists resulted in lowered outputs and increased vulnerability to recurrent droughts (Illius et al. 1998), but that such policies were advantageous to commercial farmers because they reduce inter-annual variability of sales and do not adversely affect profitability (Campbell et al. 2000; Beukes et al. 2002). Ward et al. (2004) has suggested an appropriate way to calculate optimal local stocking densities by establishing multiple raingauges (and associated grass production measurements) across the range rather than using mean rainfall isohyets to determine forage production in arid and semi-arid environments. This would allow for a more accurate tracking system in commercial pastoral systems.

The essence of livestock raising

The OvaHerero culture revolves around their cattle and for them, cattle had always been the basis of their existence (Pool 1991). Mr. N. Mukungu, a senior resident of Oukango, said that “they (cattle) are the owners of the struggle for the land” (pers. comm. 2002). Thus, had there been no cattle, they would probably not have engaged themselves in the numerous battles for grazing areas against the Nama people over a period of 40 years during the latter half of 1800’s (Pool 1991), the liberation war against the German colonial establishment at the beginning of the 20th century, which resulted in the destruction of between 65 000 and 75 000 lives, with only about 15 000 starving and fugitive Ovaherero remaining alive by the end of 1905 (Silvester & Gewald 2003), and recently the struggle for independence from South Africa, which ended in 1990.

However, the purpose of raising cattle is gradually changing. Historically, cattle were kept for consumptive uses, religious rituals and as a status symbol (Pool 1991). In this study, the respondents clearly raised cattle primarily for consumption of milk and milk by-products (93 % of respondents) and equally so to generate cash income (82 % of respondents). The high offtake of male weaners and young adults in particular is an indication that the pastoralists have commercialized their production system. The estimated annual cattle offtake in the study area (15.3 – 16.5 %) was above the national offtake (12.6 %) for all herds in 2004 (Meat Board of Namibia 2005). In agreement with a Zimbabwean study, social and cultural functions of livestock raising were important, but these were generally secondary or tertiary to economic functions (Barrett 1992). Pastoralists hold onto their female animals for longer, unless the animals were old or the male stock was depleted (A. Kauta, pers. comm.). Thus, female animals were kept to stabilize or increase the breeding stock to ensure a sustainable flow of benefits in an otherwise unpredictable environment.

The ovaHerero people remain attached to their culture, despite the challenges of modern life to diversify their sources of income to meet the growing need for cash to provide for school fees, modern medication, transport and food, among other needs. Hence, the second priority of raising cattle was to retain a cultural identity (35 %), achieve a good social standing by possessing a sizeable number of cattle (33 %) and to ensure that the younger generation continue with pastoralism (31 %). Goats and sheep were mainly used for meat consumption (77 % and 69 %). Other livestock, such as donkeys and horses, were used in the production of cattle and other household activities such as collecting firewood and water, and tracing stray animals.

Vegetation change and browse utilisation

Vegetation composition and structure have changed significantly over the past 32 – 51 y of sedentarization of pastoralists in the northern Kalahari. Bush encroachment is usually viewed as

reducing rangeland productivity (Moleele et al. 2002; De Klerk 2004). However, the generalization that bush encroachment in Namibia has led to a decline in beef production nationally (De Klerk 2004) is a simplistic one. This widely accepted notion is based solely on bush encroachment on freehold rangelands with specific production objectives, and which are largely confined to the Thornbush Shrubland, Highland Shrubland and the Karstveld vegetation types (Bester & Reed 1997). The northern Kalahari is predominantly vegetated by broad-leaf deciduous trees, a number of which constitute key browse for cattle during the hot-dry season when grass availability (and presumably quality) is at its lowest (Moleele 1998). Key resources are those that: 1) increase the probability of livestock survival until sufficient primary production is attained in the coming rainy season, and 2) sprout sufficiently to provide forage that sustains a given (profitable) number of livestock, even with minimal rainfall. Examples of key resources for cattle would be: perennial grasses, evergreens, pre-rain flushing deciduous trees, shrubs and leaf litter (Illius & O'Connor 1999). In this study, the respondents regarded *T. sericea*, *P. nelsii* and *C. collinum* as the key browse species during the hot-dry season. The pastoralists' knowledge compared well with actual browse consumption ($r = 0.70$). *Terminalia sericea*, *Bauhinia petersiana* and *P. nelsii* constituted 74.5 % of the total browse consumed during the hot-dry season, and of these browse species *P. nelsii* was the most preferred species (Chapter 3 in press).

