EFFECT OF STOCKING RATE AND RAINFALL ON RANGELAND DYNAMICS AND CATTLE PERFORMANCE IN A SEMI-ARID SAVANNA, KWAZULU-NATAL

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DECLARATION

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution.

Signed .... Date 21/04/98

Richard Warwick Sinclair Fynn

All this I tested by wisdom and said,
"I am determined to be wise"
but this was beyond me.
Whatever wisdom may be,
it is far off and most
profound - who can discover it?
So I turned my mind to understand,
to investigate and to search out
wisdom and the scheme of things
(King Solomon, in Ecclesiastes 7:23.)

ABSTRACT

Considerable understanding of the functioning of semi-arid systems is still needed to enable range managers to formulate management policies, with a degree of confidence. Long term data sets that encompass a wide range of interactions between the various major components of a semi-arid system (vegetation, herbivory, animal performance, landscape and rainfall), are unfortunately rare but essential to provide sufficient depth of data to adequately test various hypotheses about rangeland dynamics. This study comprises an analysis of a ten year data set derived from two cattle stocking rate trials in the semi-arid savanna of KwaZulu/Natal.

Statistical analysis revealed that the most pronounced and rapid compositional change was due to rainfall, but that stocking rates between 0.156 and 0.313 AU ha^{-1} had an important effect as well. Sites on steeper slopes with heavy stocking rates, exhibited the greatest amount of compositional change between 1986 and 1996 (40 Euclidean points in heavy stocking rate treatments on slopes vs 21-24 Euclidean points in heavy stocking rate treatments on flatter land, or 11-24 Euclidean points in low stocking rate treatments). Heavy stocking rates in conjunction with low rainfall tended to cause decreases in densely tufted perennial grasses and increases in annuals and weakly tufted perennials.

Multiple regression analysis revealed that seasonal peak grass production (measured as disc height) declined between 1986 and 1996 only at those sites on steeper slopes with heavy stocking rates. The camps that declined in productivity also underwent the greatest degree of compositional change. The decline in grass productivity in certain high stocking rate camps did not translate into a decline in cattle performance. Depending on rainfall, cattle gained on a seasonal basis between 112 and 241 kg at low stocking rates, 82 and 225 kg at medium stocking rates and 84 and 217 kg at high stocking rates

Rainfall, compared with stocking rate, accounted for the greatest amount of variance in seasonal peak grass production and cattle performance. Cattle performance had a strong curvilinear response to rainfall, which also proved to be a better predictor of cattle performance than grass biomass.

There were no clear trends in soil physical and chemical characteristics between low and high stocking rates that could provide convincing evidence that loss of soil nutrients was an important mechanism of range degradation. The total standing crop of plant nitrogen but not of phosphorus tended to decline at high stocking rates. Plant nutrient and van Soest analyses

suggested that forage quality was higher at heavy stocking rates.

The results of this study generally supported traditional concepts of rangeland dynamics with regard to rainfall and grazing effects on compositional change and seasonal grass production. The results were important in being able to show quantitatively that heavy stocking rates result in a decline in grass production and that this effect is dependent on an interaction between stocking rate and landscape position or slope, and that there is a link between a decline in seasonal grass production and compositional change. The results also highlighted areas for future research that would be useful for furthering our understanding of various aspects of rangeland dynamics and mechanisms of degradation.

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CHAPTER 1

INTRODUCTION

Semi-arid savannas cover extensive portions of the land mass of the Earth. Their low, variable and unreliable rainfall generally render them unsuitable for most forms of crop production except where irrigation is possible. A consequence of this is that these savannas, are on the whole, only suitable for pastoral and agropastoral activities, such as commercial ranching and communal subsistence agriculture. In commercial ranching the primary objective is the management of the system in such a way as to make a profit from the sale of livestock products, such as beef, mutton, wool and hides. On the other hand in communal subsistence agriculture, which is very common in the savannas of developing countries, the primary objective is not profit making, but rather survival. Livestock is kept as a means of providing food such as milk and meat, also for draught power, secondary products and a form of wealth.

Whether land is under commercial ranching or communal subsistence farming the primary concern of the various authorities such as governments or conservation and agricultural organisations is that these exercises are sustainable. In a country with an economy based on agriculture and more specifically livestock production, or where a significant proportion of the population depends on subsistence agriculture, the destruction of its grazing resource through injudicious management would lead to political instability, poverty and human misery. Commercial livestock farmers are dependant on an improved and more reliable understanding of grazing systems, in order to be able to refine their management strategies, thereby leading to a more efficient and profitable enterprise.

Stocking rate rather than the system of grazing has been recognised as the most important variable affecting the productivity and sustainability of a grazing system (Gammon 1978, O'Reagain & Turner 1992). Excessive grazing of a rangeland has generally been regarded as deleterious to the productivity of that system as a result of compositional changes and reduced grass production (Milchunas & Lauenroth 1993, Van de Koppel *et al.* 1997). Deshmukh (1984) and Milchunas & Lauenroth (1993) have shown that there is a strong linear relationship between mean annual precipitation and above ground net primary production. In turn Fritz & Duncan (1994) have shown that the ability of a system to support large ungulate biomass is strongly linearly related to mean annual precipitation. The critical theme that emerges from this is that the carrying capacity of a rangeland is determined by its primary production. If overgrazing drives a system to a point where it can no longer achieve optimal primary production, then the carrying capacity for that system has been reduced. The recognition of this feature of rangelands has resulted in numerous attempts to define a carrying capacity for a specific rangeland with the intention of determining maximum stocking rate levels that the land can absorb without degradation of the vegetation resource occurring. With this in mind it is understandable that there is a large amount of concern over the level that rangelands are stocked at, to the degree that many countries have laws over permissible stocking rates. There has been international and local concern over the stocking rates of Africa's communal regions, which are perceived as overstocked. There is a fear that overgrazing "will permanently reduce" the productivity of these systems, and as a result contribute further to Africa's poverty, instability and poor productivity. This has resulted in one of the major debates in rangeland science; are Africa's communal regions being degraded through perceived overgrazing (Ellis and Swift 1988, Livingstone 1991, Tapson 1991, Scoones 1992, Shackleton 1993, Dodd 1994, Dougill & Cox 1995, Hary *et al.* 1996)?

It is hard to accept that long term overgrazing will not reduce rangeland productivity. Some have questioned, however, whether livestock numbers are able to reach excessive levels in harsh and highly variable systems (Ellis & Swift 1988 and Behnke *et al.* 1993). Scoones (1992) has proposed that even if overgrazing results in degradation in certain regions of the Landscape the redistribution of soil and nutrients in other regions will maintain the overall productivity of the system.

While many rangeland scientists accept that traditional concepts of rangeland management are not suited to African or any other semi-arid systems, they contend that neither are those based on the non-equilibrium models of Ellis & Swift (1988) and Behnke *et al.* (1993). It is evident that rangeland science is, ironically, not at equilibrium with regards a unified consensus of how ecosystems function.

Whether one is dealing with a commercial or communal system, stocking rate is the variable over which man has greatest control and thereby ability to manipulate the grazing system. Thus it is important that there is a clear understanding of how stocking rate interacts with various environmental factors such as rainfall, vegetation, soils and landscape in order to be able to formulate workable management strategies that will yield sustainable production and optimum performance for relevant countries, communities and individuals.

Thus the aims of this study were to utilise information collected over ten years from two grazing trials located in a semi-arid savanna, with the intention of examining a number of integrated features that were considered important for furthering our knowledge and understanding of the mechanisms and processes that structure and drive semi-arid systems.

Key objectives were the following:

1) Determine the abundance of soil and plant nutrients and above - and below - ground biomass at high and low stocking rates, with the intention of gaining insights into mechanisms that may cause a reduction in productivity with heavy stocking rates, and also to determine whether the standing crop of plant nitrogen and phosphorus is diminished at high stocking rates.
2) Assess the role that rainfall and grazing play in driving compositional changes over time, with the intention of determining whether grazing has any effect on compositional change in a variable system. Also to see how specific species react to various environmental variables. It is important to be able to elucidate the separate effects of rainfall and grazing on compositional change because range condition assessments use species composition as a measure of the condition of a particular range. If there is a clear understanding of how various species react to rainfall and grazing then better advice can be given to range managers on achieving a desired species composition.
3) Evaluate the contribution of a range of factors such as rainfall, grazing and species composition to seasonal peak grass biomass dynamics, and establishing whether heavy stocking rates have resulted in a long term decline in seasonal peak grass biomass. Although heavy grazing has always been considered to degrade the vegetation resource, little documentation of such effects exist, and it is therefore important to be able to show that heavy grazing does reduce grass productivity and to see if this effect if present is linked to compositional change. It was also hoped to determine whether rainfall, grazing and species composition interact with each other because an understanding of such interactions could add greater flexibility to grazing management. For example, if it can be shown that grass production is less sensitive to grazing with a particular species composition or higher rainfall then heavy stocking could be implemented under favourable conditions (after good rainfall or in an area with resilient species) and lower stocking during unfavourable conditions.

4) Determining the effect of rainfall, grass biomass and stocking rate on cattle performance, with particular emphasis on establishing whether there has been a long term decline in cattle performance over time with heavy stocking rates. Very little direct evidence has been documented to show that changes in species composition and reductions in grass production translate into declines in animal production. Hard evidence is needed to be able to support strategies that require conservative stocking rates. Understanding how cattle performance is affected by various variables may help in improving livestock management.

It was intended to link the results of these various studies, to demonstrate how grazing affected compositional change, if this in turn affected seasonal grass biomass, and the consequence of this for cattle production.

CHAPTER 2

EFFECT OF STOCKING RATE IN SEMI-ARID SAVANNAS: A REVIEW

INTRODUCTION

Stocking rate has been a variable of importance to scientists and range managers alike because the performance of livestock is affected by it. The question of sustainable livestock production has become more important as human population levels have increased, resulting in greater pressure on the land. Due to the economic and ecological implications of livestock production a large amount of research has been done this century into effects of stocking rate and various grazing management strategies. Three main models of rangeland or ecosystem functioning have evolved overtime: succession model, state and transition model, and nonequilibrium model, each of which is reviewed in turn.

Succession model

Traditional approaches to rangeland management have been based on a linear deterministic model of plant succession where in the absence of disturbance the plant community will tend through a progression of seral stages towards a single outcome or climax (Clements 1916). The degree of grazing pressure will determine in which stage along that linear progression the plant community will lie. Each stage will have a characteristic species composition, with a particular agricultural potential. The rangeland manager must therefore stock at the correct levels to maintain the plant community in the optimum stage for livestock production (Dyksterhuis 1949). Thus it has been assumed that equilibrium conditions exist in all environments and that a particular equilibrium condition can be achieved by manipulating the forces that determine those equilibria. According to the succession model, high succession or climax grasses will come to dominate a grazing system with very low stocking rates, and will be replaced by low succession or pioneer grasses with heavy stocking rates. The theory (which has as yet to be disproved) predicts that excessive stocking rates will drive the system backwards to a degraded state, which is in most cases a soil - depleted system, that has very low agricultural potential and cannot recover within a time frame relevant to mankind. This because soil formation and succession is immensely slow, and because the productivity of the system is determined largely by the quality of the soil resource, recovery rates will be determined by soil formation rates. Succession theory predicts that if a grazing system is reduced to annual dominated vegetation as a result of heavy stocking rates, the removal of grazing from that system will result in a recovery to a sward dominated by perennial species. Empirical observations do not always support this prediction, suggesting that the theory does not have widespread application.

State and transition model

An alternative to the range succession model was proposed by Westoby *et al.* (1989) for variable environments such as semi-arid savannas. This model proposes a number of alternate states not linked in any linear progression, and the transition from one state to the next is determined by a combination of stochastic or manipulated events. There is not necessarily any linear order in the movement from one state to the next as in the succession model. The important factors determining the particular state that is achieved is an interaction with the latter state and the particular combination of environmental factors to which it is subject. According to this model heavy stocking rates may result in the replacement of perennial grasses by annual grasses. Contrary to the predictions of the succession model, however, that with a return to low stocking rates the system will return to a perennial dominated state, may rather enter into an alternative stable state within a new domain of attraction. For example overgrazing in the Sahel resulted in the perennial grasses being replaced by annual vegetation. After 20 years of reduced herbivore numbers, the vegetation has remained in a barren state (Van de Koppel *et al.* 1997). These observations do not support the succession model, and suggest that the state and transition model, rather than the succession model is more applicable for semi-arid systems.

Although the state and transition model is essentially different from the range succession model with regards to vegetation development, direction and equilibria, it still assumes strong biotic influence (eg grazing pressure) in determining vegetation states. Thus it is not intrinsically nonequilibrial, there is a strong influence on system dynamics from factors within the system, and therefore there are likely to be density-dependent feedback mechanisms affecting productivity. Any policy makers accepting this model for determining strategies for grazing management in semi-arid systems would, therefore, still have to consider the effects of stocking rate as a factor that may lead to degradation if applied at excessive levels.

Non-equilibrium model

Ellis & Swift (1988) claimed that the traditional (western) approaches to the management of many of Africa's communal systems may not be valid. The basis of their argument is that in systems with low and highly variable rainfall, rainfall may have such a dominant effect on the dynamics of the system such that there is little opportunity for the development of feedback mechanisms within the system. Thus the effects of stocking rate on grass biomass are inconsequential in comparison with the effects of rainfall. While animal populations may track carrying capacity very closely in equilibrial environments, the highly variable and dynamic carrying capacity of nonequilibrial environments does not allow close tracking. The critical factor in their argument is that owing to frequent droughts, livestock numbers are never able to reach levels where they have a significant impact on the vegetation.

An outline of the differences in the characteristics between equilibrial and nonequilibrial grazing systems as visualised by Ellis & Swift (1988) is displayed in Table 2.1.

Table 2.1 Characteristics of equilibrial and nonequilibrial grazing systems (from Ellis & Swift 1988).

	Equilibrial system	Nonequilibrial system
Abiotic patterns	Abiotic conditions relatively constant	Stochastic/variable conditions
	Plant growing conditions relatively invariant	Variable plant growing conditions
Plant-Herbivore interactions	Tight coupling of interactions	Weak coupling of interactions
	Feedback control	Abiotic control
Population patterns	Density dependence	Density independence
	Populations track carrying capacity	Carrying capacity too dynamic for close tracking
	Limit cycle	Abiotically driven cycles
Community/ Ecosystem Characteristics	Competitive structuring of communities	Competition not expressed
	Limited spatial extent	Spatially extensive
	Self-controlled systems	Externalities critical to system dynamics

Ellis & Swift (1988) found in Turkana that despite the fact that livestock consume only a small proportion of the resource in a good year their nutritional status and production rates closely track the seasonal dynamics of plant production. This is because the nutritional status of the vegetation is strongly correlated with production. For livestock the quality of the diet declines during the dry season to the point where animals are no longer able to maintain condition. In drought years forage quantity and quality become limiting. This depletion of the foraging resource is due, not only to removal by livestock but also due to termites and weathering. Although there is some sort of density-dependent effect on forage biomass in drought years, termites, microbes, and abiotic factors deplete the resource regardless of the number of livestock. Thus the main factor determining the survival or mortality of livestock is not livestock density but rather the length of the drought. Thus external rather than internal factors seem to regulate livestock populations. The implications of this are that traditional approaches to rangeland management in these systems cannot work, because they aspire to obtain a particular stocking rate that is in equilibrium with the vegetation, and no such interaction exists in a non-equilibrium system. Thus in Turkana and related environments livestock will not cause a degradation of the environment under current pastoral strategies if the theory holds true.

Spatial scale

Turkana is a spatially extensive environment where the people are nomadic and are able to compensate for high environmental variation by being able to exploit the spatially variable system available to them (Ellis & Swift 1988). Thus they are able to move their livestock in times of drought to areas that are inherently able to produce more forage during dry periods, and to those areas that by chance have received more rain. This situation is rare in most communal areas of Africa and the world today, which are spatially restricted. There is little opportunity for nomadic activity due to restricted land available for movement, as a result of increasing human populations and political and social boundaries. The fact that human and especially livestock populations are able to persist in the face of destabilizing forces such as variable rainfall in the Turkana system, and that there is little evidence of degradation may be the result of the extensive spatial scale of the system. Spatial scale has been shown to be an important stabilizing feature in mathematical models, where populations are prevented from going to extinction by increasing the spatial scale of the model (DeAngelis & Waterhouse, 1987). Scoones (1992) contended that cattle had been able to maintain their levels over time in the communal regions of Zimbabwe by use of key resource areas in dry periods, as it is these areas that provide fodder at the end of dry periods. This is supported by Hary *et al.* (1996) who concluded that the availability of dry season forage resources in Northern Kenya, sets an upper limit to the number of livestock that can be held. Also that degradation is likely to occur on dry season grazing reserves when rest periods are shortened and pressure increased, due to a reduction in the spatial scale of pastoral resource exploitation. Stafford Smith & Ash (1995) found that the decline in cattle gain with increasing stocking rate increased as camp size decreased.

Therefore spatial scale may be important for secondary production and system resilience such that heavy stocking rates at small spatial scales may represent more of a threat to land degradation than at larger spatial scales. The density-independent effects described by Ellis & Swift (1988) for Turkana and Breman & de Wit (1983) for the Sahel, may only be valid for those spatially extensive systems. A fenced commercial ranching system in the same region may, over time, experience the negative effects of overstocking.

What is degradation

The word "degrade" according to the Oxford dictionary means to reduce to a lower rank or status, or to bring disgrace or contempt on something. The first definition however is more meaningful, the reduction to a lower rank or status fits in rather well with succession theory where, less complex undeveloped and probably less productive vegetation states are considered as being of low rank or status in the successional process. In other words the vegetation is not at its potential complexity, structure, diversity, and, importantly to mankind productivity. What the definition in the Oxford dictionary does not address, however, is whether this state of degradation is permanent or temporary (i.e. when the word degrade is applied to vegetation, is it possible for this degraded state to return to its former state within a time frame relevant to mankind). This is important because the implications for the welfare of mankind are vastly different for land that has altered state only temporally and that which has changed permanently. Dodd (1994) considers the modern usage of the word degradation as referring to decreases in productivity or unfavourable changes in species composition, but not indicating whether the changes are permanent or the result desert like. Binns (1990) defines degradation as change that is reversible with good weather and a little time. He associates desertification with irreversible change. Desertification is not a good word to use for permanent changes in the vegetation or productivity of a system, as this conjures up pictures of an area of rolling sand dunes devoid of almost all vegetation. A permanent change in the productivity of a system does not have to be so severe. The definition of degradation by Abel & Blaikie (1989) for the permanent decline in productivity of a system is probably the most useful and reads as follows: "Range degradation is an effectively permanent decline in the rate at which land yields livestock products under a given system of management. This definition excludes reversible vegetation changes even if these lead to temporary declines in secondary productivity. It includes effectively irreversible changes in both soils and vegetation."

With the concept of degradation now defined it would be suitable to continue with a discussion on how stocking rate can lead to range degradation and continue with a review of what evidence may exist for such effects in semi-arid rangelands.

Mechanisms of range degradation

Animal production model

In the previous discussion on degradation it was established that the critical symptom of degradation is a loss of secondary productivity. Secondary production will be some function of the quantity and quality of primary production according to a general linear model in the form of:
Animal production = *f* (forage production, forage quality).
The expected relationship of these two variables with animal production is positive, so that a reduction of one or both of them would be expected to reduce animal production.

Processes affecting forage quantity and quality

What processes will have a negative impact on forage production and quality? This is an important question because this will affect animal performance. For optimum growth a plant needs a decent rooting substrate that is well aerated and suitable for root development, sufficient available soil-water over the period of the growing season, macro- and micro-nutrients in the soil at levels that are not limiting, and minimal herbivory. The intrinsic potential for the amount of growth a plant may attain may be determined genetically. Thus the species composition of a sward is important in terms of forage production. This is also true for the quality of forage available to animals, because different species vary in forage quality (Norton 1982).