The abovementioned key browse resources are perennial, and therefore experience minimal inter-annual fluctuations in biomass production, providing a steady flow of benefits to cattle production. However, it is possible that cattle feeding on browse may not achieve a comparable body condition to those foraging on grass, as woody plants are usually chemically defended with anti-nutritive substances such as condensed tannins and have high crude fiber concentrations which reduce the digestibility of dietary tissues (Launchbaugh 2001). However, it has been demonstrated that a number of woody species on African savannas reduce the synthesis of anti-herbivore substances when frequently browsed (Du Toit et al. 1990; Augustine & McNaughton 1998; Ward & Young 2002). Katjiua & Ward (unpublished data) have recorded lowered condensed tannin concentrations in *Grewia flava* and *T. sericea* exposed to

frequent herbivory under field conditions in the current study area. In addition, cattle browsing resulted in elevated crude protein content in *T. sericea* under natural conditions (Chapter 4).

Extent of vegetation change

Livestock foraging distance from water points contracts as forage resources become abundant during the wet season, but expands with increasing food shortage, particularly during the hot-dry season (pers. obs.). Thus, cattle impact may overlap with neighbouring villages during the dry seasons, especially where the inter-village distance is shorter than 10 km (Walker et al. 1987). The mean \pm SD shortest distance between two adjacent villages in the Otjinene constituency was 6.6 ± 4.5 km, while the longest distance was 14 ± 11.95 km ($n = 44$ villages) (Ministry of Agriculture, Water and Forestry, unpublished data). Thus, the impact of cattle on rangelands accentuates with the scarcity of forage resources and shorter inter-village distances. In the current study area, vegetation change has extended far into the range in tandem with foraging distance (Chapter 2).

Perception of woody proliferation

The current state of vegetation change in the northern Kalahari had beneficial outcomes for the livelihoods of pastoralists. Woody vegetation provided browse for livestock production, and served as a source of firewood and timber for construction of houses and livestock pens. Other uses of woody vegetation included shelter for livestock and wildlife. In the arid region of southern Ethiopia, the Borana pastoralists also perceived vegetation change in the form of bush encroachment as beneficial to the productivity of camels and goats as well as to cattle production (Oba & Kotile 2001). Woody vegetation in arid and semi-arid environments has increasingly been recognized as an important component in supporting both people and animal populations (Bergström 1992).

Implications for management

The Otjinene constituency, and much of the northern Kalahari communal rangelands, has a potential for sustainable livestock production. A combination of factors, such as biophysical, socio-economic factors and institutional arrangements, attest to this:

1) **Biophysical factors** – The abundant browse species such as *T. sericea*, *P. nelsii*, *B. petersiana* and *Grewia* species may sustain profitable livestock herds and flocks if their regenerative vigor is maintained by promoting appropriate harvesting practices such as frequent herbivory that minimize the accumulation of carbon-based secondary compounds, while enhancing foliage protein content of browse.

2) **Socio-economic factors** – Diversifying sources of income to include options such as poultry, community-based wildlife conservation (conservancies), high value dryland crops such as dates and olives, and remittances from off-village incomes rather than relying solely on livestock would promote sustainable livelihoods. Increased livestock offtake and value addition to livestock products will further enhance income from livestock production.

3) **Institutional arrangements** – The presence of a water point committees and village heads, and the recently approved National Land Tenure Policy (Ministry of Lands and Resettlement 2005) which devolves exclusive user-rights to communities at village-level, will provide framework conditions that are conducive to sustainable range resources management at the community level. Exclusive land tenure rights at community level were identified as key conditions for sustainable resource management, and can significantly facilitate efforts to reduce and / or reverse causes of land degradation (Dewdney 1996). Furthermore, the relatively low human densities (0.8 persons/km²) (Namibian National Planning Commission 2001 census) in the northern Kalahari have made it possible that some areas are lightly utilized, with the potential for rotational rangeland utilization.

CONCLUSIONS

1. Cattle raising is the dominant source of livelihood among the OvaHerero pastoralists of Otjinene constituency.
2. Livestock production around permanent water points has had a significant impact on the structure and composition of plant species over the past 32 to 51 years in the northern Kalahari. However, the resultant vegetation change has been beneficial to pastoral production, and has acted as a source of fire wood and construction materials. Bush encroachment may have decreased herbage production, but has increased browse abundance and thereby benefits pastoral production, particularly during the hot-dry season.
3. The OvaHerero raised cattle primarily for consumption of milk and milk products, and to generate cash income. Although not a priority, livestock, especially cattle, remain central to their culture and existence, and serve as a symbol of social status.

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CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1. INTRODUCTION

The establishment of artificial water points in the northern Kalahari, resulted in permanent pastoral settlements, which led to the expansion of livestock production in this semi-arid environment (De Klerk 2004). The combined effects of overgrazing by domestic cattle and proportionally less browsing by large mammalian herbivores have tilted the balance between woody species and grasses into woody plant-dominated rangelands (Aharoni and Ward 1997, Moleele 1998, De Klerk 2004). The impact of livestock accentuates with proximity to the water points (Perkins and Thomas 1993, Van Rooyen et al. 1994), but can extend beyond 7 000 m from water points (Jeltsch et al. 1997).

Overgrazing and bush encroachment have reduced the biomass of grasses available for grazers (Moleele et al. 2002, De Klerk 2004), particularly during the dry seasons on Namibia's rangelands (Ward et al. 1998). However, the role of increased availability of browse (resulting from bush encroachment) in providing feed to domestic livestock in arid and semi-arid environments has been recognized (Bergström 1992, Moleele 1998, Illius and O'Connor 1999). Browse possesses physical and chemical features that may deter mammalian herbivores (Shipley and Yanish 2001). These include, among others: thorns, prickles and secondary metabolic compounds such as polyphenols (Launchbaugh 2001). Herbivores are faced with the challenge to forage optimally to maximize the rate of nutrient or energy intake from an array of defended woody plants (Illius et al. 1999), particularly in the advent of bush encroachment. Patch and diet selection are important elements to achieve diet optimization (De Vries and Daleboudt 1994).

Plants have evolved two basic adaptive traits in response to herbivore damage, these are: resistance and tolerance traits (Van der Meijden et al. 1988, Mauricio 2000). A resistance trait is any plant character that influences the amount of damage a plant suffers (Mauricio 2000). Resistance traits such as thorns and secondary compounds deter herbivory (Rohner and Ward 1997), while tolerance traits allow plants to experience damage without a reduction in fitness (Tiffin 2000). Regrowth capacity is a character of plants that allows them to maintain fitness in the face of potentially fitness-reducing damage (Mauricio 2000, Pilson 2000). These traits can coexist in the same individual of a particular species, but the extent of both intrinsic and extrinsic factors that a plant experiences may determine the ratio in which resistance and tolerance traits are expressed (Mauricio et al. 1997, Tiffin and Raucher 1999, Mauricio 2000).

Knowledge of the dynamics of range resources and the response of such resources to grazing and browsing have a major influence on livestock husbandry and options for sustainable rangeland utilisation. Pastoral production in arid and semi-arid environments demonstrated that pastoralists are able to cope with the variability and dynamics of rangeland resources, by following their herds to suitable resource patches or simply migrating to high resource patches (Ellis and Swift 1988). Thus knowledge on what the animals feed on or where and when they feed on the forage species is important for the long-term pastoral livelihoods.