Effect on soil physical and hydrologic characteristics

A compaction of the soil would be expected to reduce its suitability as a growing media. Rauzi & Hanson (1966) found that the pore space of the soil of a heavily grazed rangeland was lower than the soil of a lightly grazed rangeland. One may expect this to have a negative effect on root development. Decreases in pore size will be associated with increased soil bulk density. An increase in soil bulk density with increasing stocking rates has been documented (Rhoades *et al.* 1964, Rauzi & Hanson 1966, Warren *et al.* 1986, Pluhar *et al.* 1987). Warren *et al* (1986) found that soil bulk density was negatively correlated with infiltration rate of water into the soil.

The rate at which water can enter the soil is a crucial factor in determining the efficiency of a rangeland in utilizing rainfall. The reduction of forage biomass and increased runoff leads to reduced rain use efficiency (Le Houerou 1989). This is especially so in semi-arid and arid rangelands where water is limiting. It is intuitive that the standing crop biomass of a rangeland will have a negative relationship with stocking rate and this is supported in the literature (Fourie *et al.* 1985, Ralphs *et al.* 1990). This will therefore have a negative effect on rain use efficiency. If the infiltration rate of the soil has been so reduced that most of the water during a rainfall event is lost from the system as runoff, then the functioning of that system has been impaired. This is because a certain percentage of the water that used to enter the soil for use by plants and storage, is no longer available to the plant and one may expect reduced plant growth. It may be true to state that reduced soil infiltration rates in rangelands may represent one aspect of degradation, especially when dealing with environments where water is limiting.

There is strong evidence that heavy stocking rates reduce infiltration rates in soil and increase runoff, and thereby accelerate soil erosion, though there are examples on sandy soils where heavy stocking rates have not reduced the infiltration rates of water into soil. Sandy soils due to their high porosity, are less susceptible to surface capping, and therefore, heavy stocking rates are less likely to result in lower infiltration rates. On other soil types, however, heavy stocking rates are likely to have an effect on infiltration. Johnston (1962) found that infiltration rate was inversely proportional to stocking rate in south western Alberta. Soil loss increased slightly under medium and heavy stocking rates but was greatly increased at very heavy stocking rates. Rauzi (1963) found that infiltration rate on ungrazed rangeland was four times as great as that on the heavily grazed rangeland. Rhoades *et al.* (1964) showed that infiltration rate was inversely proportional to grazing intensity at a site in Oklahoma. Sharpe *et al.* (1964) found that run off from heavily grazed watersheds was 10 times higher than from lightly grazed watersheds in South Dakota. Rauzi & Hanson (1966) found that infiltration rates on lightly grazed watersheds were four times that of heavily grazed watersheds. They noted that this was related to vegetal cover. Multiple linear regression analysis showed that total herbage and mulch accounted for 71 % of the variation in infiltration rate. Kincaid & Williams (1966) showed that there was a highly negative relationship between crown cover percentage and surface runoff in an experiment in Arizona. Kelly & Walker (1976) working in the lowveld of Zimbabwe, found that infiltration was higher under nil and light utilization regimes than in the intensive regime. Macdonald (1978) working at Matopos, Zimbabwe showed that the heavily grazed patches of rangeland had greatly reduced infiltration rate compared with the lightly grazed patches. Warren *et al.* (1986) working at the Texas A&M research station found that after trampling by cattle at high stocking rates infiltration rate was lower and sediment production higher than before trampling. There was not much difference in these factors before and after trampling at lower stocking rates. Snyman & van

Rensberg (1986) observed that a change from a perennial- to a pioneer-dominated grassland may be associated with increased rates of soil loss and runoff and reduced infiltration. Pluhar *et al.* (1987) reported from a grazing trial in the Texas rolling plains that regression analyses indicated that infiltration rates increased and sediment production declined as vegetation standing crop and cover increased. Thurow *et al.* (1988) found on the Edwards plateau in Texas that moderately grazed pastures were able to recover from droughts and maintain infiltration and erosion rates, whereas heavily grazed pastures had decreased infiltration rates and increased erosion. Zobish (1993) observed that grazing may increase the rate of soil loss and runoff in semi-arid and subhumid locations of Eastern Kenya through a reduction in grass cover. Milchunas & Lauenroth (1993) found that soil-water content decreased in 13 out of 15 sites as a result of grazing.

Other factors can play a role, a reduction in densities of soil dwelling insects and other fossorial animals can further reduce water penetration into the soil (Dean 1992). Grazing may also affect the particle size distribution of the soil. Strang (1974) found on the sandveld of the Zimbabwean highveld that sites that had been heavily grazed tended to have a coarser sand fraction than protected sites.

Heavy grazing therefore has large potential to reduce primary productivity in rangelands through its effect on runoff and soil moisture. This effect is likely to vary in its importance, however, according to soil type. Very sandy soils are less likely to experience large compaction and runoff.

Effect on soil nutrients

Soil macro- and micro-nutrients are essential for plant growth. A deficiency of these in the soil would lead to a reduction in plant growth, as is attested to by the amount of fertilizer farmers have to apply to lands to optimize crop yields. However there is very little evidence to suggest that heavy stocking rates lead to a run down in levels of soil nutrients, although there is evidence that they may cause a significant increase in the concentration of certain nutrients in areas where they congregate. Tolsma *et al.* (1987) sampled along transects at increasing distances from two waterholes in eastern Botswana and found that there was an increase in soil nutrients near the waterholes. This was attributed to cattle concentrating around the waterhole at drinking times and increasing the concentration of dung and urine at these points.

In a similar study to that of Tolsma *et al.* (1987) by Dougill & Cox (1995) in the Kalahari, soil inorganic phosphorus had higher concentrations near the waterhole relative to the surrounding rangeland. Nitrogen however showed no increase in concentration. These studies would support the hypothesis of Breman & de Wit (1983) that animals add heterogeneity to soils and vegetation in the landscape through attraction to puddles formed from runoff and subsequently increase the concentration of dung and urine in these areas. This leads to higher concentrations of soil nutrients at these spots which as a result are more favourable for the establishment of woody plants.

The increase in concentration of nutrients at points where animals congregate means that the animals must be removing these nutrients from other regions of the rangeland. The studies of Tolsma *et al.* (1987) and Dougill & Cox (1995) did not detect any reduction in the nutrient concentration in the zone between 50 and 1000 m from the waterhole (where one may expect heaviest grazing) relative to the zone of greater than 1000 m from the waterhole (where grazing levels should be lower). Milchunas & Lauenroth (1993) in an analysis of a 236 site worldwide data set found no evidence of grazing induced changes in soil organic carbon, soil nitrogen, soil phosphorus and soil pH. Tongway & Ludwig (1997a) note, however, that there is overwhelming evidence of reduced soil nutrient reserves in Australian rangelands that are degraded through overstocking. This is mainly due to the erosion of the upper few cm of soil where the largest proportion of the nutrient reserve is located.

It seems, therefore, that loss of soil nutrients through heavy grazing is dependent on the soil type and erodability of the landscape. Landscapes that are resistant to erosion are less likely to lose soil nutrients than erodible landscapes.

Effect on grass basal cover

The reduction of grass basal cover will facilitate soil erosion in two ways. There will be an increase in runoff rates (Kincaid & Williams 1966), (though this may not happen on very sandy soils) and reduced binding of the soil by roots. Barnes & Franklin (1970) found that rates of soil loss on areas kept bare were tenfold those of protected areas. Snyman & Van Rensberg (1986) found that soil loss was significantly related to basal cover. There is good evidence to show that heavy grazing does reduce basal cover. Kennan (1969) reported variable results on the response of basal cover to grazing from two grazing trials at Matopos. One trial was in the thornveld on clay soils while the other was in the sandveld. Basal cover in the thornveld showed a clear negative response to grazing, while there was no clear trend in the sandveld. Thus it appears that there may be an interaction between grazing and soil type and its effects on basal cover, where the effect of grazing on basal cover on sandy soils is buffered. Fourie *et al.* (1984) showed that both heavy rotational and continuous grazing caused a decline in basal cover during a trial in the Northern Cape. Mott (1986) reported that patch grazing in a north Australian savanna resulted in the basal cover of grasses in heavily grazed patches being reduced. Fuls & Bosch (1991) showed that there was a lower total basal cover in patches of heavily grazed grassland compared with lightly grazed patches. A similar study by Macdonald (1978) in Zimbabwe showed the same trends in basal cover.

It seems that generally, there is a reduction in basal cover with heavy grazing, but that soil type may influence this trend.

Effect on species composition

Morphological and physiological differences between species, such as growth habit, perenniality, proportions and distribution of leaf and stem and flowering behaviour, have significant effects on both the quantity and quality of forage available to grazing animals (Norton 1982). Shifts in species composition are likely to alter the quantity, quality and variability of plant production by modifying the amount and pattern of energy flow through the ecosystem (Briske 1991). Various grass species inherently have different potentials for growth. Certain species will always be small and without much leaf material regardless of the availability of water and nutrients. Thus a change from a sward dominated by high producing grasses to one dominated by low producing grasses, will represent a loss of primary and most possibly secondary production.

Different species are inherently dissimilar in forage quality. Breman & de Wit (1983) note that the crude protein content of grass should be at least seven percent to keep livestock in good condition in the Sahel. Livestock cannot compensate for poor quality by consuming more. On the contrary with decreasing quality, activity in the rumen decreases so that the rate of digestion decreases and therefore intake rate decreases. Ellis & Swift (1988) note that livestock performance in Turkana is limited in the dry season by low forage quality, even though forage quantity is adequate. Compositional change is likely to bring with it changes in the forage quality of the sward. Thus grazing induced compositional changes are likely to affect animal production and, if permanent, represents a form of degradation.

Compositional change through heavy grazing has, however, been recorded not to affect animal performance and even to improve animal productivity. Harrington and Pratchett 1974 noted in a grazing trial in Uganda that a change in a *Themeda triandra* and *Hyparrhenia* *filipendula* dominated sward to almost total dominance of *Brachiaria decumbens* between tufts of *Cymbopogon afronardus,* lead to a higher than expected production from the high stocking rate treatment (i.e. did not follow the Jones & Sandland (1974) relationship between stocking rate and animal production).

Compositional changes may result through selective grazing which results in differential frequency and intensity of defoliation of plants on a site, and thereby causes a shift in competitive interactions. Plants grazed less frequently gain an advantage over more frequently utilized plants. These grazing induced shifts in competitive interactions contribute to changes in plant community composition over time (Archer & Smeins 1991).

The most likely mechanisms for grazing induced compositional changes in semi-arid environments, may be through more palatable species being selected for by grazers, or differential defoliation intensities on grasses that are able to avoid excessive defoliation by means of their growth habit (creeping or prostrate species) and those that are not (Briske, 1991). Species that are unable to avoid intensive defoliation may be more prone to mortality during droughts and die more frequently than creeping or prostrate species. Another mechanism could be through different abilities for recruitment under heavy grazing, as a result of a life cycle geared towards a perennial habit and low seed output, as opposed to an annual habit with high seed output (O'Connor & Pickett 1992).

There is a large amount of evidence for grazing induced compositional change. Harker & Mckay (1962) working in Buganda, East Africa, observed the conversion of a grassland that was dominated by *Pennisetum purpureum* and *Imperata cylindrica* to one dominated by *Cynodon dactylon, Panicum maximum, Setaria sphacelata* and *Brachiaria* sp. This an example of high successional species (*Pennisetum purpureum* and *Imperata cylindrica*) being replaced as a result of heavy grazing by mid-successional species, demonstrating how grazing acts against successional progression. Replacement of long lived, densely tufted perennials by short lived and weakly tufted perennials as a result of heavy grazing has been documented by Heady (1966) in East Africa, Kennan (1969) at Tuli, Zimbabwe, Kelly and Walker (1976) in south east Zimbabwe, Macdonald (1978) in Matopos, Zimbabwe, Ralphs *et al.* (1990) in Texas, O'Connor & Pickett (1992) in the eastern Transvaal South Africa, and Guevara *et al.* (1996) in Argentina. These examples illustrate how heavy stocking rates act against the successional process, resulting in a sward dominated by lower successional species.

Dougill & Cox (1995) in a study of vegetation and other parameters around waterholes in the Kalahari found that there were distinct zones of vegetation around these points. The most heavily impacted areas around the waterholes were dominated by low degraded vegetation, this was followed by a bush encroached zone up to about two kilometres from the waterhole and only then did grass species begin to dominate. The same pattern around waterholes was observed by Tolsma *et al.* (1987) in eastern Botswana. It is important to note that the study of Dougill & Cox (1995) was on Kalahari sands while that of Tolsma *et al.* (1987) was on higher clay soils and yet a similar pattern was observed. This pattern is in effect an example of changes of vegetation state due to grazing intensity as described by the state and transition model of Westoby *et al.* (1989). O'Connor (1994) studied how *Themeda triandra, Bothriochloa insculpta* and *Heteropogon contortus* responded to applied light and heavy grazing treatments over five growing seasons. Species abundance was more responsive to rainfall variability than grazing although there were distinct trends in population turnover between light and heavy grazing treatments.

A consideration of the results from O'Connor & Pickett (1992) where long term heavy grazing had reduced longer lived perennials, and resulted in a sward characterised by short lived perennials, and the results from this shorter term study suggest that there are two distinct trends in populations of semi-arid grass species. 1) A short term relatively dramatic fluctuation corresponding to variation in rainfall, and 2) a more subtle trend in population density over longer time periods that reflects a particular species response to grazing severity. This is supported by the results of Hatch (1994) who studied the effects of grazing and rainfall on the species composition of a grazing trial in Zululand. Long-lived perennial grasses such as *Panicum maximum* and *Themeda triandra* tended to increase in good rainfall years and decrease in drought years. The decline in dry years was enhanced by heavy grazing. The weakly tufted perennial *Urochloa mosambicensis* tended to increase in abundance in response to decreased rainfall and this was facilitated by heavy grazing. Milchunas & Lauenroth (1993) in the analysis of a worldwide data set, found that the percentage change in the dominant species increased with increasing duration of grazing treatments and intensity of grazing.

O'Connor (1995) observed drought to have an overriding effect on community change but with grazing history having an additional effect. For example, severe drought in combination with heavy grazing almost eliminated the palatable perennials and increased the abundance of the shorter-lived unpalatable perennials. The lightly grazed grassland was able to maintain its longer lived perennials but was dramatically changed in the relative proportion of these. O'Connor & Roux (1995) in a study of a grazing trial in the Karoo which lasted 23 years found that community change was largely rainfall driven, but that the influence of grazing treatments on longer lived plants became more important over time. Grazing did not eliminate perennials from the sward. One would assume that with heavier grazing there would be a more pronounced effect on the perennial component.

In conclusion, rainfall has the most conspicuous effect on compositional change in semi-arid environments, but there is also an important grazing effect, whereby heavy grazing causes a reduction in densely tufted, long lived perennial grasses and an increase in weakly tufted perennial and annual grasses.

Effect on bush encroachment

Bush encroachment adds a new dimension to compositional change because it means not only replacement of herbaceous species and a suppression of grass growth (Kennard & Walker 1973, O'Connor 1985), but also means a change in vegetation structure that may not suit grazers. Very severe encroachment as a result of severe grazing pressure such as that described by Tolsma *et al.* (1987) and Dougill & Cox (1995) is likely to have a negative impact on grazers.

Other evidence for grazing induced bush encroachment has been documented by Skarpe (1990) in Botswana and Ash *et al.* (1991) in Australia. Heavy stocking rates may not always have consistent effects on bush encroachment but may interact with the type of soil or vegetation as is illustrated by the study of Kennan (1969). In this study at Matopos, responses of trees to grazing appeared to differ between fine-leafed trees and broad-leafed trees. Acacias increased in abundance in the grazing treatments but remained stable under complete protection, while broadleaved species in one case declined under grazing and showed large increases with complete protection. Grazing may create gaps suitable for the establishment of Acacias while broadleaved species generally establish in protected areas, thus may have found nongrazed treatments more suitable for establishment due to an accumulation of moribund material.

The two-layer model (Walker & Noy-Meir 1982) has been proposed to explain the mechanisms by which grazing leads to bush encroachment. The thrust of this model is that the balance between the woody and herbaceous layers is determined by the availability of water and nutrients in different rooting zones. Grasses are more efficient in taking up water and nutrients than woody plants in the topsoil due to their shallow rooting habit, while woody plants with their deep root systems are more able to access water and nutrients in the subsoil. However in a system dominated by grasses most of the water from rainfall and nutrients released by mineralisation do not move to the subsoil as they are intercepted by grass roots in the topsoil. The hypothesis is that with heavy grazing there is a reduction in root biomass in the topsoil and therefore less interception of water and nutrients, which are then able to move into the subsoil thereby advantaging trees. As a result grasses lose their competitive edge and bush encroachment occurs.

The data from the study by Dougill & Cox (1995), does not support this. This study shows that there appears to be no difference in the hydraulic properties of soils in the bush encroached zone and the control site (grassland). The predominance of water transport as uniform matrix flow in both the bush encroached zone and grassland, suggests that the susceptibility of surface nutrients to leaching is limited and that their movement to depth is unlikely. Also there was no difference in nitrogen and phosphorus levels in the bush encroached and control zones in the subsoil.

Dougill & Cox (1995) state that results from nutrient profile measurements and mineralization and leaching column experiments, suggest that nitrogen and phosphorus cycling is rapid, efficient and restricted to the topsoil. There was no evidence that heavy grazing encourages the movement of nutrients and water to depth as proposed in the two layer model. They suggest that bush encroachment is caused by the reduction in grass density and the preferential selection of grasses over woody plants by grazers that removes the competitive dominance of grasses over woody species. Also the reduction of grass biomass by heavy grazing, means that fire frequency and intensity will be lower, minimizing the negative impacts on the woody layer.

Throughout this section it has been shown that there is sufficient evidence to conclude that grazing has a significant effect on soil physical, chemical and hydrologic characteristics as well as plant community composition and structure.

Evidence for degradation

Livingstone (1991) produced a very useful analysis of current thinking on and processes involved with range degradation. He proposes that degradation is most likely to take place during certain window periods such as in a drought, rather than the longer inter-drought periods. At the beginning of a drought cattle numbers will be high, while vegetal cover will rapidly decline. If the drought is severe enough almost all cover may disappear. With the onset of the first heavy rains after the drought there is likely to be severe soil loss and resultant loss of seed banks.

Livingstone (1991) comments on the work of Abel and Blaikie (1989) who measured effective vegetation cover at a communal area (62.8%) and a non-communal grazing area (57.5%) in Zimbabwe. They used the method of Abel & Stocking (1987) adapted from the SLEMSA model (soil loss estimation model for Southern Africa) of Elwell & Stocking (1982), and concluded that there would be negligible differences in the rate of soil loss from the two areas.

Livingstone (1991) notes that there is a flaw in this argument because they are not taking the vulnerable post-drought period into account. It is during this period that the two areas will most likely not have the same effective vegetative cover. The reason being that if one considers the work of Kelly (1973) who found that herbaceous production in a more heavily grazed communal area was only 9% below that of the commercial area in a normal rainfall year, but that during a drought year it was 80% lower. Therefore during a drought year the communal area as predicted from the SLEMSA equation, should lose a lot more soil. Livingstone (1991) states " The main problem with the literature is the failure to distinguish between normal and drought years."

Hary *et al.* (1996) used a principal components analysis on nine variables for 87 range units in Kenya to identify a structure behind the occurrence of rangeland degradation. The variables used were availability of permanent water, drought risk, length of first and second growing period, median rainfall during the first and second rainy season, erosion status factor , range condition factor and permanent accessibility factor. The first three components accounted for 78% of the total variance. The first component, which accounted for 48% of the variance was interpreted as a production-potential gradient as it had high loadings on availability of permanent water, drought-risk, length of first and second growing period, median rainfall during the first and second rainy season. The second component was considered a range degradation gradient as range condition factor and erosion status factor had high loadings on this axis. Permanent accessibility factor was the only variable to have high loadings on the third component, and thus could be interpreted as a range accessibility gradient. A subsequent regression analysis of erosion status factor and range condition factor on the orthogonal axes revealed a significant negative relationship between theses two variables and the production potential gradient.

These results lead Hary *et al.* (1996) to conclude that range degradation increases with the production potential of the range (i.e. as a system decreases in drought risk, increases in rainfall, and increases in length of the growing period, it becomes more susceptible to degradation). This result is supported by the study of Milchunas & Lauenroth (1993) who found that compositional changes and declining above ground net primary production were significantly related to increasing site productivity. This is probably because these systems have higher human populations, with more pressure on the land through higher livestock populations, than more arid systems. This in a way, supports the argument of Ellis & Swift (1988) in that in a semi-arid system the environment does not allow livestock numbers to reach high levels, thus reducing the impact that livestock have on the vegetation.

Scoones (1992) notes that the long term impact of herbivores is dependant on soil type. He cites Barnes (1965) who showed that 15 years of high stocking rates on sandy soils did not result in significant changes, whereas Carew (1976) showed that on clay soils high stocking rates may result in long term lowering of production.

The main test for degradation is whether the land is declining in its ability to yield livestock products. Tapson (1991) presents evidence of cattle numbers from the Kwazulu region between 1974 and 1988. These areas have been heavily grazed over time and there have been numerous predictions of the imminent collapse of the system. Cattle numbers have shown a slight increase over time while mortalities a slight decrease. Moreover this time series comes at the end of a 50 year period of similar management. If the land is being degraded due to heavy stocking rates, why has the cattle population not crashed as predicted?

Scoones (1992) presented similar evidence from the heavily utilized communal areas of Zimbabwe. In a 25 year time series there was no sign of a decline in cattle numbers. Regression analyses indicate a slight but not significant positive increase in cattle numbers.

These two data sets would suggest that heavy stocking rates have not resulted in degradation. However a maintenance of cattle numbers may not equate with no loss of productivity. Scoones (1992) notes that although the numbers of cattle are being maintained, the data gives no indication of the production quality (in terms of weight, ability to pull ploughs or milk production), and that it is plausible that the degradation of the natural resource may be felt in terms of these factors first, before any decline in numbers.

Milton *et al.* (1994) note that as the land degrades ranchers may make use of increasingly hardy and more agile types of domestic livestock. They give an example of Schofield & Bucher (1986) from arid northern Chile and semi-arid Argentina where cattle have largely been replaced by goats.

Mace (1991) says that multi-species herding is the norm in Africa and that pastoralists may adapt to changes in the environment by switching emphasis on species. As an extreme hypothetical example, cattle may change from productive milkers such as Frieslands and beef producers such as Brahman to less productive (though probably more economical) Inguni.

Walker (1980) presented an informative modelling exercise where he showed that communal areas may be in a more resilient state less likely to degrade than the well managed commercial areas, if subjected to sudden heavy grazing. The reason for this is that communal areas that have been subjected to high grazing levels for long periods of time, have developed a grass sward which is dominated by species with a large ungrazeable fraction, ie creeping species. On the other hand better managed areas are dominated by tufted species that have a low ungrazeable fraction. In the case of a change of management where heavy grazing is suddenly implemented, an area dominated by tufted species may lose all the grass cover, leading to severe soil erosion and bush encroachment. Walker (1980) contends that these results are supported by real examples where well managed areas in game reserves have been given over to communal grazing, resulting in far more devastating effects than occurred in the constantly heavily grazed areas. The situations reported by Tolsma *et al.* (1987) and Dougill & Cox (1995) on severe bush encroachment, after waterholes had been established in areas that were previously inaccessible to livestock, could be further support for the results of Walker (1980). These could be regarded as examples of degradation, as the encroached zones are effectively permanent changes. Only a large amount of time, labour and expense would be able to restore these zones to a grassland state. Severe bush encroachment is likely to reduce the carrying capacity for grazers, because it restricts their access to the range and reduces grass production.

Grass production in arid and semi-arid systems is water limited. A long term reduction in the mean annual rainfall or changes in the distribution thereof, would reduce the productivity of these systems. A question then arises as to whether negative feedbacks exist by means of reduced rainfall, through the effect of grazing intensity on plant biomass? Dodd (1994) investigated this topic and concluded that studies by Neilson (1986) and Pielke & Avisar (1990) using sophisticated modelling have shown that there is little doubt that feedback exists between land surface properties (including amount of vegetation standing crop) and atmospheric processes. However they have not determined how much, and at what geographic scale, grazing related change must take place on arid rangelands to affect the climate at a significant level. Thus the possibility exists that overgrazing may in addition to affecting the productivity of a system through effects on soil and plant dynamics, also influence plant growth by reducing rainfall.

Ellison (1960) noted that to see the effects of overgrazing one has only to look at the rocky hillsides of many Mediterranean countries. Whether this is the result of soil erosion through overstocking or rather the inherent nature of the landscape, we probably will never be sure. However seeing that this is where land has been subject to the effects of civilization and high population densities for thousands of years, there quite likely has been heavy utilization of these regions in periods over time. It is possible that this is the final resilient state of a system subjected to long periods of abusive grazing. With continued heavy grazing in Africa's rangelands, it may be a matter of time before many of its rangelands settle in a state similar to that of the Mediterranean countries.

According to Wilson & Macleod (1991) confirmation of the loss of productivity requires the measurement of departures from the linear relationship between animal productivity and stocking rate. They note that in the *ex-ante* situation of an experiment, overgrazing will be observed as a loss of linearity with time. In the *ex-poste* situation of a comparison between two paddocks of the same range type, but different grazing history, overgrazing will be observed as a difference in the optimum stocking rate.

Another factor that may suggest that a particular area of land is degrading is an increasingly negative slope in the relationship between biomass and stocking rate. The reason for this is that if heavy stocking rates are leading to a reduction in productivity and the lighter stocking rates not, production in the high stocking rate treatments relative to the low, will become increasingly disparate, leading to increasingly negative slopes.

Conclusion

There was consistent evidence for rainfall having the most conspicuous effect on vegetation dynamics in semi-arid systems. The processes, mechanisms and effects of the various components of arid and semi-arid systems under various grazing regimes reported in the literature, would suggest that most of the semi-arid areas of the world are not exempt from the effects of overstocking. There is no convincing evidence to suggest that stocking rate is unimportant. Whether exceptionally harsh and variable systems such as Turkana, experience density-dependent effects and are vulnerable to degradation by livestock (under conditions of natural mortality and recruitment, i.e. no supplementary feeding and livestock imports) has however not been satisfactorily resolved. The assumptions of systems being limited to natural mortality and recruitment amongst livestock are rarely met, and this suggests that most semi-arid systems in

Africa have the potential to be overstocked and are therefore vulnerable to degradation through heavy stocking rates. This will be manifest as increased runoff and reduced infiltration of water into the soil, unacceptably high levels of soil loss, replacement of perennial grasses by annuals, reduced and more variable grass production, bush encroachment and reduced animal production. No system is exempt from the destructive effect of artificially inflated long term heavy stocking rates on vegetation and soils. Examples of vegetation destruction and desertification as a result of heavy stocking rates have been documented in Africa, the USA, the Russian Federation and Australia (Van de Koppel *et al.* 1997).

It is essential therefore to ensure that rangelands are not subjected to heavy stocking rates for extended periods of time, if their productivity is to be maintained. Controls should be set in place by relevant authorities, on the levels at which farmers (commercial or subsistence) should be allowed to stock at. The high variability of grass production as a result of rainfall variability however, complicates the issue of calculating carrying capacities for various regions. Farmers should attempt to employ an opportunistic management strategy by buying in livestock during above average rainfall years and selling off livestock during below-average rainfall years.

The mechanisms and time frame in which heavy stocking rates degrade rangelands are not satisfactorily understood, and this should be the thrust of future stocking rate research; understanding how stocking rate interacts with climate, soils, landscape and vegetation, with the purpose of developing a robust theoretical framework to predict the effect of stocking rate in various environments.

CHAPTER 3

STUDY AREA AND EXPERIMENTAL DESIGN

Site factors

Location

The trials on which this study is based are located on the farms Llanwarne (27° 35' S 31° 45' E) and Dordrecht (27° 36'S 31° 46' E) which are situated in the Pongola region of the Zululand bushveld (fig 3.1) (altitude = 274m).

Climate

The climate is typical of a semi-arid environment with a low and variable rainfall (fig3.2), with most of the rain falling in the summer months (table 3.1). Temperatures are high in the summer and mild in the winter with no frost occurring (table 3.1).

Soils

Basalt is the dominant rock type at both sites hence yielding generally medium to fine textured soils with a blocky structure. The soils of the Llanwarne site are predominantly of the Clovelly and Swartland forms (appendix 1a), while the Dordrecht site is dominated by the Swartland form (Soil Classification Working Group 1991) (appendix 1b).

Vegetation

The vegetation is included in the Savanna biome, namely a tropical vegetation type co-dominated by woody plants and grasses (Scholes 1997). At a finer scale the vegetation of this region has been classified as Lowveld (Acocks 1953). This vegetation type occupies the plains at altitudes between 150 - 600 metres above sea level, between the eastern foot of the interior plateau and the western foot of the Lebombo range (fig 3.3).

Characteristic vegetation is an *Acacia nigrescens, Sclerocarya caffra, Themeda triandra* savanna (Acocks 1953)(all plant species nomenclature is according to Arnold & DeWet (1993)). The study area is dominated by fine leafed trees such as *Acacia nilotica, Acacia gerrardii, Acacia tortilis, Acacia nigrescens, Acacia burkea, Acacia grandicornuta, Acacia luederitzii, Acacia senegal* and *Dichrostachys cinerea*. Other common trees include *Sclerocarya birrea* subsp *caffra,* *Ziziphus mucronata, Maytenus heterophylla, Maytenus senegalensis, Schotia brachypetala, Combretum apiculatum, Combretum zeyheri, Berchemia zeyheri and Euphorbia ingens*. A characteristic feature of this bushveld is the formation of bushclumps dominated by broadleaved trees. These clumps are unrelated to soil, but rather are the result of facilitative succession under an *Acacia* tree, evidence for which is the growth of juvenile broadleaved trees under *Acacia* species and the invariable occurance of an old *Acacia* stump within bushclumps. Common woody species in these clumps are *Euclea schimperi, Euclea divinorum, Euclea undulata, Cassine transvaalensis, Carissa bispinosa* and *Dovyalis caffra.* Another common feature of this vegetation is the occurrence of dense stands of *Spirostachys africana* on the toeslopes adjacent to watercourses. Vegetation along dry watercourses is dominated by *Euclea* species, *Spirostachys africana, Dinocanthium hystrix, Schotia brachypetala* and *Schotia capitata*, with *Ficus sycomorus, Acacia robusta, Phyllanthus reticulatus* and *Phoenix reclinata* becoming common along the larger watercourses. The average bushdensity of the study area is 5797 trees ha^{-1} with an average canopy cover of 46.1 % (Walters 1995).

The grass layer, when in a higher successional state, is dominated by *Themeda triandra, Panicum maximum, Panicum coloratum, Digitaria argyrograpta, Bothriochloa insculpta, Cenchrus ciliarus, Cymbopogon excavatus, Sporobolus fimbriatus, Sporobolus ioclados*, and *Cenchrus ciliaris*. In a lower successional state common grasses are *Aristida congesta, Urochloa mosambicensis, Tragus racemosus, Sporobolus nitens, Eragrostis superba*, and *Chloris virgata*.

Experimental design

The trials were established in 1986 (see Turner 1988) and terminated in 1995 at Llanwarne and 1996 at Dordrecht. At the start of the trials in 1986 the Llanwarne site was said to be in good condition, while the Dordrecht site was determined to be in poor condition (Turner 1988). The experimental design of both trials consisted of three stocking rate treatments replicated twice (fig 3.4). The stocking rates for the light, medium and heavy treatments were 0.156, 0.238 and 0.313 animal units (AU) per hectare respectively at Llanwarne and 0.164, 0.208 and 0.278 AU ha^{-1} at Dordrecht, where the medium stocking rate is the recomended stocking rate for this region. By comparison the stocking rates of communal areas in this region were estimated to be about 0.4 AU ha^{-1} . Llanwarne made up a total area of 114.7 ha where the light, medium and heavy treatments made up 51.3, 34.2 and 29.2 ha respectively, while Dordrecht made up 90.5 ha where the light, medium and heavy treatments make up 36.6, 28,6 and 25.3 ha respectively.

In the text of this thesis the low, medium and high replication 1 treatments will be referred to as L1, M1 and H1 respectively and the low, medium and high replication 2 treatments will be referred to as L2, M2 and H2 respectively

A two camp rotational grazing system at each stocking rate was used, where the camps received alternate spring and autumn rests, and the period of stay was variable depending on the season (Hatch 1994). The sites were burnt before the start of the trial (winter 1985) and the Low replication one (L1) and medium replication one (M1) camps at Llanwarne were burnt again in the winter of 1990 following an accumulation of rank grass after a series of above average rainfall years (Hatch 1994).

The drought of the 1991/1992 season resulted in severe fodder shortages and the experimental cattle in all treatments had to be supplemented with sugar cane tops during the winter of 1992, and the medium and heavy stocking rate treatments at Dordrecht in the winter of 1993. More detailed information on the experimental cattle and their management is described in the methods section on cattle performance (chapter 6).

Data were initially collected by Turner (1988) followed by Hatch (1994) and by the author in the final year (1996). Details of data collection are described in the methods sections of the relevant chapters of this thesis.

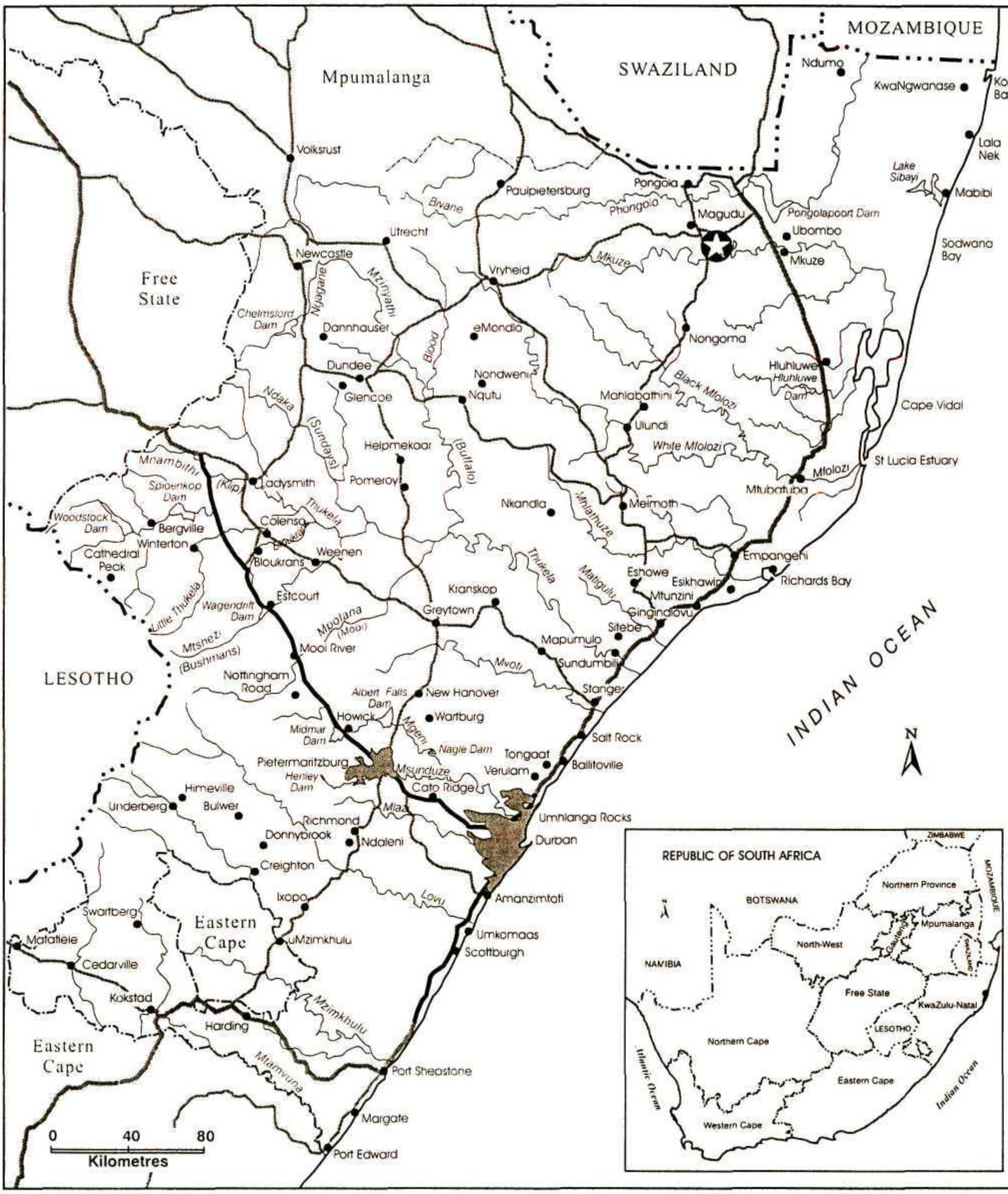


Figure 3.1 Map of KwaZulu-Natal showing roads and towns, with the location of the study site indicated.

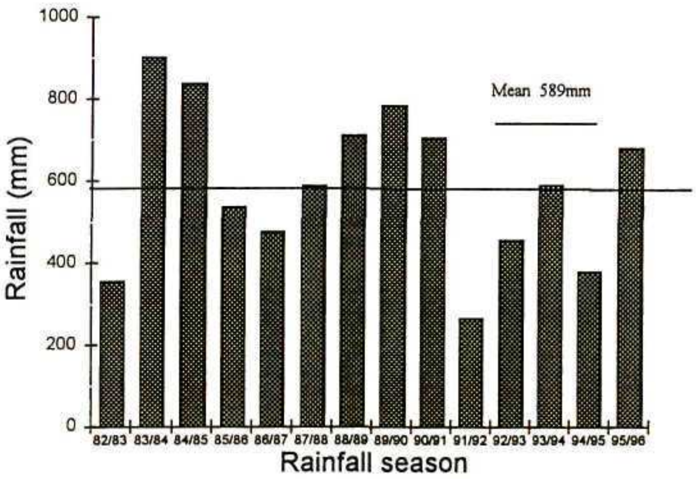


Figure 3.2 Seasonal rainfall data collected at the Llanwarne meterological station between 1982 and 1996, CV = 32%.

Table 3.1 Local climate characteristics at Llanwarne and Dordrecht, taken from the Llanwarne meterological station, over a ten year period(Clemence et al. 1987).