This study therefore focused on: firstly, the impact of livestock production on the rangelands of the northern Kalahari; secondly, cattle diet selection during the hot-dry season when grass biomass is usually at its lowest level; thirdly, the response of a major browse species, *Terminalia sericea*, to cattle herbivory in terms of its regrowth capacity (tolerance traits) and production of condensed tannin (resistance trait); and finally, the study investigated indigenous knowledge and perceptions of livestock impacts on the rangelands, cattle diet selection, and livestock management practices.

7.2 LIVESTOCK IMPACTS ON VEGETATION AND SOIL OF THE KALAHARI

The impacts of livestock on plant structure and composition, and on soil were accentuated with proximity to the artificial water points, and differed from measurements taken further away from the water points (Chapter 2). These findings were in agreement with previous studies in the Kalahari (Tolsma et al. 1987, Perkins and Thomas 1993) and elsewhere in arid and semi-arid environments (Pickup 1994). Livestock impacts around artificial water points appeared to be confined to the immediate area around water points. Woody species diversity and structure, and herbaceous diversity and abundance did not differ significantly from 600 m to 4000 m away from water points. The high abundance of the few herbaceous species, such as the unpalatable *Sida cordifolia*, near water points is consistent with the suggestion that high above-ground interspecific herb competition would reduce species diversity, but increases the abundance of a few species (Wilson and Tilman 1991). Woody and herbaceous species diversity at the water points (200 m) was 29 and 55 % respectively of the diversity measured 600 – 4000 m away from the water points. High livestock trampling and selective feeding near the artificial water points may have facilitated the establishment of species such as *S. cordifolia*.

In contrast to the limited extent of livestock impacts around water points highlighted in chapter 2 of this study, simulation models predict that such impacts may extend as much as 7000 m further into the range (Pickup 1994, Jeltsch et al. 1997). This apparent contradiction emanates from the absence of long-term data on historical impacts of livestock that includes measurements before permanent settlement by pastoralists. Long-term observations by pastoralists in the northern Kalahari (this study) revealed that vegetation change has occurred all over the range and that bush densities have increased since they settled in the area some 32 to 51 y ago (Chapter 6). This observation is generally consistent with the simulation models.

7.3 CATTLE DIET SELECTION

Cattle, under conditions of low grass biomass, consumed more browse than grasses during the hot-dry season in the northern Kalahari communal rangelands (Chapter 3). Heightened browse consumption of growth resulting from a pre-rainflush during the hot-dry season has been attributed to higher quality of browse during this period than later in the growing season (Owen-Smith 1994, Augustine and McNaughton 1998). Sprouting deciduous plants are under pressure to allocate resources to new growth rather than to anti-herbivore secondary compounds (Augustine and McNaughton 1998). Furthermore, heavy and frequent herbivory increased crude protein, but lowered condensed tannin and fiber contents (Chapter 3). Similar trends regarding crude protein and condensed tannin were recorded by Du Toit et al. (1990) in the Kruger National Park (South Africa) and Ward and Young (2002) in the Mpala Research Centre in north-central Kenya.

In contrast with McArthur et al. (1993) and Aerts et al. (1999), that condensed tannin is one of the most important and abundant secondary compound that deter herbivory, this study found no evidence to suggest that condensed tannin content in *T. sericea* deters herbivores. However, browse quality and the ratio of nutrient to secondary compounds were more important than nutrients (crude protein or phosphorus content) alone in foraging decisions (Chapter 3). Cattle browsed in a way that showed that diet optimization, involving a trade-off between diet quality, quantity and availability on the range explained browsing behaviour much better (Chapter 3). This is consistent with Illius et al.'s (2002) contention that diet optimization determines herbivore foraging behaviour. A multiple linear regression explained much of the variation ($R^2 = 93.9$) in diet selection, and highlighted that crude protein, phosphorus and acid detergent lignin were most important features of diet quality which determined browse selection by cattle (Chapter 3).