Rainfall (mm)	
Mean annual rainfall	558.5
Highest mean monthly rainfall (Jan)	122.7
Lowest mean monthly rainfall (July)	9.5
Temperature (°C)	
Mean annual temperature	21.2
Highest mean monthly temperature (Jan)	31.2
Lowest mean monthly temperature (June)	6.2
APAN Evaporation (mm)	
Mean annual evaporation	2040.3
Highest mean monthly evaporation (Dec)	240.7
Lowest mean monthly evaporation (Jun)	98.3

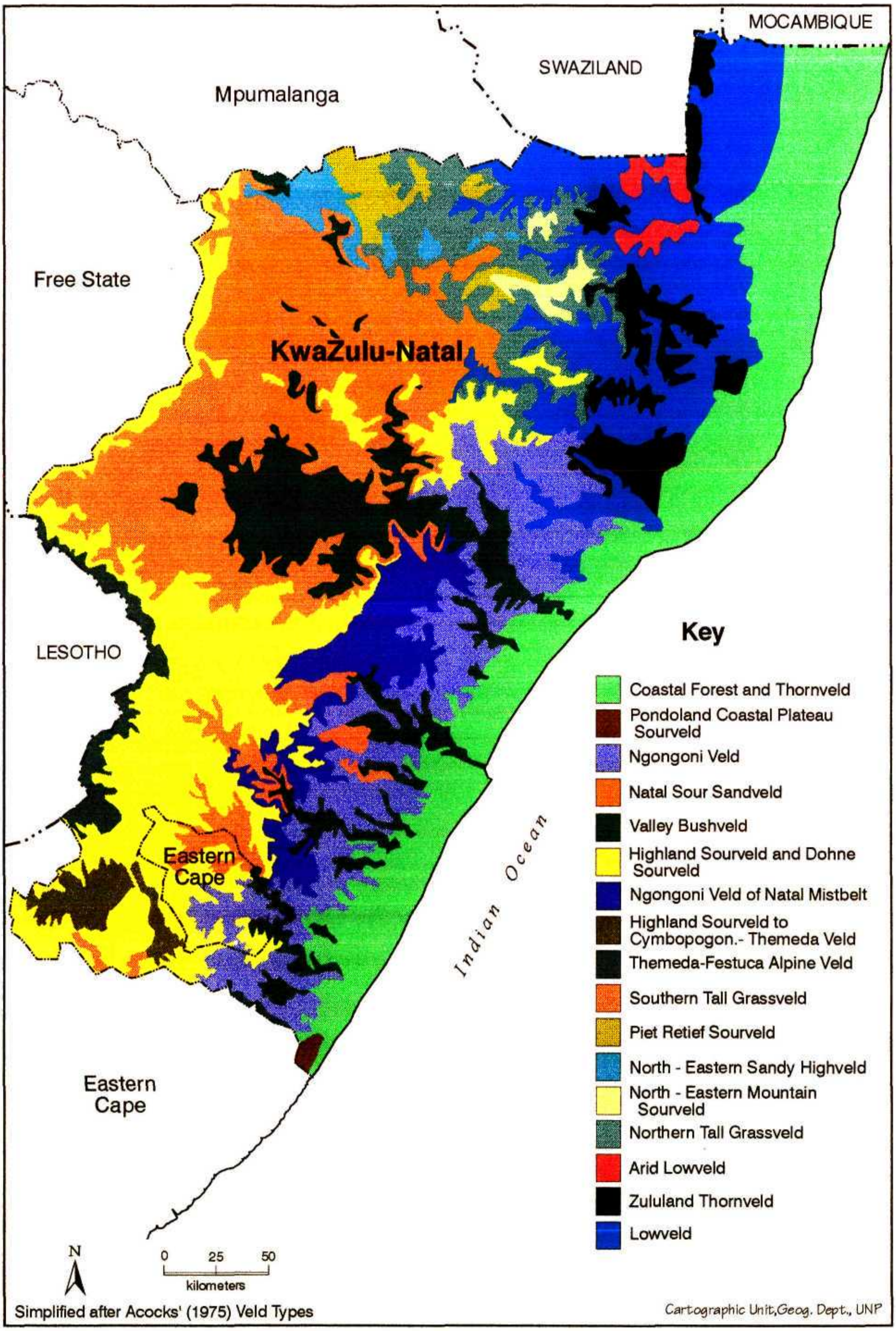


Figure 3.3 Map of Acocks (1975) veld types of Natal (study site location indicated).

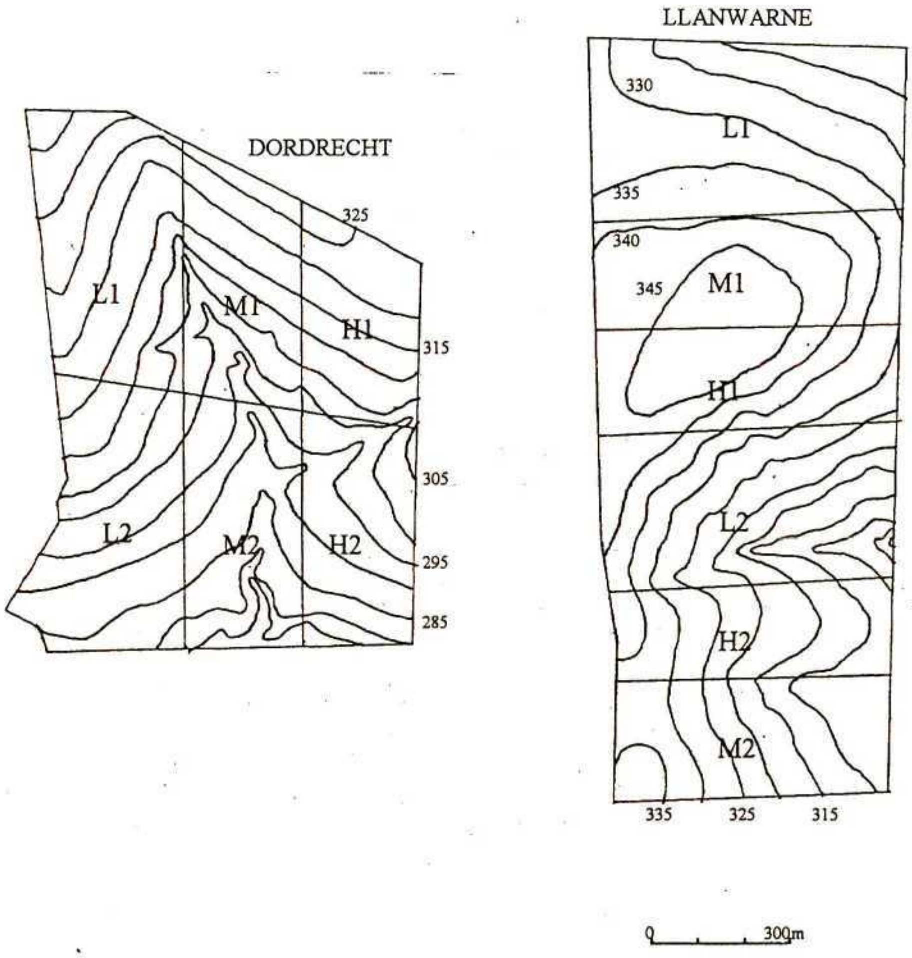


Figure 3.4 Experimental design of the trials at Llanwarne and Dordrecht

CHAPTER 4

EFFECT OF STOCKING RATE AND RAINFALL ON SPECIES COMPOSITION DYNAMICS IN A SEMI-ARID SAVANNA

Introduction

Species composition has been a tenet of the philosophy of rangeland management, largely due to it being an integral component of succession theory. Composition has been the framework upon which rangeland management theories have been based (Dyksterhuis 1949). Grazing pressure is considered a disturbance factor that acts as a force against successional progression. A sere in the successional sequence is characterised by a particular species composition and structure. Rangeland scientists have postulated that at some point along the successional sequence a particular sere exists that will yield optimum animal performance. Thus the prime objective of rangeland managers has been to maintain rangeland in this ideal compositional state, by means of finding a balance between grazing pressure and successional progression. For this balance to be possible there has to be an assumption of equilibrial ecosystem functioning. Recently questions have been raised over the validity of the concept of the equilibrial nature of plant communities, especially in semi-arid environments (Ellis & Swift 1988). The concept of linear deterministic succession has also been questioned with suggestions that the state-and-transition model may be more appropriate for semi-arid environments (Westoby *et al.* 1989).

The basic question needing resolution in this debate is the relative importance of the roles that stocking rate and rainfall play in determining species composition over a range of climatic environments. Evidence exists for grazing induced changes in species composition in semi-arid and humid environments (Van de Koppel *et al.* 1997). It appears that compositional change in semi-arid environments is largely rainfall driven on a short time scale, with stocking rate becoming more important on a larger time scale. (O'Connor 1995, O'Connor & Roux 1995).

The aim of this study was to determine the magnitude and direction of compositional changes over time in response to stocking rate and rainfall by the use of ordination techniques (i.e. what is the degree of species change over time under various stocking rates, what are the optimal conditions for increases or decreases of certain species, and how strongly are they dependent on those conditions?) It was intended to assess how these results supported or contradicted contempory thinking on how various growth forms or strategies of grasses (i.e. annual, weakly tufted perennial, tufted perennial) reacted to grazing and rainfall, as well as to determine whether the results supported the succession model or state-and-transition model, or both. This was especially relevant to range condition assessment techniques, where heavy stocking rates are considered to drive succession back to an annual and weakly tufted perennial dominated sward.

Methods

Survey method

Surveys of species composition were conducted in each treatment camp at Llanwarne and Dordrecht in the summer every two years between 1986 and 1996. The survey method consisted of the nearest plant method (Foran *et al.* 1978) with 150 samples taken systematically along two diagonal transects across a camp (300 samples per camp in total). If the nearest plant to a point was a grass, it was identified to the species level, sedges were lumped, and other herbaceous species were recorded as forbs. If no herbaceous plant (woody species were ignored) occurred within 20 cm of the point then bare ground was recorded.

Data analysis

To examine the magnitude of compositional change between 1986 and 1996, Euclidean distances were calculated for each camp in 1986 and 1996. These distances were compared with the 99% confidence interval about the mean Euclidean distance between treatments in 1986. This was done separately for Llanwarne and Dordrecht because the high, medium and low grazing treatments at Llanwarne were not the same as the high, medium and low treatments at Dordrecht. A one-tailed t - value was used to calculate confidence intervals because the objective was to determine if the sites had moved more between 1986 and 1996, than the original Euclidean distances among treatments in 1986 (i.e. had a camp moved outside the bounds of the original composition at the start of the trial).

A correspondence analysis (CA) and a canonical correspondence analysis (CCA) were done on a combined Llanwarne and Dordrecht data set, using the multivariate statistical program CANOCO (ter Braak 1988).The reason that a combined data set was used was to test whether the different starting conditions of the two sites had an affect on compositional change. Thus the data was subjected to an unconstrained analysis (CA) and to one constrained by the environmental variables included in the analysis (CCA). By using a constrained analysis one is able to test directly whether the included environmental variables account for a significant amount of the variance in the species data and also to identify which species are related to specific environmental variables. A problem with a constrained ordination arises if one wishes to examine the trends in site trajectories through time, because it distorts the representation of sites in their trajectories over time. Unconstrained ordinations provide an undistorted perspective of the change over time in site trajectories. The effect of repeated measures on the same site or auto-correlation (Swain & Greig-Smith 1980), was first removed by including a covariable matrix of dummy variables which coded for sites and years. The ordination was conducted thereafter on the residual variance. A Monte Carlo permutation test (restricted form, with 99 permutations) was used to test whether the ordination and first axis were significant (Ter Braak 1988).

Environmental variables

Stocking rate has a known influence on species composition over time (Van de Koppel *et al.* 1997), and therefore a stocking rate-by-time variable was used in the analysis, where time was the number of years that the trial had been running.

Rainfall at Llanwarne and Dordrecht is low, variable and typical of a semi-arid environment (see fig 3.2, chapter 3). As a result water is likely to be a limiting factor in this region and thereby may have marked influences on species composition. Summer rainfall immediately preceding the survey is likely to be important, but the previous seasons rainfall may also be important. For example the previous seasons rainfall may result in abundant seed production, which then provides the potential for good germination and establishment in the following year. Thus two rainfall variables were included in the analysis: summer rainfall preceding the survey and product of rainfall preceding the survey and the previous seasons rainfall.

A dummy variable distinguishing between the Llanwarne and Dordrecht sites was included because of the different starting condition of these sites (Turner 1988). An interaction between the site variable and the grazing-by-time variable was included to determine if the starting condition of the sites had an influence on the effect of grazing on compositional change.

Dynamics of individual species

The relative abundances of two species of the three main growth forms or strategies of grasses in the L 2 and H 2 camps at Llanwarne, were graphed over the duration of the trial with rainfall overlaid. The objective was to see the individual reaction of species of different functional groups to rainfall and stocking rate, and to illustrate some of the results from the ordinations. The H 2 camp at Llanwarne was chosen because it had shown a decline in productivity and greatest compositional change over time.

Results

Correspondence analysis

The first four axes accounted for 57.5% of the variance in the species data with axis 1 and axis 2 accounting for 19.6 % and 14.3% of the variance respectively. Axis 1 accounted for 30.5%, while axis 2 accounted for 22.3% of the species-environment relations (table 4.1).

Table 4.1 Summary of the overall performance of the correspondence analysis in terms of the variance accounted for by each axis and species-environment relations

Axes	1	2	3	4	Total inertia
Eigenvalues	.107	.078	.068	.061	.716
Species-environment correlations		.680	.683	.704	.623
Cumulative percentage variance					
of species data	19.6	33.9	46.3	57.5	
of species-environment relation	30.5	52.8	73.6	88.1	
Sum of all unconstrained eigenvalues (after fitting covariables)					.545
Sum of all canonical eigenvalues (after fitting covariables)					.162

There was little divergence in the correspondence analysis site trajectories through time among the various stocking rate treatments (fig 4.1). The trajectories are essentially correlated with time rather than with treatment.

The trajectories move mainly along axis 1 which is essentially a rainfall gradient with some influence of grazing. The product of rainfall preceding the survey and the previous seasons rainfall (rain 2) is significant and most strongly correlated with this axis followed by grazing (fig 4.2 and table 4.2). The drought of the 1991/1992 season precipitated a pronounced compositional change as seen by the large distance moved by the 1993 sites (fig 4.1). With the return of average though not high rainfall seasons (see fig 4.2, chapter 3) the sites tended towards the original positions, though were deflected on axis 2 possibly as a result of a grazing effect, seeing that the grazing-by-time variable is most strongly correlated with this axis (fig 4.2 & table 4.2).

The only conspicuous difference among treatment trajectories was that at high stocking rates species composition appeared to be less stable (i.e. moved further in ordination space, though the effect was site specific). This was confirmed formally by comparing the Euclidean distances between sites in 1986 and 1996 with the confidence limits of the mean Euclidean distance between treatments in 1986. At Llanwarne, all except the L 2 treatment had changed outside the bounds of the Euclidean distances between treatments by 1996 (fig 4.3 A). At Dordrecht only the H 1 treatment had changed outside the bounds of the Euclidean distances between treatments (fig 4.3 B).

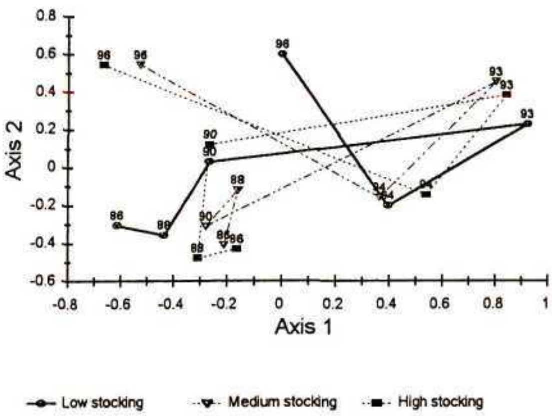
The original composition of the sites (Llanwarne & Dordrecht) did not affect the influence of grazing on species composition change, as shown by the short site by grazing interaction arrow and its direct correlation with the grazing time variable (fig 4.2).

Rainfall as a product of the rainfall season preceding the survey and the previous season's rainfall (rain 2) was more important in driving compositional change than a single seasons rainfall, as indicated by the longer arrow of rain 2 (fig 4.2) and the significant effect of the drought of the 1991/1992 season as shown by the large distances that the sites moved in ordination space from positions in 1990 compared with the 1993 positions (fig 4.1). The length of the grazing-time arrow, although not as long as the rainfall arrow, indicated a significant contribution of grazing over time to compositional change (fig 4.2).

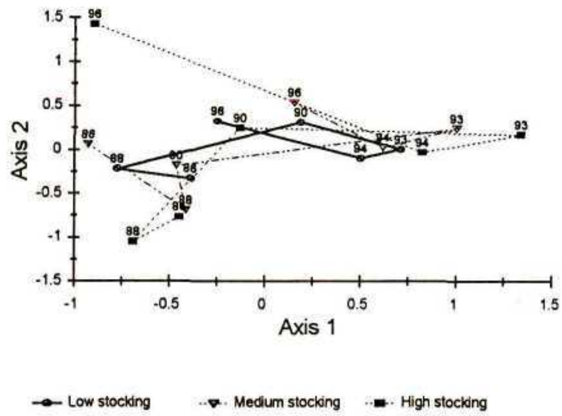
Species that exhibited greatest increases under low rainfall conditions especially with a combination of low rainfall years (rain 2), were short lived perennials such as *Aristida congesta, Sporobolus nitens, Urochloa mosambicensis* and *Fingerhuthia africana*, and the annual *Tragus racemosus* (fig 4.2). These increases most likely occurred at the expense of densely tufted perennials such as *Cymbopogon excavatus, Themeda triandra, Eragrostis superba, Digitaria argyrograpta* and *Sporobolus ioclados,* which exhibited greatest increases with combinations of years of high rainfall (rain 2) and low grazing over time (fig 4.2). Generally those species that increased with combinations of years of low rainfall also increased with high grazing conditions (fig 4.2).

The opposite effect was observed with the annuals *Aristida adscensionis* and *Enneapogon cenchroides*, the creeping perennial *Dactyloctenium australe* and the weakly tufted perennial *Trichoneura grandiglumis*, which increased most rapidly with combinations of high rainfall seasons but also depended on conditions of high grazing over time (fig 4.2). Thus these species probably needed disturbance in the form of gaps created by grazing, to optimize their recruitment, but at the same time needed high rainfall for germination. *Eragrostis curvula, Melinis repens* and *Eustachys paspaloides* tended to increase during a single high rainfall season, rather than a combination of high rainfall seasons (fig 4.2) but only under low grazing conditions.

Interestingly bare ground and forbs tended to increase optimally with combinations of high rainfall years and low grazing. *Panicum* species, *Bothriochloa insculpta* and *Cenchrus ciliarus* did not appear to respond to high levels any of the environmental variables in the analysis, suggesting that optimum conditions for increases in these species occurred at moderate levels of these variables. The classical antagonistic effect of high rainfall with low grazing causing increases in long lived perennials such as *Themeda triandra, Cymbopogon excavatus, Digitaria argyrograpta* and *Sporobolus ioclados* and high grazing with low rainfall causing increases in annuals and short lived perennials such as *Urochloa mosambicensis, Aristida congesta, Tragus racemosus* and *Sporobolus nitens*, supports the Clementsian model (fig 4.2).



A



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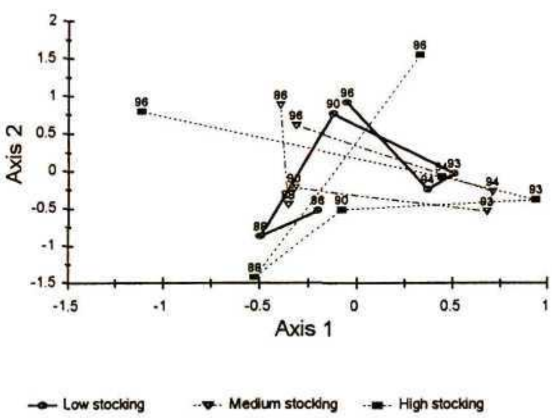

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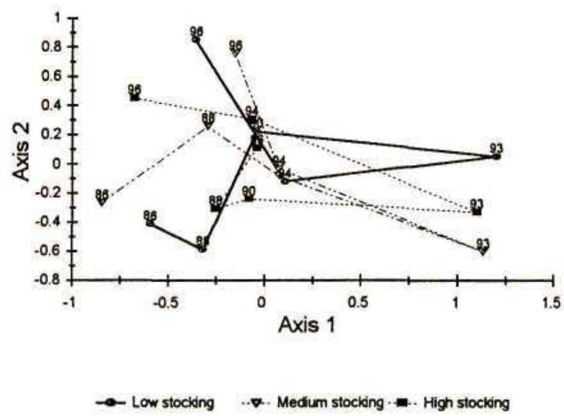


D

Figure 4.1 Site trajectories between 1986 and 1996 on the first two axes of a correspondence analysis of a combined Llanwarne and Dordrecht data set. Llanwarne replication 1 (A), Llanwarne replication 2 (B), Dordrecht replication 1 (C), Dordrecht replication 2 (D).