The role of browse component in livestock production in arid and semi-arid environments has been

recognized (Bergström 1992, Woodward and Coppock 1995, Scoones 1995, Moleele 1998, Illius and O'Connor 1999). Declining grass biomass for grazers due to overgrazing and bush encroachment in arid and semi-arid environments demands that research is focused on quantifying browse carrying capacity, browse nutritional value and browse responses to herbivore damage to ensure long-term exploitation of this key resource.

7.4 BROWSE RESPONSE TO HERBIVORE DAMAGE

The allocation of photosynthetic products into resistance and tolerance traits by *T. sericea* was a complex function of the factors that determine the internal resource status of the plant. These factors were: soil nutrients, soil moisture and the degree of damage the plant suffered. Condensed tannin concentration was 22.5% and 21.5% higher under low soil nutrients and low soil moisture conditions than under conditions of high soil nutrients and high water contents (Chapter 5). These results are in agreement with the reviews by Herms and Mattson (1992) and Stamp (2003), which stated that nutrient limitation and drought conditions slow down growth more than photosynthesis, resulting in excess photosynthetic products being shunted into storage and production of secondary compounds. Improved soil moisture and soil nutrients enhanced growth in the present study. The latter result is consistent with the Resource Availability Hypothesis (Coley 1985).

Furthermore, the responses of resistance and tolerance traits to herbivore damage depend on the resources available to the plant (Strauss and Agrawal 1999, Meyer 2000) and the degree of damage a plant suffers (see review by Stowe et al. 2000). In this regard, *T. sericea* compensated for damage in three ways: over-compensation, full-compensation or under-compensation (Chapters 4 and 5). Compensation, in the context of this study, refers to the extent *T. sericea* recovered from damage in terms of the production of phytochemicals, fiber or replacement of lost tissues. Over-compensation occurred under conditions of low resources which may have constrained growth, as a result which may

have increased storage (see review by Koricheva et al. 1998), which in turn is proposed to aid over-compensatory responses to herbivory (Hochwender et al. 2000). In addition, this study further suggests that herbivory should either be moderate or, if it is high, should be of short duration and sporadic for over-compensation to occur. Otherwise, when damage is high and frequent, as was the case with *T. sericea* and *Grewia flava* near water points, under-compensation is likely to occur. Similar results, but for secondary compounds, were reported by Du Toit et al. (1990), and Ward and Young (2002) working on *Acacia* species. Thus under-compensatory responses appear to result from exhaustion of plant reserves which limits the allocation of photosynthetic products to storage structures and production of secondary compounds, but instead directing such products primarily to regrowth. Consequently the regrowth of frequently damaged plants becomes relatively more palatable with high nutrient contents than with carbon-based secondary compounds.

Full-compensatory response occurred under conditions of high resource availability. This major result suggests that resources available to plants enables plants to achieve an internal resource balance which is sufficient to sustain plant fitness, therefore over-compensation would have potentially represented a marginal opportunity cost to plant fitness. According to Hochwender et al. (2000), over-compensation results from storage prior to plant damage in resource-poor environments. Thus over-compensatory response may contribute to fitness probably because recurrent damage could threaten the survival of plants in resource-poor environments. This may be in agreement with the hypothesis that plants use information from their environment to induce defensive traits if past or current herbivory is a reliable predictor of future risk of herbivory, and if herbivory reduces plant fitness (Karban et al. 1999).

This study also demonstrated that the resistance and tolerance traits of *T. sericea* do not occur independently. This important result was consistent with findings by Abrahamson and Weise (1997) and Mauricio (2000). *Terminalia sericea* used both defensive strategies with varying degree of expression, depending on the resources available and the degree and frequency of herbivory. This was

also consistent with the results of Van der Meijden (1988) that resource availability determines the extent to which a plant allocates resources to tolerance and resistance traits. Furthermore, the compensatory responses of both resistance (e.g. condensed tannin, acid detergent fibre and neutral detergent fibre) and tolerance traits (e.g. leaf size and leaf cluster size) behaved in the same manner upon plant damage (Chapters 4 and 5).