Numbers represent year, i.e. 86=1986

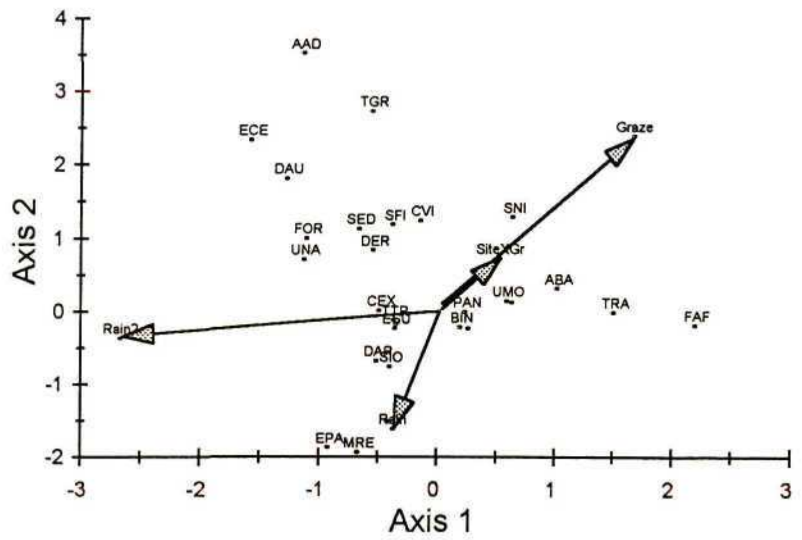


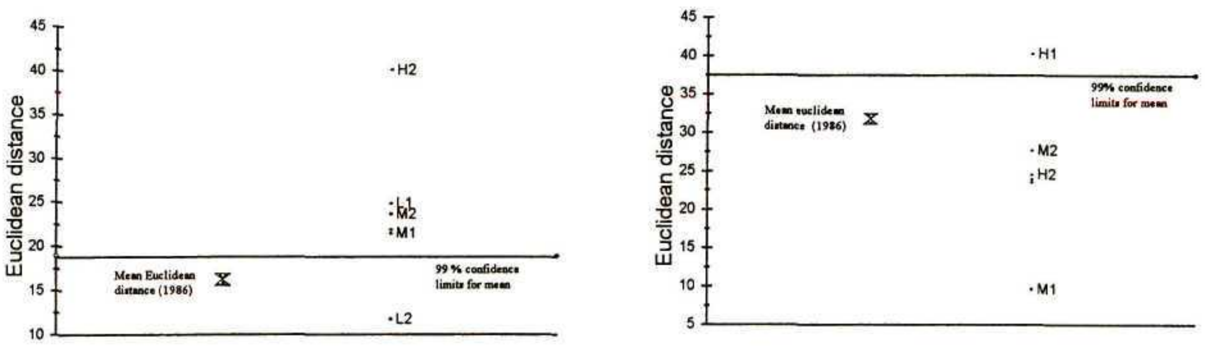
Figure 4.2 Plot of the species scores of the first two axes of a correspondence analysis of a combined Llanwarne and Dordrecht data set.

Key to species: AAD:Aristida sp, ABA:Aristida congesta, BIN:Bothriochloa insculpta, CEX:Cymbopogon excavatus, CCI:Cenchrus ciliarus, CVI:Chloris virgata,DAU:Dactyloctenium australe, DAR:Digitaria argyrograpta, DER:Digitaria eriantha, ECE:Enneapogon cenchroides, ECH:Eragrostis chloromelas, ECU:Eragrostis curvula, ESU:Eragrostis superba, ESP:Eragrostis sp, EPA:Eustachys paspaloides,FOR:Forbs, FAF:Fingerhuthia africana, HCO:Heteropogon contortus, MRE:Melinis repens, SFI:Sporobolus fimbriatus, SIO:Sporobolus ioclados, SNI:Sporobolus nitens, TGR:Trichoneura grandiglumis, TRA:Tragus racemosa, TTR:Themeda triandra, UMO:Urochloa mosambicensis, UPA:Urochloa panicoides, UNA: bare ground, Rain:Rainfall immediatly preceding the survey, Rain2:Product of the seasons rainfall preceding the survey and the previous seasons rainfall, Graze:Stocking rate X time since start of trial, SiteXGr:Interaction between site (Llanwarne & Dordrecht) and the grazing time variable.

Table 4.2 *t*-values of regression coefficients and correlations of environmental variables with axis 1 & 2

t-values		
Variable	AX1	AX2
Rainfall	**4.8598**	**-4.0971**
GrazeXtime	1.3430	**5.1535**
Rain2	**-6.0479**	**4.4488**
SiteXgraze	-1.0440	-1.4650
Correlations		
Variable	AX1	AX2
Rainfall	-.0661	-.3085
GrazeXtime	.3153	.4890
Rain2	-.4703	-.0701
SiteXgraze	.1439	.2138

Rain 2 is the product of seasonal rainfall preceding the survey and the previous seasons rainfall. SiteXgraze is the interaction between site (Llanwarne or Dordrecht and the graze time variable. Numbers in bold denote significance ($p<0.05$).



A **B**

Figure 4.3 The Euclidean distances between species composition in 1986 and 1996 for each treatment camp, compared with the Euclidean distances between treatments in 1986. Llanwarne (A), Dordrecht (B)

Canonical Correspondence Analysis

The Monte Carlo permutation test showed that the ordination and the first axis were significant ($p<0.01$). The first four axes of the ordination accounted for only 29.8% of the variation in the species data of which axis 1 and 2 accounted for 10.3% and 10% respectively (table 4.3). Thus the first two axes were almost equally important in terms of the species variance accounted for. Axis 1 accounted for 34.6% of the species-environment relations while axis 2 accounted for a further 33.4% (table 4.3). Once again the first two axes were of similar importance when relating species to environmental factors.

Table 4.3 Summary of the overall performance of the canonical correspondence analysis in terms of the variance accounted for by each axis and species environment relations

Axes	1	2	3	4	Total inertia
Eigenvalues	0.056	0.054	0.040	0.012	0.716
Species-environment correlations		0.791	0.820	0.798	0.544
Cumulative percentage variance					
of species data	10.3	20.3	27.7	29.8	
of species-environment relation	34.6	68.0	92.9	100.0	
Sum of all unconstrained eigenvalues (after fitting covariables)					0.545
Sum of all canonical eigenvalues (after fitting covariables)					0.162

There was essentially one important difference between the CCA and the CA. In the CA the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2) and the graze-time variable were inversely correlated in their effects on compositional change (fig 4.2) while in the CCA analysis they were orthogonal (fig 4.4). However seasonal rain preceding the survey remained in opposition to grazing although more so than in the CA analysis.

Although the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2) had changed in relation to the graze-time variable the basic species environment relations had not changed. *Themeda triandra* and *Cymbopogon excavatus* were still positively associated with the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2), while *Tragus racemosus, Fingerhuthia africana, Aristida congesta* and *Urochloa mosambicensis* were still negatively associated with this variable (fig 4.4). *Melinis repens* and *Eustachys paspaloides* were still shown to increase optimally with a single seasons high rainfall and low grazing (fig 4.4). Of interest is that the strongly tufted perennial *Heteropogon contortus* appears to increase optimally under conditions of low rainfall and low grazing, rather than high rainfall and low grazing as exhibited by similar tufted perennials (fig 4.4).

Changes that did take place were with *Sporobolus ioclados* and *Eragrostis superba* which were positively related to the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2) in the CA analysis, but were negatively correlated with it in the CCA (fig 4.4). The annuals *Aristida adscensionis* and *Enneapogon cenchroides*, the creeping perennial *Dactyloctenium australe* and the short lived perennial *Trichoneura grandiglumis* were shown to increase most under conditions of high rainfall and grazing, more so than in the CA (fig 4.4). *Sporobolus fimbriatus* was more strongly associated with the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2) in the CCA than the CA.

The site positions in the CCA analysis showed groupings according to year rather than treatment as in the CA, thus showing the strong effect of rainfall on compositional change (fig 4.5). Preceding rainfall and the product of the rainfall season immediately preceding the survey and the previous seasons rainfall (rain 2) still had significant effects on this axis. Grazing still had the strongest effect on axis 2 (table 4.4).

As with the CA the site-by-grazing interaction was weak and directly correlated with grazing (fig 4.4), indicating that site had little effect on the response of species to grazing.

Table 4.4 T values of regression coefficients and correlations of environmental variables with axis 1 & 2

t-values		
Variable	AX1	AX2
Rainfall	-6.7792	-0.7072
GrazeXtime	3.2557	-6.4615
Rain 2	9.3837	2.2058
SiteXgraze	1.2383	0.6993

Rain 2 is the product of seasonal rainfall preceding the survey and the previous seasons rainfall. SiteXgraze is the interaction between site (Llanwarne or Dordrecht and the graze time variable

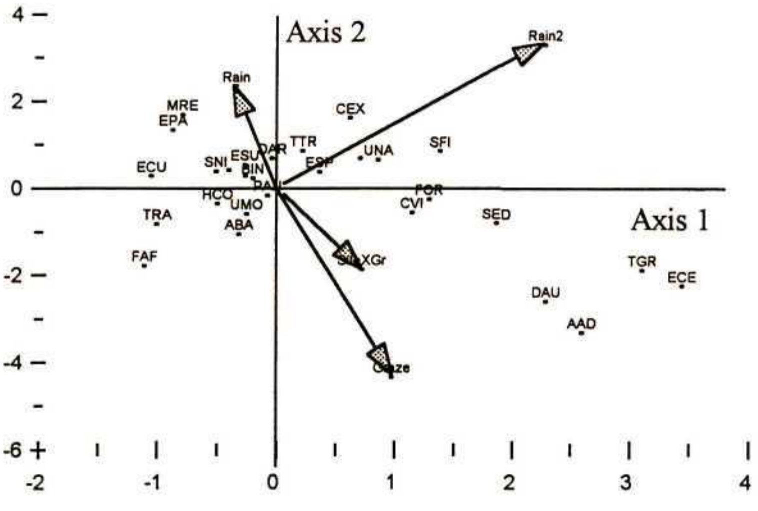
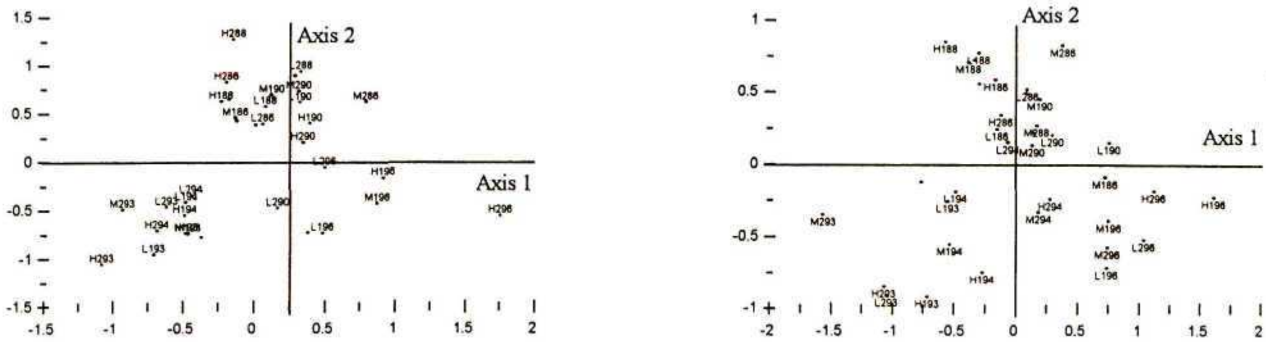


Figure 4.4 Plot of species scores for Llanwarne and Dordrecht, of the first two axes of a CCA analysis on the combined Llanwarne and Dordrecht data set.

Key to species: AAD:Aristida sp, ABA:Aristida congesta, BIN:Bothriochloa insculpta, CEX:Cymbopogon excavatus, CCI:Cenchrus ciliarus, CVI:Chloris virgata, DAU:Dactyloctenium australe, DAR:Digitaria argyrograpta, DER:Digitaria eriantha, ECE:Enneapogon cenchroides, ECH:Eragrostis chloromelas, ECU:Eragrostis curvula, ESU:Eragrostis superba, ESP:Eragrostis sp, EPA:Eustachys paspaloides, FOR:Forbs, FAF:Fingerhuthia africana, HCO:Heteropogon contortus, MRE:Melinis repens, SFI:Sporobolus fimbriatus, SIO:Sporobolus ioclados, SNI:Sporobolus nitens, TGR:Trichoneura grandiglumis, TRA:Tragus racemosa, TTR:Themeda triandra, UMO:Urochloa mosambicensis, UPA:Urochloa panicoides, UNA:Unallocated bare ground, Rain:Rainfall immediately preceding the survey, Rain2:Product of the seasons rainfall preceding the survey and the previous seasons rainfall, Graze:Stocking rate X time since start of trial, SiteXGr:Interaction between site (Llanwarne & Dordrecht) and the grazing time variable.



A B

Figure 4.5 Plot of the site scores for Llanwarne (A) and Dordrecht (B), of the first two axes of a CCA analysis on the combined Llanwarne and Dordrecht data set.

Key to sites - L1:low stocking rate camp (replication 1), M1: medium stocking rate camp (replication 1), H1: high stocking rate camp (replication 1)
L2:low stocking rate camp (replication 2), M2: medium stocking rate camp (replication 2), H2: high stocking rate camp (replication 2) 86: 1986, 88: 1988, 90: 1990
93: 1993, 94: 1994, 95: 1995, 96: 1996. Llanwarne (A), Dordrecht (B).

Dynamics of individual species

The densely tufted perennials *Panicum* species (*Panicum maximum* and *Panicum coloratum* lumped) and *Themeda triandra* did not exhibit marked changes in abundance that could be attributed to rainfall or stocking rate (fig 4.6). Surprisingly *Panicum* species tended to become more frequent after the 1992 drought, rather than showing a marked decline after the drought. This could be due to the ameliorating effect of tree cover where these Panicums grow. The drought appears to have had more of an effect on *Themeda triandra* at high stocking rates where it declined as a result of the drought. There was a consistent trend, however, of lower frequencies of these species at high stocking rates. Densely tufted perennials are favoured by low stocking rates, so this was not unexpected.

The weakly tufted perennials *Aristida congesta* and *Urochloa mosambicensis* reacted in a similar fashion to the 1992 drought (fig 4.7). At high stocking rates both species increased in relative abundance after the drought, but remained constant at low stocking rates. Several higher rainfall seasons after the drought resulted in inconsistent trends between the two species, with *Aristida congesta* declining and *Urochloa mosambicensis* increasing.

Some change in the system (possibly due to drought) favoured a rapid increase of *Urochloa mosambicensis*, especially at high stocking rates.

The 1992 drought appeared to have a negative impact on the relative abundance of the annual *Chloris virgata* (fig 4.8), while the annual *Tragus racemosus* increased rapidly in relative abundance as a result of the drought. *Chloris virgata* appears to favour high stocking rates with high rainfall (see 1990) while *Tragus racemosus* favours high stocking rates with low rainfall (see 1993). The reasons for this interaction of these two annuals with rainfall is left to speculation at our present state of knowledge of these species.

Caution needs to be used in the interpretation of the trends in relative abundances of perennial grasses however, because a large increase in the abundance of annual grasses will reduce the frequency at which perennials are recorded even though their absolute abundances have not declined.

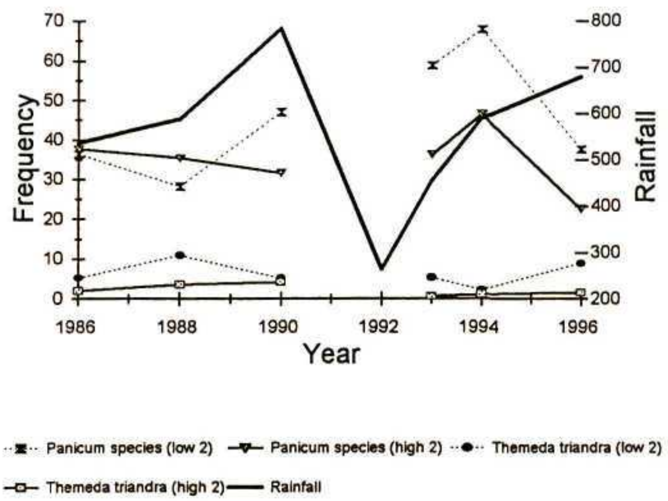


Figure 4.6 Changes in relative abundance of the long lived perennial grasses *Panicum* species (*Panicum coloratum* and *Panicum maximum*) and *Themeda triandra* in response to rainfall and stocking rate.

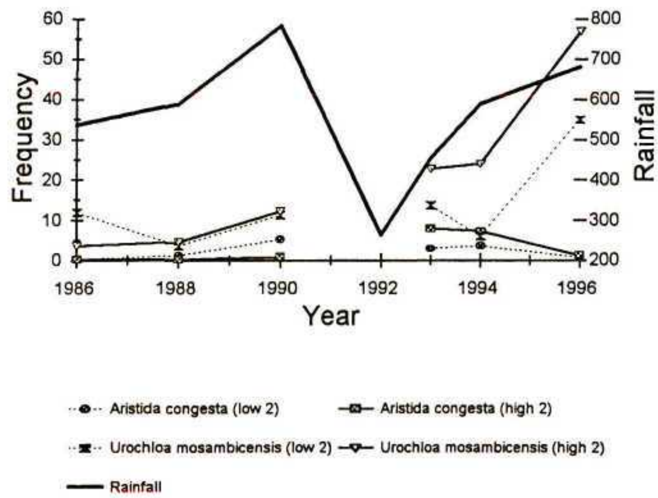


Figure 4.7 Changes in relative abundance of the short lived perennials *Aristida congesta* and *Urochloa mosambicensis* in response to rainfall and stocking rate.

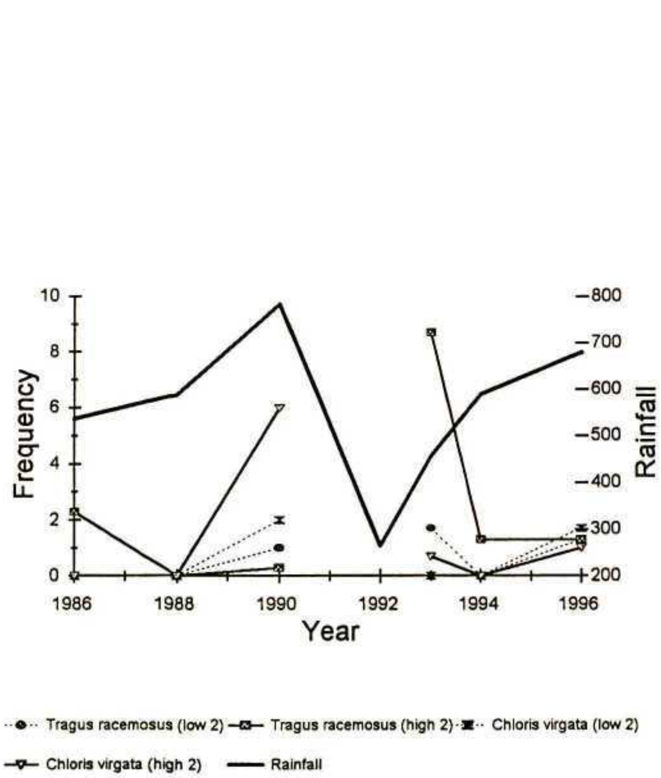


Figure 4.8 Changes in relative abundance of the annuals *Tragus racemosus* and *Chloris virgata* in response to rainfall and stocking rate.