The response of *T. sericea* to herbivore damage in the semi-arid savanna ecosystems of the northern Kalahari (Chapters 4 and 5), suggests that if the natural levels of carbon-based secondary compounds are acceptable to herbivore consumption, then browse consumption on resource-rich soils can be maintained without the plant having to over-compensate secondary compounds. However, if the natural levels of the secondary compounds are high under resource-poor conditions and are able to reduce herbivory, then high and frequent plant damage under high stocking density will improve palatability through limited allocations to secondary compound relative to regrowth. But if herbivory is not sufficiently frequent, over-compensatory response will further make browse unacceptable to herbivores. This is probably a safer strategy for *T. sericea* under resource-poor conditions of the Kalahari, because under natural conditions herbivory in broad-leafed savanna in the southern Kalahari is generally low (less than 10% of above-ground primary production) (Scholes and Walker 1993) and could result in over-compensation. However the commonly high and frequent herbivore damage near water points would result in increased palatability, thus making survival of *T. sericea* difficult. Livestock impacts through trampling may also prevent plant recruitment. This may be the reason for the absence of *T. sericea* within 600 m of the artificial water points (Chapter 2).

7.5 PASTORALISTS' OBSERVATIONS AND PERCEPTIONS

The OvaHerero are traditional cattle pastoralists, and are more animal-dependent than any other group in Namibia. Historically, they kept large herds of cattle for consumptive uses, religious rituals and as a

status symbol (Pool 1991). However, this situation has changed, because nowadays cattle are mainly raised to generate cash income and for consumption of milk and milk products, while maintaining a cultural identity had a lower priority (Chapter 6). Cattle are no longer killed just for meat consumption, but only at special occasions such as religious and wedding ceremonies. Sheep and goats are the ones kept primarily for meat consumption. The results suggest that various uses of livestock can evolve parallel to maintaining a cultural identity – that of keeping livestock, particularly cattle for religious purpose.

Pastoralists' observations of bush encroachment and cattle browse consumption were consistent with field data collected during the same period of the study (Chapter 6). The majority of pastoralists had observed extended spread of bush encroachment since they settled in the villages, while field data revealed a sparse bush density at the water points but a consistent high density away from the water points (600 – 4000 m).

The pattern of browse consumption by cattle was highly correlated with pastoralists ranking of browse consumption, in terms of the amount of different browse species contributing to cattle diet (Chapter 6). However, pastoralists' observations did not take into account the abundance of browse on the range, hence could not determine browse preference. In addition to being a valuable perennial asset for domestic animals, woody vegetation was used for the construction of livestock pens, houses and for fire wood. Thus these multiple uses of woody plants made the current state of bush encroachment in the northern Kalahari not being perceived degradation but as a beneficial process to the local pastoral communities. A similar positive perception regarding increasing bush densities was reported in southern Ethiopia among the Borana pastoralists where bush encroachment was perceived as beneficial to the productivity of camels, goats and cattle (Oba and Kotile 2001).

This study raises a number of outstanding questions for future research for the pastoralist system under consideration and the ecology of the Kalahari rangelands in general. These questions are:

- How much browse is produced and what portion of it is consumed by the domestic animals in relation to the available herbage?
- Given that deciduous plants do not flush at the same time during the hot-dry season, how does this temporal variability affect the foraging behaviour of cattle?
- What is the nutritional value of the key browse species and if deficient in some ways, how best (in terms of affordability and accessibility of supplements) can pastoralists minimise the shortfall particularly during the hot-dry season?
- What frequency of herbivory should be maintained to ensure a healthy regrowth of browse while enhancing its palatability?
- How best, in terms of physical constraints and financial costs, can pastoralists improve the soil fertility of the rangelands to enhance foliage quality? and
- How best, in terms of overcoming problems associated with common-pool resources such as prisoner's dilemma and the logic of collective action (Ostrom 1990), should local-level resource management institutions be moulded and or strengthened to create incentives for pastoralists to maintain or improve land productivity for domestic animal production?

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APPENDIX

QUESTIONNAIRE USED FOR INTERVIEWING PASTORALISTS

Management of Livestock and Range Resources in the Omaheke

BUSH ENCROACHMENT

BROWSE UTILISATION

A Questionnaire Survey

Village name : _____

Village Age : _____

Number of households : _____

Date : _____

Interviewer : _____

A: Household

1. Head of household : Female ; Male
2. Age of household head : _____
3. Period of residence in the village (years) : _____
4. Household size : _____
5. Number of children : _____

B: Farming activities

6. Use the numbers 1,2, and 3 to **prioritise the utilization** associated with each of the livestock that the household has. (For example, the numbers 1 and 3 in the box below would mean that pigs are **mainly** kept for social status and **rarely** sold to generate money). 1 = most of the times, 2 = sometimes, 3 = very rare situation.

C:

	To Sell or to make money	(Ombazu): Culture and wedding, funeral, rituals	(Ombuniko motjwana): Social status	(Pe kare ovirumatwa): Inheritance	(Okukekera ovanatje): gift to children	For meat	For milk	For draught power, to be used in work
Cattle								
Sheep								
Goats								
Donkeys								
Horses								

Ownership

7. Indicate number of livestock owned by the household.

	Cattle	Sheep	Goats	Donkeys	Horses
Numbers					

8. How are livestock usually acquired? Indicate with a 1 for the most used method by which livestock are acquired and 3 for the least method. 2 would be intermediate.

Methods of acquisition	Choose 1, 2 and 3
Purchase	
Gift (okukekerwa)	
Inheritance (okurumata)	

D: Livestock Management

9. Provide the names of the supplements you offer to your livestock.

10. During which period (s) of the year do you provide fodder supplements?

11. How many bags (or kg) of each supplement did you buy (will still buy) this year?

12. From which diseases do your livestock usually suffer?

13. When do they usually suffer from diseases? (Which period of the year?)

14. How many **times** during last year did you sell cattle/sheep/goats?

Cattle: _____; Sheep: _____; Goats: _____

15. In total, **how many** cattle/sheep/goats did you **sell** last year?

Cattle: _____; Sheep: _____; Goats: _____

16. In total, **how many** cattle/sheep/goats did you **buy** last year?

Cattle: _____; Sheep: _____; Goats: _____

17. In your opinion, during which period (s) were there many more cattle in this village?

1940s

1950s

1960s

1970s

1980s

1990s

E: Browsing

18. **Name** the trees and shrubs commonly browsed by cattle and goats. **Prioritise** your list in (decreasing) order of preference. (**Best first**).

Cattle browsed trees/shrubs	Goats browsed trees/shrubs

19. During which months of the year is browsing critical to the survival of cattle?

20. Which of the browse species do insects or larvae usually attack?

21. When did you observe a severe insect or larvae attack on (which) browse species?

22. Do locusts (also) defoliate browse species? (YES or NO ?)

23. Do cattle browse less or more in recent years than before? Select your answer from the following:
- They are browsing **less** than before
- They are browsing **more** than before
- There is no change over the years
- I do not know
24. If you say 'they are browsing less or more than before', what could the course of this change be?

F: BUSH ENCROACHMENT

25. Has there been any change in the density of bushes in your village over the past 20 to 30 years?
- No, there is no change
- Yes, there is a change
- I do not know
26. Has bush density **expanded** closer or further away from watering points? Or has density distribution remained the same over the years?

27. Which tree/shrub species have increase in density of the years?

28. With what will you associate the localities with dense bushes in your village?

29. Is it better or worse with more trees? If better, with which species? and Why?

30. Which trees in your village are mainly used for firewood?

31. Which trees in your village are mainly used for construction of kraals, fences and houses?

G: Watering points (boreholes)

32. How many boreholes are operating in your village? _____

33. How many of them are no longer operating? _____

34. In which year was the oldest water point dug or drilled? _____

35. Are watering points in the village too close together? _____

36. Do you experience competition for water with other cattle owners since new watering points have been introduced?

37. Did you have any say in the decision about watering point placement?