Discussion

The findings of this study are largely in agreement with the results of other workers in semi-arid environments (O'Connor 1995, O'Connor & Roux 1995), which show that on an annual scale rainfall tends to have the major influence on compositional change, with stocking rate playing an additional less conspicuous role in the short term, but increasingly larger effect in the long term. For example the year to year changes in the site positions (fig 4.1) are largely due to rainfall with little evidence of a stocking rate effect, as indicated by very little divergence in site trajectories amongst stocking rate treatments. Very little movement through ordination space can be attributed to stocking rate, except the H 2 stocking rate treatment at Llanwarne (fig 4.1 B), and the H 1 treatment at Dordrecht (fig 4.1 C). This was confirmed by the conspicuously larger Euclidean distances between 1986 and 1996 for these two camps compared with other camps (fig 4.3).

These two high stocking rate camps occurred on steeper slopes than the H 1 camp at Llanwarne and the H 2 camp at Dordrecht, which suggests that compositional changes are less likely to occur with heavy grazing on flat land or gentle slopes than heavy grazing on steep slopes. Compositional change as a result of heavy grazing have been observed worldwide (Milchunas & Lauenroth 1993, Van de Koppel *et al.* 1997), but little has been said of the interaction of stocking rate with landscape and its effect on compositional change. Vegetation change as a result of heavy grazing is more likely on steeper slopes than on flat land for a number of reasons. Soil loss is more likely on steeper slopes owing to the greater potential for runoff. There is a large amount of literature relating vegetation shifts in semi-arid grasslands to soil degradation (Van de Koppel *et al.* 1997). Another likely factor that may precipitate vegetation change on steeper slopes, is a reduction in soil moisture status. Milchunas & Lauenroth (1993) observed grazing induced reductions in soil water at 13 out of 15 sites. Grazing induced reductions in basal cover will have a larger effect on runoff on steeper slopes than flat land. Slopes are generally more moisture stressed than flat land owing to better drainage, and therefore any reduction in water capture on slopes will have a larger effect on plant growth than on flat land. In fact, flatter down slope zones benefit from runoff from the slopes, receiving considerably more water than they would otherwise (Hodgkinson & Freudenberger 1997). Perennial grasses may be more prone to mortality with heavy grazing in a moisture stressed environment. In Australian mulga rangelands, the grass *Monachather paradoxa* was found to suffer greater mortality in stands of *Acacia aneura* where soil moisture was lower than outside the stands, owing to soil moisture extraction by the trees (Freudenberger *et al.* 1997). This illustrates how this effect may have caused, or at least contributed to vegetation change on the steeper slopes at Llanwarne and Dordrecht.

Grazing, although second to rainfall, has been an important vector of compositional change over time as shown by the length of the grazing-by-time arrow. More direct evidence for a grazing effect is the negative response of densely tufted perennials such as *Themeda triandra* and *Cymbopogon excavatus* and the positive response of weakly tufted perennials such as *Aristida congesta* and *Urochloa mosambicensis* to grazing (fig's 4.2 & 4.4), as well as the positive response of *Dactyloctenium australe, Trichoneura grandiglumis, Enneapogon cenchroides* and *Aristida adscensionis* to high rainfall and grazing (fig's 4.2 & 4.4). Although responses to grazing are clear, they have only been strong enough to result in a divergence in site trajectories amongst the H 1 treatments at Dordrecht and the H 2 treatment at Llanwarne.

The conclusion then is that in these two trials, rainfall has been the major cause of compositional change, with evidence to show compositional changes due to heavy stocking rates only being observed in those camps on steeper slopes.

Recent research suggests that owing to the sampling strategy, greater vegetation changes may have taken place than actually detected. Friedel (1997) found that compositional changes caused by grazing could not be detected without stratifying for spatial patterns at fine scales. There were strong spatial patterns in the Llanwarne and Dordrecht trials represented by sub-habitats beneath tree canopies and between tree canopies, which was unaccounted for by the survey method.

The lack of response of *Panicum* species to any of the environmental variables included in this analysis, is most likely due to the ameliorating effect of the trees under which it grows. There will be reduced water stress and temperature fluctuations, enabling it to cope better with the effects of grazing . Also *Panicum maximum* is probably a better competitor than most other grasses in shaded environments, due to superior CO_2 assimilation rates and better water use efficiency in the shade (Kinyamario *et al.* 1995).

The reaction of species to environmental variables was not strictly according to growth forms or strategies of species. A similar result was obtained by Friedel (1997). Patterns, however, were observed amongst similar growth forms or strategies of species. Annuals and weakly tufted perennials tended to increase under conditions of heavy grazing while strongly tufted perennials tended to increase under conditions of high rainfall and low grazing. This was observed in the

Sahel, where perennial vegetation was replaced by annual vegetation under conditions of low rainfall and heavy grazing (Van de Koppel *et al.* 1997). There were two distinct responses of annuals and weakly tufted perennials to rainfall, those that increased with high grazing and high rainfall and those that increased with high grazing and low rainfall.

The increase in the relative abundance of *Urochloa mosambicensis* after the 1992 drought (fig 4.7) provides support for the state-and-transition model where a large perturbation such as a severe drought may change a system in such a way that elicits an entirely different response after the drought. With succession theory one may expect a weakly tufted perennial such as *Urochloa mosambicensis* to increase directly after the drought relative to higher successional species and then with better rainfall years to decline relative to higher successional species, yet it appears to continue to increase. There was also support for the Clementsian model of succession and was particularly evident in the correspondence analysis where grazing and rainfall were in opposition to each other, with high rainfall and low grazing causing increases in strongly tufted grasses (i.e. promoting change towards a higher successional community).

The results of this study support the continued use of conventional methods of range condition assessment for this region, but also emphasize the role that rainfall plays in affecting range condition.

CHAPTER 5

FACTORS CONTROLLING GRASS PRODUCTION IN A SEMI-ARID SAVANNA

Introduction

The greater the amount of grass produced in a season the more livestock one should be able to support in that season. Thus most methods used for calculating the carrying capacity of a region take into account total end of season herbaceous dry matter per hectare (TDM ha^{-1}) (de Leeuw & Tothill 1993). Although the validity of the carrying capacity concept in semi-arid environments is questionable, due to variable grass production (Stoddart 1960, Mcleod 1997), there is a link between the performance of livestock and the quantity of forage produced (Jones & Sandland 1974).

The amount of forage produced in a season is dependent on a range of abiotic factors such as temperature, rainfall and soil fertility (Tainton 1988), as well as biotic factors such as the particular species composition of the sward (Grime 1997) and stocking rate (Van Poolen & Lacey 1979).

Thus a loss of soil from a particular landscape may reduce grass productivity (Biot 1993, Van de Koppel *et al.* 1997). Heavy stocking rates usually reduce infiltration in soils and increase runoff and erosion and thereby reduce the water use efficiency of the rangeland (Van de Koppel *et al.* 1997).

The notion that many of Africa's communal areas are overstocked (see Sandford 1983, Cossins 1986, Boonzaier *et al.* 1990, Tapson 1991), has produced fears of widespread degradation of vegetation, desertification and the agricultural productivity of many countries being reduced to a fraction of their original potential. This fear has not only been restricted to communal farming, but also to commercial farming where increased use of supplements has led to reduced mortality and improved calving percentages of livestock, allowing a large increase in livestock numbers. This factor in combination with prevailing economic pressures, often forces farmers to increase the number of livestock on their farms (Ash *et al.* 1991). Livestock numbers usually increase in good wet cycles (combination of above average rainfall seasons) usually as a result of improved fecundity and farmers buying-in animals. It is in these times that farms become overstocked, usually with no adverse effects on the vegetation, while rainfall continues to be above average (Ash *et al.* 1991). In the event of a sudden drought overgrazing results (Ash *et al.* 1991), because there is insufficient grass available to support the high livestock numbers, and farmers cannot easily sell their livestock due to the markets being flooded, with a resultant crash in market values of animals. It is in these periods that range degradation is most likely, due to greatly reduced grass cover, thereby exposing the soil to erosion or surface compaction and sealing (Livingstone 1991). This scenario is most relevant to semi-arid regions rather than humid regions where rainfall is more reliable. Both communal and commercial farming regions are likely to experience overgrazing during droughts. A long-term grazing trial in a semi-arid system is likely to be affected by droughts, and is therefore a useful means of testing whether periods of heavy grazing during droughts result in degradation, because heavy stocking rates are maintained throughout the drought. Grazing trials offer the opportunity to establish how vegetation reacts to specific stocking rates and within what time frame. They provide insights into the interactions between various grazing intensities and environmental effects, on plant species composition and plant biomass dynamics. They are also useful for providing guidelines to commercial farmers in these regions to know at what stocking rates on average they are able to safely stock at.

The aims of this study were to determine whether factors such as rainfall interacted with stocking rate in affecting seasonal peak grass biomass. The reason being that if it can be shown that during high rainfall years grazing has minimal impact on seasonal peak grass biomass, then during such periods heavy stocking rates are unlikely to degrade the vegetation or result in fodder shortages in winter (the reverse will also be true). Using the same logic it was also intended to determine whether swards differing in composition were more resistant to grazing than others.

It was also intended to determine how much of the variance in peak grass production was accounted for by each variable, with the intention of understanding the relative importance of each variable in the system (with regards its effect on seasonal peak grass biomass). The key thrust of this study was to test whether the various stocking rate levels used in these trials have led to a decline in grass production over time, because this is important for determining the sustainability of farming practices in this region, and assessing the maximum average stocking rate that a region can absorb on a sustainable basis. This will be to the benefit of the farmers of that region.

Methods

Grass biomass estimates in each treatment camp, were taken every three weeks over the duration of the trial using the disc pasture metre method (Bransby & Tainton 1977). Fifty points were taken along a diagonal transect in each camp with the pasture metre, and a mean value was calculated from this. In addition species composition surveys were carried out for all treatment camps, using the nearest plant method (Foran *et al.* 1978) with 300 points taken along two diagonal transects per camp (150 per transect). An initial survey was done at the start of the trial followed by surveys every two years. Rainfall data were collected at both Llanwarne and Dordrecht for the duration of the trial.

Multiple regression analysis was used to examine the effects of rainfall, species composition and grazing on grass biomass. In this analysis *a priori* hypotheses were constructed on what factors would affect grass biomass, which were set up as variables in the regression model to test these hypotheses.

The Llanwarne and Dordrecht data sets were analysed separately because the starting conditions of the two trials was different, Dordrecht being in poor condition and Llanwarne in good condition (Turner 1988). This could have significant implications for further vegetation responses to grazing treatments. Also separate analyses would enable closer examination of characteristics unique to each site. For example it was possible to distinguish between up slope and down slope sites in the Dordrecht analysis, but not the Llanwarne analysis.

In addition the slope of the line for the relationship between stocking rate and grass biomass was determined for each year, for each replication set of high, medium and low stocking rate treatments at Llanwarne and Dordrecht. The reason being that with a loss of grass productivity over time at high stocking rates, one would expect that the slope of the line in this relationship will become more negative, because reduced productivity at high stocking rates would "drag" it down. Thus if one can confirm that there is a significant trend in an increasingly negative slope of the line over time for a particular replication, then one can conclude that the grass resource is degrading in the high stocking rate treatment of that replication. Once the slopes of the lines had been determined for each year, they were regressed against time using simple linear regression, to see if there was any significant negative trend in the slope of the line over time.

Theory behind the model

The response variable

Seasonal peak grass biomass was used as the response variable. Data for grass biomass from the trial was collected in the form of disc heights using a disc pasture metre (Bransby & Tainton 1977). Calibration equations to convert the disc values to biomass values were determined by Turner (1988) in the 1986/87 season only. Thus there was no benefit in converting the disc heights to grass biomass values, due to there being a linear relationship between grass biomass and disc height (Turner 1988). It would also create a double variance effect. Therefore an assumption of the analysis is that the relationship between disc height and grass biomass has not changed over the period of the study.

To determine the peak grass biomass for each treatment camp for a particular season the mean disc height value for each three week sampling period from the 1st of July to the 30th of June was graphed and rainfall superimposed on this (fig 5.1).

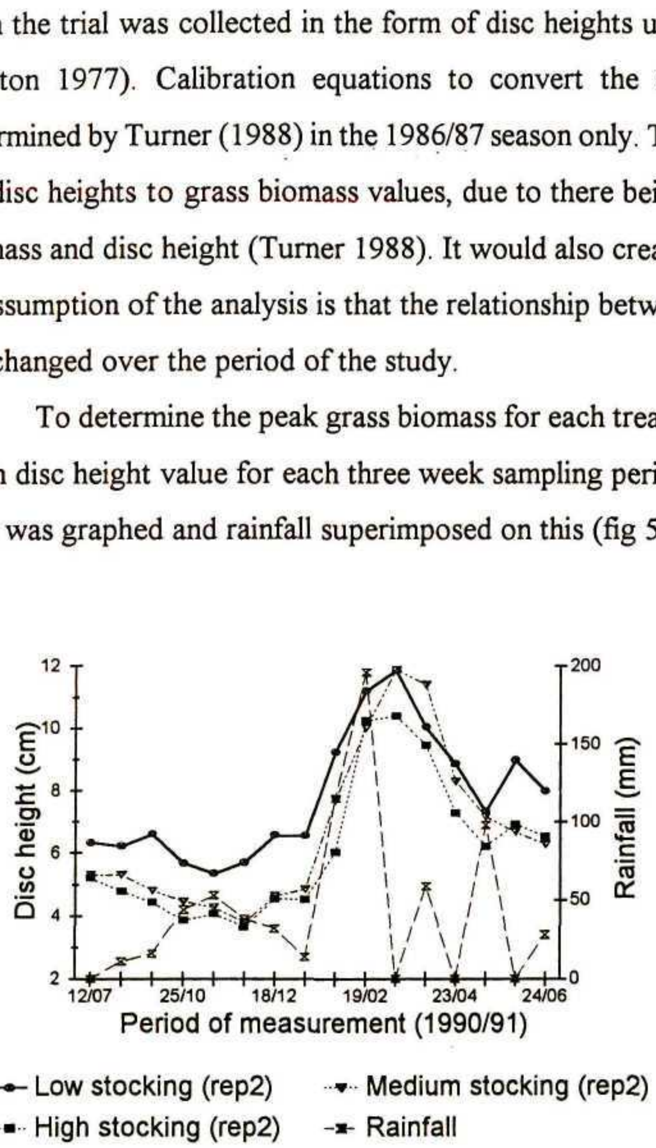


Figure 5.1 Example of changes in disc heights over the season (1990/91) at Llanwarne with rainfall overlaid.

The reason for rainfall being considered in the determination of peak grass biomass was that only the peak growth from the new season was wanted, not residual biomass from the previous season. Thus the peak in the graph of disc height against time after the first significant rain for the season (> 50 mm) was considered as the peak grass biomass for that season.

The response variable was log transformed, because this removed any pattern in the residuals and resulted in a better r^2 for the model.

Predictor variables

Rainfall has an obvious effect on seasonal grass production, especially in an environment where water is limiting (Deshmukh 1984, Milchunas & Lauenroth 1993) and was therefore considered an important variable to include in the model.

The stocking intensity in a particular season may have an effect on the peak grass biomass for that season (Ralphs *et al.* 1990, Fourie *et al.* 1985). Grazing days ha^{-1} was used as a measure of stocking intensity. This is the number of days an area was grazed, multiplied by the stocking rate in AU ha^{-1}. Grazing is only likely to depress peak grass biomass after the initiation of grass growth. Therefore to calculate grazing days ha^{-1} for a particular treatment, the number of days that the cattle were in a particular camp from the first rains until peak grass biomass was attained, was determined and multiplied by the stocking rate for that treatment.

The accumulated amount of grazing (sum of grazing days ha^{-1} for all years, from start of trial up to and including year in question) that a treatment had sustained over time, was used as a variable to elucidate any long term trends in grass biomass. This is because it has a time directional trend and a differential trend between treatments that will elucidate any stocking rate by time effects on grass biomass.

Another factor that is likely to affect grass biomass is the particular species composition of an area. For example a sward dominated by the pioneer *Tragus racemosus*, is likely to have a lot less biomass than a sward dominated by *Panicum maximum*. It was decided that the best way to represent species composition in a regression analysis would be to ordinate the data and use the site scores from the ordination in the analysis. The site scores from the correspondence analysis (CA) in chapter 4 was used for this purpose.

Panicum species (*Panicum maximum*, *Panicum coloratum* and *Panicum deustum*), were lumped because of the possible inconsistencies in identification by different field workers over the years. Owing to the species composition surveys being conducted biennially, site scores for each camp could not be obtained for every year for the regression analysis. Thus for every alternate year that the survey was not conducted, the mean of the previous and following years site score was used. The site scores from the first two axes were used, as they capture most of the variance.

The interactions between the amount of grazing sustained by an area and rainfall may be important because with low rainfall, heavy grazing may have a large effect on peak grass biomass, but may have little or no effect with high rainfall. Therefore an interaction of rainfall and grazing days ha^{-1} was included in the model. The particular species composition of the sward, may interact with grazing to affect grass biomass. For example heavy grazing may not affect peak grass biomass with one particular species composition, but may do so with another composition more susceptible to grazing. Thus interactions between species composition (axis 1 or axis 2), and grazing days ha^{-1} were included in the regression model.

An interaction between site (up-slope or down-slope) and accumulated grazing days ha^{-1} was included in the Dordrecht analysis, because it was suspected that accumulated grazing may affect peak grass production differently, at up-slope and down-slope sites. This is because the up-slope sites are likely to have a greater potential for erosion than the down-slope sites.

Care was taken when selecting variables for the model that they would not be collinear with each other. The effect of certain interaction terms that were correlated with certain variables in the model, was taken into account and checked by omiting these from the model.

Results

Regression analysis

Llanwarne

All predictor variables included in the regression model, except previous years biomass and the interaction terms, were significant (table 5.1). As is to be expected grazing (grazing days/ha) has a negative impact on the peak grass biomass attained that season, as indicated by its negative coefficient. Grazing days/ha accounted for 17.24 % of the variance in seasonal peak grass biomass (table 5.2). Accumulated grazing days/ha had a negative coefficient (at the 10% level), indicating that heavy stocking rates over time had resulted in a decline in peak seasonal grass production.

Axis 1 accounted for 19.6% of the species variance in the ordination, and appears to be a contrast of vegetation that responds to high rainfall and that which responds to drought. For example sites with negative scores are associated with high rainfall years, while sites with positive score are associated with low rainfall years (see figures 4.1 & 4.2, chapter 4). In addition the variable consisting of the product of rainfall preceding the survey and the previous years rainfall, had a significant influence and was correlated with axis 1 (see table 4.2, chapter 4). This would explain why this specific feature of species composition, had a significant effect on grass production. Surprisingly it did not account for much of the variance in grass production, even though it was strongly significant (table 5.2).

Axis2 accounted for 14.3% of the species variance in the ordination. There is a general time trend along this axis where sites associated with the early years of the trial have negative scores, sites associated with the middle years of the trials have neutral scores, and sites associated with the end of the trial have positive scores (see figure 4.1, chapter 4). Also the grazing-by-time variable is strongly associated with this axis (see table 4.2, chapter 4), and could therefore represent a vegetation response to accumulated years of grazing, or some particular aspect of degradation, which would explain its significance in this analysis. In fact both axis 1 and axis 2 could represent some particular aspect of vegetation degradation. Degradation due to drought (axis 1), and degradation due to years of heavy grazing (axis 2).

The previous years biomass was non-significant indicating that, little residual herbage contributes to the following seasons biomass at Llanwarne. Rainfall had a highly significant effect on peak grass biomass, which is to be expected, seeing that water is one of the most limiting elements in a semi-arid system. In this analysis rainfall accounted for more of the variance than any other variable (table 5.2), confirming the dominant (but not exclusive) role of rainfall in a semi-arid system.

The interaction between rainfall and grazing was non-significant, indicating a consistent effect of grazing on grass biomass at a range of rainfall levels. This is surprising because at high rainfall, grazing may not have much effect on peak grass biomass, but at low rainfall is likely to have a significant effect, where heavy grazing should reduce grass biomass to a greater degree than light grazing. Grazing generally reduced peak grass biomass significantly across all levels of rainfall (fig 5.2).

The interaction between grazing and axis 1 was not significant. One would expect vegetation under drought conditions (positive score on axis 1) and heavy grazing, to produce less biomass. Although there is a general trend of this (fig 5.3), a few points did not follow this trend probably giving rise to the non-significant result.

The interaction between grazing and axis 2 was also non-significant. There is an expectation that vegetation that has suffered many years of heavy grazing will produce less biomass than lightly grazed vegetation, especially in years of high grazing intensity. There is a general trend of declining productivity with increasingly positive scores on axis 2 (vegetation response to accumulated grazing), and heavy grazing during the season, but once again a few points are against the trend, thus weakening the interaction (fig 5.4).

Table 5.1 Estimates of the regression coefficients of factors hypothesized to affect peak seasonal grass biomass at Llanwarne (r^2 = 62.6).

Variable	Coefficient	t prob
Constant	1.841	<.001
Graz	-0.01037	0.027
axis1	0.2236	0.001
axis2	0.2794	0.003
Accum	-0.000272	0.071
Prev	0.0099	0.421
Rain	0.000862	0.003
Graz_ax1	-0.00301	0.399
Graz_ax2	-0.00040	0.927
Rain_Gr	0.00001184	0.131

Key to variables: Graz:Grazing days/ha for season, Axis 1 & 2: Site scores of correspondence analysis, Accum: Accumulated grazing days/ha, Prev: Previous seasons biomass, Rain: Rainfall, Graz_ax1: Interaction between grazing and axis1, Graz_ax2: Interaction between grazing and axis2, Rain_Gr: interaction between grazing and rainfall.

Table 5.2 Analysis of variance showing the percentage of the variance in peak biomass accounted for by various factors.

Variable	D.F	S.S.	%Var explained
+ Graz	1	0.67953	17.24
+ axis1	1	0.01754	0.44
+ axis2	1	0.10541	2.67
+ Accum	1	0.41870	10.62
+ Prev	1	0.07660	1.94
+ Rain	1	1.22094	30.98
+ Graz_ax1	1	0.13130	3.33
+ Graz_ax2	1	0.00129	0.03
+ Rain_Gr	1	0.06572	1.67
Residual	44	1.22404	
Total	53	3.94105	

Key to variables: Graz:Grazing days/ha for season, Axis 1 & 2: Site scores of correspondence analysis, Accum: Accumulated grazing days/ha, Prev: Previous seasons biomass, Rain: Rainfall, Graz_ax1: Interaction between grazing and axis1, Graz_ax2: Interaction between grazing and axis2, Rain_Gr: interaction between grazing and rainfall.

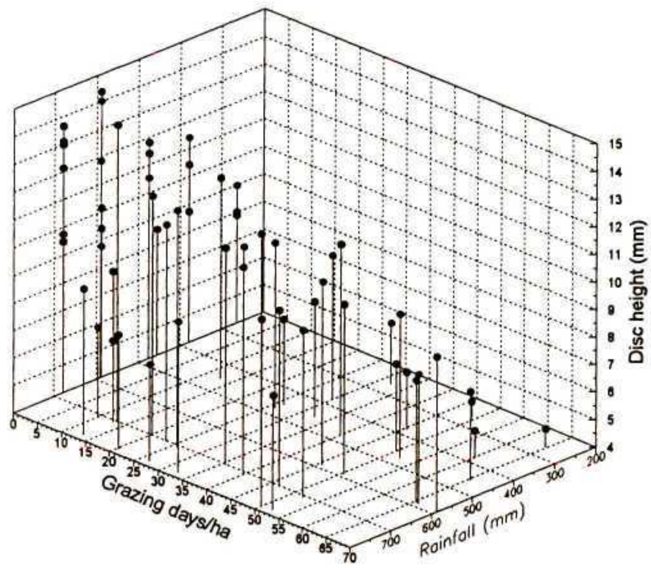


Figure 5.2 The interaction between rainfall and grazing and it's effect on peak seasonal grass biomass at Llanwarne.

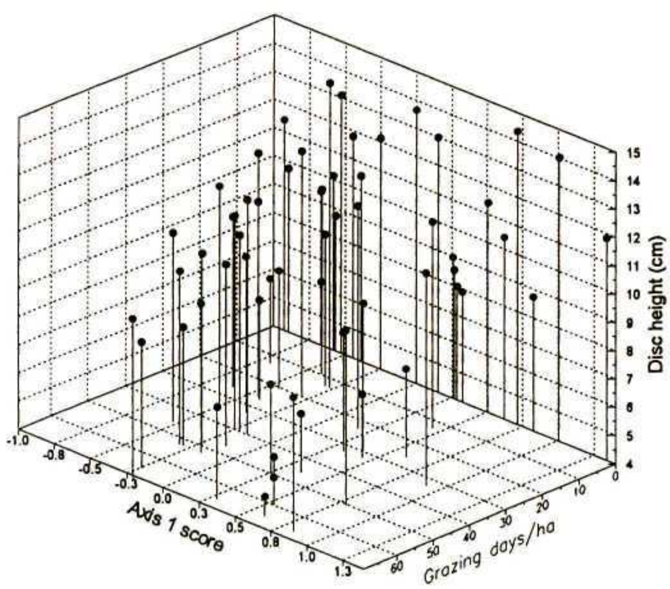


Figure 5.3 The interaction between species composition as represented by axis 1 scores and grazing and its effect on peak seasonal grass biomass at Llanwarne.

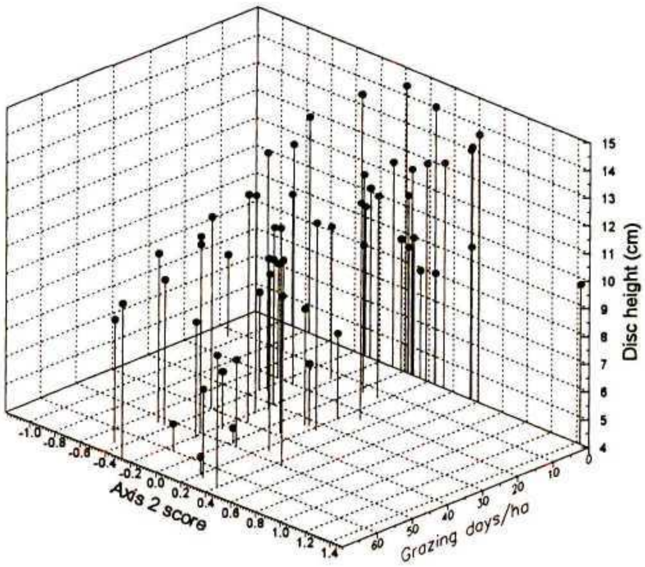


Figure 5.4 The interaction between species composition as represented by axis 2 scores and grazing and its effect on peak seasonal grass production at Llanwarne.

Dordrecht

Unlike Llanwarne there was no compositional effect of axis 1 on peak grass biomass. This result was surprising considering that axis 1 appeared to be a rainfall induced successional gradient, which would be expected to affect grass production at Dordrecht. There was an effect of certain vegetation characteristics represented by axis 2 on grass production. This axis was considered to be a grazing induced successional gradient.

The previous year's biomass had a significant positive effect on peak grass biomass, which indicated that residual herbage was contributing to the following season's biomass. Once again rainfall was highly significant, and had one of the dominant influences on peak grass biomass (table 5.4).

As at Llanwarne, there was no interaction between grazing and rainfall indicating that grazing effects on grass biomass were consistent across all levels of rainfall, encountered at Dordrecht (fig 5.5). It is surprising that heavy grazing did not have a more pronounced effect on peak grass biomass during low rainfall years. A detailed examination of the data revealed that even in the drought of the 1991/1992 season, 190 mm of rain fell between November and March allowing a modest peak biomass to be achieved during that period.

The interaction between grazing and axis 1 was non-significant. This is probably because grazing had little effect on peak grass biomass with high scores on axis 1 (fig 5.6). The particular vegetation after the drought (positive scores) appears to have generally produced low yields irrespective of grazing intensity. Species such as *Tragus racemosus, Aristida congesta* and *Urochloa mosambicensis,* which increased as a result of the drought of 1991/1992, are low yielding species whether grazed or not.

The interaction between grazing and axis 2 was significant indicating that the effect of grazing was inconsistent across the features of species composition represented by axis 2. Heavy grazing had less effect on grass biomass when the vegetation had been subject to few years of accumulated grazing (negative scores), compared with when it had been subject to many years of accumulated grazing (positive scores)(fig 5.7). It was proposed earlier that axis 2 may represent some form of degradational gradient, as a result of grazing. If this is so, less biomass was produced by vegetation in a degraded form, and particularly so at high stocking rates.

There was no statistically significant effect of grazing days ha^{-1} on peak grass production, which was at odds with the result from the Llanwarne analysis (table 5.3). Accumulated grazing days ha^{-1} as in the Llanwarne analysis had a significant negative coefficient, indicating that heavy stocking rates had resulted in a decline in peak grass biomass over time. There was a strong interaction, however, between accumulated grazing days ha^{-1} and landscape position, which accounted for a large percentage of the variance in peak grass biomass (table 5.4) (i.e. grass production declined over time as accumulated grazing days ha^{-1} increased but not consistently across up-slope and down-slope sites). This result encouraged further investigation as it was evident that site-specific (up-slope or down-slope) degradation at heavy stocking rates had occurred, but it was unknown whether it was associated with up-slope or down-slope sites. The hypothesis that heavy grazing was more likely to degrade up-slope sites rather than down-slope sites, was then tested by analysing the up slope and down slope site data separately. The analysis confirmed that there was a declining trend in grass biomass with heavy stocking over time (significant negative coefficient of accumulated grazing), in the up-slope sites, but not with the down-slope sites (table 5.5). When fitting the full model with all the interaction terms included, this effect was not evident, yet it was known that a site-specific effect was present due to the significance of the site-by-accumulated grazing variable (table 5.3). Further investigation revealed that accumulated grazing and axis 2 are colinear (see fig 4.2, chapter 4), thereby masking the accumulated grazing effect. The removal of the grazing-by-axis 2 interaction from the model revealed the significance of the accumulated grazing variable for the down slope sites (table 5.5).

This was well illustrated by examining the trends in the slope of the line of stocking rate against grass biomass for each replication of the high, medium and low treatments at Llanwarne and Dordrecht (fig 5.8). It is evident that the down-slope sites (replication 2) at Dordrecht, although variable, have no significant trend of increasing negative slope over time, while the up-slope sites do (table 5.6). Replication 1 at Llanwarne had no significant trend of increasing negative slopes over time, while replication 2 did (table 5.6). This shows that at both Llanwarne and Dordrecht a decline in peak seasonal grass production at high stocking rates was only present on steeper slopes (the H 2 camp at Llanwarne was on a steeper slope than the H 1 camp).

Table 5.3 Estimates of the regression coefficients of various factors hypothesized to affect seasonal peak grass biomass at Dordrecht (r^2 71.0).

Variable	Coefficient	tprob
Constant	1.003	<.001
Graz	-0.00297	0.518
axis1	0.1178	0.154
axis2	0.2679	0.003
Accum	-0.000729	0.022
Prev	0.0589	<.001
Rain	0.001177	<.001
Site_Acc	0.000455	0.005
Graz_ax1	-0.00362	0.221
Graz_ax2	-0.00699	0.040
Rain_Gr	-0.00000220	0.760

Key to variables: Graz:Grazing days/ha for season, Axis 1 & 2: Site scores of correspondence analysis, Accum: Accumulated grazing days/ha, Prev: Prevoius seasons biomass, Rain: Rainfall, Graz_ax1: Interaction between grazing and axis1, Graz_ax2: Interaction between grazing and axis2, Rain_Gr: interaction between grazing and rainfall.

Table 5.4 Analysis of variance showing the percentage of the variance in peak grass biomass accounted for by various factors.

Variable	D.F.	S.S.	% var explained
+ Graz	1	0.50302	8.44
+ axis1	1	0.10321	1.73
+ axis2	1	0.32995	5.53
+ Accum	1	0.16812	2.82
+ Prev	1	0.51346	8.61
+ Rain	1	2.21457	37.14
+ Site_Acc	1	0.57681	9.67
+ Graz_ax1	1	0.00032	0.01
+ Graz_ax2	1	0.14624	2.45
+ Rain_Gr	1	0.00309	0.05
Residual	43	1.40408	
Total	53	5.96288	

Table 5.5 Estimates of regression coefficients of various factors at up slope and down slope sites at Dordrecht.

	Coefficient	tprob
Up slope sites (r^2 82.6)		
Constant	0.077	0.792
Graz	0.00641	0.442
axis1	0.283	0.179
axis2	-0.0248	0.703
Accum	-0.000413	0.057
Prev	0.1368	<.001
Rain	0.001447	<.001
Rain_Gr	-0.0000042	0.763
Graz_ax1	-0.00375	0.390
Down slope sites (r^2 57.2)		
Constant	1.453	0.002
Graz	0.00283	0.756
axis1	0.0932	0.342
axis2	0.292	0.056
Accum	0.000153	0.422
Prev	0.0136	0.524
Rain	0.001133	0.033
Graz_ax1	-0.00720	0.191
Graz_ax2	-0.00485	0.349
Rain_Gr	-0.0000110	0.412

Key to variables: Graz:Grazing days/ha for season, Axis 1 & 2: Site scores of correspondence analysis, Accum: Accumulated grazing days/ha, Prev: Prevoius seasons biomass, Moist: Rainfall multiplied by soil depth, Site_Acc: Interaction between Accum and site (up slope or down slope),Mgr_ax1: Interaction between Moist, axis1 and Graz, Mgr_ax2: Interaction between Moist, axis2 and Graz.

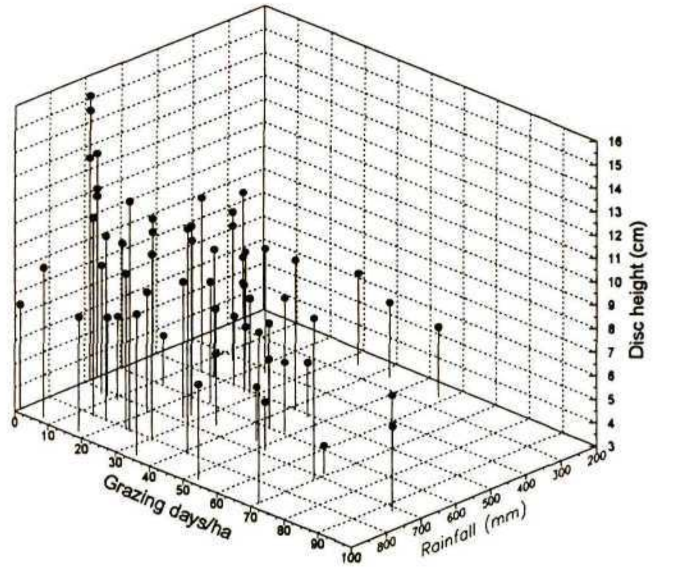


Figure 5.5 The interaction between rainfall and grazing and its effect on peak seasonal grass biomass at Dordrecht.

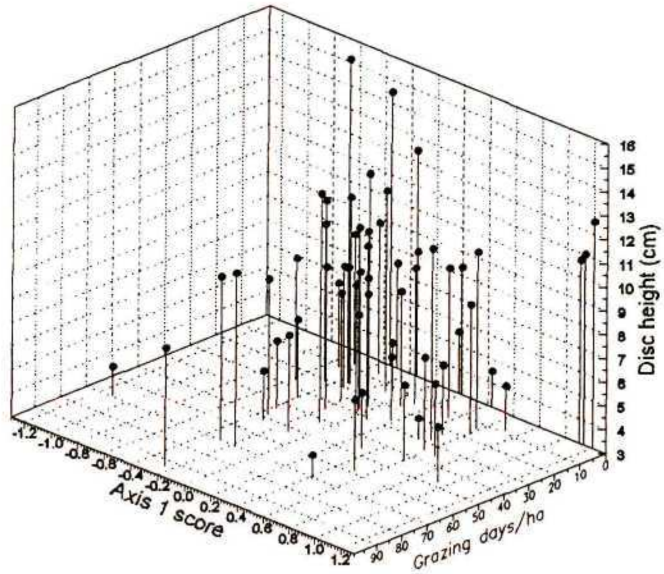


Figure 5.6 The interaction between species composition as represented by axis 1 scores and grazing and its effect on peak seasonal grass biomass at Dordrecht.

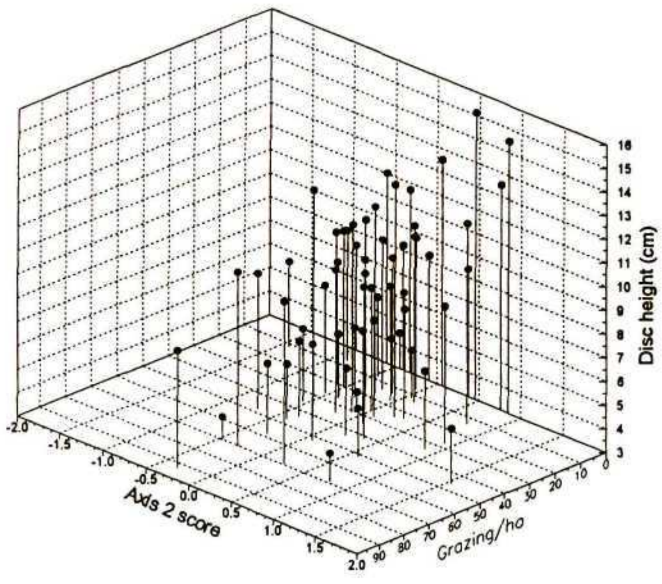


Figure 5.7 The interaction between species composition as represented by axis 2 scores and grazing and its effect on peak seasonal grass biomass at Dordrecht.

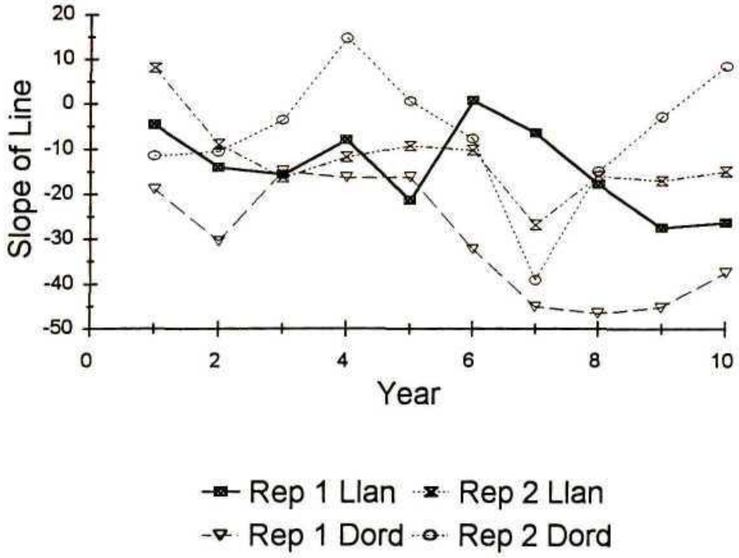


Figure 5.8 Trends over time of the slope of the line, in the relationship between stocking rate and grass biomass at Llanwarne and Dordrecht.

Table 5.6 Estimates of regression coefficients of the trends over 10 years, in the slope of the line, of the relationship between stocking rate and grass biomass.

Replication 1 Llanwarne (r^2 18.8)		
	Coefficient	t prob
Constant	-4.94	0.421
Year	-1.648	0.117
Replication 2 Llanwarne (r^2 32.8)		
	Coefficient	t prob
Constant	-1.95	0.705
Year	-1.862	0.049
Replication 1 Dordrecht (r^2 50.6)		
	Coefficient	t prob
Constant	-12.53	0.080
Year	-3.23	0.013
Replication 2 Dordrecht (r^2 15.5)		
	Coefficient	t prob
Constant	-6.8	0.538
Year	0.05	0.977

Discussion

There is convincing evidence that heavy stocking rates at both Llanwarne (0.313 au ha^{-1}) and Dordrecht (0.278 au ha^{-1}) have resulted in a decline in peak seasonal grass biomass over time, although the effect is site specific as illustrated by only the up slope sites at Dordrecht showing a decline (table 5.5 & 5.6) and only replication 2 at Llanwarne showing a decline (table 5.6). Milchunas & Lauenroth (1993) in a multiple regression analysis of a worldwide 236 site data set, also found evidence of declining productivity, that could be attributed to increasing levels of grazing and increasing years of treatment. The reason for the site specific effects at Dordrecht is possibly that the up slope sites are in a more erodible position, where loss of soil and seed banks is more likely than the down slope sites which may receive soil and seed, thus benefiting from the degradation of the up slope sites. The distinction between the two replications at Llanwarne is not so much on landscape position, but rather the gradient of the slope. The H 2 treatment at Llanwarne is on a steeper slope than the H 1 treatment which is in a more stable landscape (almost flat). Thus the H 2 treatment at Llanwarne has greater potential for erosion than the H 1 treatment, and will therefore be more vulnerable to degradation under high stocking rates.

An important result is that the H 2 camp at Llanwarne and the H 1 camp at Dordrecht, were found to be the only two camps to exhibit large compositional change between 1986 and 1996 (chapter 4). This result provides a strong link between compositional change and its effect on grass production, and is supported by the significance of axis 1 and 2 in the Llanwarne analysis and axis 2 in the Dordrecht analysis, and the general trend of declining productivity with increasingly positive scores on axis 1 and 2 (fig's 5.3, 5.4, 5.6 & 5.7). Both axis 1 and axis 2 were interpreted to represent different forms of degradation gradients, axis 1 being due to drought, and axis 2 due to long-term heavy grazing. A link between compositional change and declining productivity was also observed in the study of Milchunas & Lauenroth (1993), where they found a significant declining trend in above ground net primary production with increasing species dissimilarity (differences in composition between grazed and ungrazed sites).

A decline in seasonal grass production is a source of concern, because in all likelihood it means that the carrying capacity of the region has been decreased. Fritz & Duncan (1994) have shown that the large ungulate biomass supported by a region, is strongly positively correlated with rainfall.

This is because seasonal peak grass biomass is strongly positively correlated with rainfall (Deshmukh 1984, Milchunas & Lauenroth 1993), meaning that a long-term decline in seasonal peak grass biomass should mean a decline in carrying capacity.

The evidence that degradation of the grass resource is more likely to occur in more erodible landscapes, suggests that the range manager should take landscape position into account and ensure that more erodible landscapes are not heavily utilised. Separation of rangelands into management areas should be based primarily on the erodability and stability of landscapes rather than vegetation and soils, which may not be sensitive to such changes in the landscape, as is generally the case at Llanwarne and Dordrecht.

A consideration of the spatial scale that erosion processes take place is important. Scoones (1992) proposed that certain top land areas may be subject to losses of productivity, but that erosion and deposition processes may result in increases in production elsewhere. Scoones (1992) referred to these areas of increased productivity as 'key resource' areas, that were able to maintain the secondary productivity of the system. He proposed that if these 'key resource' areas were degraded then the overall productivity of the system would be affected. Tongway & Ludwig (1997b) referred to this process as 'Robin Hood in reverse or robbing the poor to give to the rich'. The resource rich 'Key resource' areas continually receive soil, water and nutrients from areas already poor in these resources. A question arises as to whether there is sufficient compensation for the loss of productivity in the eroded region, by increased productivity in the deposition region, because a large proportion of the soil from the eroded region is likely to wash into stream beds and be lost from the system altogether. Also the increase in productivity in the area of deposition may not be large enough to compensate for the decline in productivity for the area that lost soil. At Dordrecht the H 2 camp which was situated directly below the H1 camp in the landscape, received soil at the expense of the H 1 camp. It appears that evidence exists that the H 2 camp has benefited from the degradation of the H 1 camp. The severe drought of the 1991/1992 season occurred in the sixth year of the trial. It was at this time that the H 1 camp at Dordrecht really showed signs of degradation (fig 5.8). Two years after the drought the H 2 camp showed a marked trend of increasing productivity (indicated by the increasingly positive slope of the line)(fig 5.8). Any major loss of soil and water from the H 1 camp would have taken place during rainfall events after the drought, when grass cover was poor. Some of this soil and water would be expected to be deposited in the H 2 camp below the area of erosion, and thereby stimulating an increase in productivity of this camp. It is not possible, however, to determine whether this increase in productivity in the H 2 camp compensates for the decreased productivity of the H 1 camp, thus it is difficult to confirm or refute the 'key resource' area claims of Scoones (1992) on these grounds.

Livingstone (1991) has contended that rangeland is most vulnerable to degradation with heavy grazing pressure during drought periods, rather than with heavy grazing pressure during normal rainfall years when grass cover is good. The evidence that the H 1 camp at Dordrecht only showed significant trends in declining productivity after the severe drought of the 1991/1992 season (year 6, fig 5.8) is good support for this hypothesis.

The decline in grass production in the H 1 camp at Dordrecht and the H 2 camp at Llanwarne could be due to observed compositional changes (chapter 4), or some soil related process, or a combination of the two. Macdonald (1978) found that soil moisture and infiltration of water into the soil in degraded patches of grassland with poor grass production, was less than in patches of better grass production. This phenomenon together with loss of soil and nutrients and compositional change are likely causes of degradation in these two camps. Fuls & Bosch (1991) observed in semi-arid patch-grazed grassland, that overgrazed degraded patches had retrogressed beyond a threshold of drought resilience, and could not recover through resting. Similar degraded patches are common in these degraded camps, especially at Dordrecht and on the basis of the observations of (Fuls & Bosch 1991) it is predicted that long-term rest will not stimulate much improvement in these patches. Van de Koppel *et al.* (1997) note that attempts in the Sahel to restore degraded areas by reducing herbivore numbers had little effect, and that the areas have remained in a barren state for at least 20 years. They propose that the degraded areas represent an alternate stable state. If this is the case degraded areas are unlikely to revert back to their former state because they are now in a new domain of attraction. Rietkerk & Van de Koppel (1997) have shown by means of a graphical model, that the interactions between water infiltration or nutrient retention and plant density, potentially give rise to the existence of alternate stable vegetation states in semi-arid systems. The general pattern emerging from the literature is that a reduction in the ability of a system to capture water and nutrients, as a result of increased runoff and reduced infiltration, which is caused mainly by reduced plant density, leads to an alternate stable state from which the system cannot return. This may be the result of a positive feedback between reduced plant density and reduced resource availability (Rietkerk & Van de Koppel 1997). Tongway & Ludwig (1997a) also emphasize the importance of plant density in capturing and maintaining resources in the system, where a reduction in plant density leads to a 'leaky system', which in turn leads to the development of the positive feedback effect described by Rietkerk & Van de Koppel (1997). With this in mind, it is likely that to restore the productivity of the degraded camps at Llanwarne and Dordrecht, will require some form of intervention to reduce runoff and improve resource capture. The degraded patches in these camps have largely lost the ability to capture and conserve resources. The concept in economics that one needs money to make money, also holds in ecology where one needs resources to capture resources. The more grass there is in a patch, the greater will be the ability of that patch to capture resources, generating a positive feedback between grass cover and resource capture. By merely resting the camps is unlikely to result in much improvement in species composition, cover and productivity.

Rainfall was confirmed from both the Llanwarne and Dordrecht analyses to be significant, and dominant over grazing in its influence on the dynamics of peak grass biomass. This is to be expected for arid and semi-arid systems where water is limiting. In a more humid environment there may be a greater influence of grazing relative to rainfall on peak grass biomass. The significant effect of rainfall on seasonal peak grass biomass is supported by the results of Deshmukh (1984) and Milchunas & Lauenroth (1993), who found a strong linear relationship between rainfall and seasonal grass production.

The hypothesis that heavy grazing in high rainfall seasons may have no effect on seasonal peak grass production was not supported in the results (fig's 5.2 & 5.5). This means that even in good seasons, farmers cannot stock excessively if they want sufficient forage left over during the winter.

CHAPTER 6

CATTLE PERFORMANCE AT LLANWARNE AND DORDRECHT

Introduction

A high proportion of African rangelands are in arid or semi-arid regions that have a low agricultural potential. Generally the rainfall is too variable, low and unpredictable to permit regular, successful dryland cultivation of crops, although subsistence type crop production is often attempted with variable results (Walker 1979). This being the case, livestock production or wildlife is often the only viable form of land use, and consequently large areas of Africa's rangelands are utilised for livestock production in either communal systems or commercial farms. Considering that land use options are limited for semi-arid rangelands sustained livestock production from these regions is of primary concern.

In the previous two chapters there was good evidence to show that heavy stocking rates had over time resulted in compositional change, and a run down in grass production at Llanwarne and Dordrecht, although the effects were limited to sites on steeper slopes. The natural progression to these results is to see if this decline in grass productivity is reflected in the performance of the cattle themselves. A decline in cattle performance is probably the most important issue in the diagnosis of range degradation, though it has been notoriously difficult to link vegetation changes with declining cattle performance. There is good evidence for changes in the state of vegetation under various grazing regimes, but nothing to show long term changes in productivity (Sandford 1983). If a change in the state of the vegetation does not translate into a decline in livestock production, then we cannot regard the system as degraded from a purely functional definition, where we are concerned with the economic or dietary requirements of individuals (Abel 1993, Biot 1993). Whether one is a pastoralist leading a subsistence lifestyle or a commercial rancher concerned with profit making, at the end of the day one is concerned with some form of animal production, whether it be milk as a source of protein or the maturation of livestock to sell. Thus a decrease in the yield of livestock products will negatively impact those dependant on rangelands in one way or another.

A detection of degradation as indicated by reduced animal productivity could be observed by means of a loss of linearity in the animal gain - stocking rate relationship (Wilson & Macleod

1991), or a significant negative coefficient in the regression of time by stocking rate (accumulated grazing pressure) on animal production (i.e. the detection of a significant declining trend over time in the performance of livestock at heavy stocking rates).

An objective of livestock farmers is to optimize the productivity of their system, in terms of livestock products. The grazing system that is used appears to be less important than stocking rate in determining livestock performance (O'Reagain & Turner 1992). This means that farmers should attempt to find the optimum stocking rate for livestock production in a particular system, at certain levels of rainfall and grass biomass. A grazing trial presents an opportunity to do this because it has a range of stocking rates over a range of rainfall seasons, thereby providing insights into the interactions between stocking rate and rainfall and their effect on livestock performance.

Thus the aims of this study were to determine how factors such as rainfall, grass biomass and stocking rate affected cattle performance. It was considered important to establish whether stocking rate interacted with rainfall in determining cattle performance, because an understanding of such interactions would enable range managers to optimise cattle production under various rainfall regimes. A primary objective was to see if cattle performance had declined over time in the heavy stocking rate treatments, especially seeing that declining trends in grass biomass, and compositional changes were detected in some of these treatments, which suggests that cattle performance may also have been affected. A detection of a declining trend in cattle performance would be a source of concern, in light of the fact that many of Africa's rangelands are considered to be over stocked.

Methods

The cattle used in the trials were weaners of the Brahman-cross type and weighed about 250 kg on introduction, attaining weights of over 500 kg during the year. The experimental cattle were replaced with new weaners each year, in October. At the Dordrecht trial there were six animals in the light and medium stocking rate treatments and seven in the heavy stocking rate treatment. Llanwarne had eight animals in the light and medium stocking rate treatments and nine in the heavy stocking rate treatment. Their weight was recorded every three weeks during their period of stay in the trial. The cattle would be penned the night before weighing. The cattle were rotated between replication 1 and replication 2 of a particular treatment of the trial, and their period of stay in a particular replication was not fixed, but was determined by the availability of forage. Thus the cattle data was not replicated within a particular year, but did not need to be seeing that a regression approach was used where years were the replications. The stocking pressure was obviously double that of the stocking rate when the cattle were present in a particular replication.

Statistical analysis

Only the first nine years of data were used for the analysis as there was no tenth year for Llanwarne, and the trial was closed midway through the tenth year at Dordrecht. Multiple regression analysis was used for the statistical analysis, using the general statistical programming package (Genstat 5). Two particular analyses were done, these being on seasonal gain animal^{-1} (the mean weight gain for the season of all the cattle in a treatment), and on seasonal gain ha^{-1} (the total weight gain of all the cattle in a treatment, divided by the area (ha) of the treatment).

There is a well known strong relationship between stocking rate and animal production (Harlan 1958, Riewe 1961, Peterson *et al.* 1965, Cowlishaw 1969, Jones & Sandland 1974), thus stocking rate was considered an important variable for inclusion in the gain animal^{-1} and gain ha^{-1} model. One would expect that with increasing stocking rates competition for forage will increase thus reducing forage intake and increasing energy expenditure by animals, owing to increased effort to obtain forage. Thus gain animal^{-1} is expected to decline with increasing stocking rate and has been shown to do so (Jones & Sandland 1974).The experimental results of Jones & Sandland (1974) would suggest that a quadratic function for stocking rate should be included in the gain ha^{-1} model, because gain ha^{-1} tends to increase with increasing stocking rate to a point and then decline. This is because at very high stocking rates individual animal performance is so poor that gain per unit area starts to decline. An examination of the data from this trial, however, shows that at the range of stocking rates used, the relationship is linear, thus not warranting the inclusion of a quadratic function for stocking rate in the gain ha^{-1} model.

The availability of grass should have an effect on the weight gain of cattle, as the more grass that is produced in a season the more forage there is available for each individual animal over the season. Also the greater the availability of grass the less energy animals have to expend to get to it, which should also contribute towards improved animal production. Therefore peak grass biomass is expected to affect both gain animal^{-1} and gain ha^{-1} and was considered a variable worthy of inclusion in the model.

Rainfall would also be expected to affect cattle growth through its effect on grass production. If rainfall in a season is low then grass production will be low and therefore cattle production should be low. Thus rainfall is an important variable to include in the model. Since grass production is likely to be some function of rainfall, however, one cannot fit both peak grass biomass and rainfall in the same model. Therefore two models were used, one with rainfall and one with peak grass biomass. This was done with the intention of seeing which would be the better predictor of cattle performance.

To address the question of whether heavy stocking rates over time are resulting in declining cattle performance, the accumulated grazing days per hectare that each treatment received over the duration of the trial was included as a variable in the model. The logic behind this is that the greater the amount of grazing days that a treatment has received, the greater the likelihood that degradation will occur. Accumulated grazing days per hectare for a particular season is calculated as the sum of the number of grazing days ha^{-1} for each season, from the start of the trial up to and including the relevant season.

Finally there is the possibility that stocking rate will interact with rainfall or grass biomass in determining animal production. For example, in a high rainfall year, low stocking rates may result in lower gain per animal than high stocking rates, because heavy grazing prevents the grass 'getting away' and becoming rank and of low forage quality. To test this, an interaction between rainfall and stocking rate was included in the rainfall model.

An interaction between stocking rate and grass biomass was included in the grass biomass model, because high stocking rates at high grass biomass levels may result in similar animal performance compared to low stocking rates, owing to a lower probability of forage being limiting, but at low grass biomass, high stocking rates are expected to result in worse animal performance, owing to a shortage of forage.

Data transformation

The response variable was log transformed in the four different regression analyses, as this was found to give a better fit, and in the case of the gain ha^{-1} analysis at Llanwarne the residual scatter indicated that the residuals were correlated. A log transformation of the response variable was found to remove this correlation.

Results

Gain animal^{-1} analysis

When fitting the model with peak grass biomass instead of rainfall it was decided to include a quadratic term for peak grass biomass, because the graph of peak grass biomass against gain/animal appeared curvilinear (fig 6.1 A). Multiple regression analysis showed that for both the Llanwarne and Dordrecht data the quadratic for peak biomass was significant (table 6.1 & 6.2). Thus an increase in peak grass biomass may translate into an increase in gain animal^{-1}, to a point, after which the rate of gain declines with further increases in peak grass biomass.

When fitting the model with rainfall instead of peak grass biomass, the quadratic term for rainfall was included in the model owing to a strong curvilinear effect in the relationship between rainfall and gain animal^{-1} (fig 6.1 B & C). The quadratic function was highly significant for both the Llanwarne and Dordrecht data (table 6.1 & 6.2), and furthermore rainfall proved to be a better predictor of gain animal^{-1} than peak grass biomass as indicated by the greater variance (r^2) accounted for by the rainfall model (table 6.1& 6.2). Thus it would be better to use rainfall rather than peak grass biomass in a predictive model. The relationship between rainfall and gain animal^{-1} at Llanwarne can be described by the equation: seasonal gain = -137.0 + 1.098(rain) - 0.000885(rain)^2 and at Dordrecht by the equation: seasonal gain = -27.4 + 0.686(rain) - 0.000505(rain)^2. Differentiation of these equations and solving for rain, shows that a farmer can expect optimal gain animal^{-1} in a rainfall year of around 620 mm at Llanwarne, and 679mm at Dordrecht. The significance of the quadratic function in the rainfall model means that with an increase in annual rainfall above these values, gain animal^{-1} will be less than optimum.

Stocking rate had a significant effect on gain animal^{-1} at Dordrecht only, and then only in the model using rainfall (table 6.2). One would expect a significant effect in the other models also, so this result is surprising. Accumulated grazing was non significant in both the grass biomass and the rainfall model at Llanwarne (table 6.1), but there is a suggestion of a positive effect on gain animal^{-1} at Dordrecht (table 6.2), though only in the rainfall model. In fig 6.1 E, however, there appears to be no trend in the relationship between accumulated grazing and gain animal^{-1}, at either Llanwarne or Dordrecht. Thus there has almost certainly been no loss of gain animal^{-1} with heavy stocking rates over time, and according to the regression analysis, perhaps a slight increase in gain animal^{-1} at Dordrecht.

Although evidence presented in chapter 5 has shown that there is a loss of primary productivity with heavy stocking, this has not been translated into a decline in cattle production.

In terms of the variance accounted for by various factors in the model, an analysis of variance revealed that at both Llanwarne and Dordrecht, rainfall (represented by the linear and quadratic function in the model) rather than stocking rate , had the major effect on gain/animal (table 6.3). The analysis of variance showed that with the Llanwarne data, rainfall (sum of linear and quadratic functions) accounted for 77% of the variance, and stocking rate only 4% of the variance (table 6.3). Rainfall also dominated gain animal^{-1} dynamics at Dordrecht where it accounted for 60% of the variance, while stocking rate accounted for only 12% of the variance (table 6.3). These results indicate that the livestock farmer in this region has very little control over the performance of his cattle in a particular season, when using a grazing system with fixed stocking rates. Over the long-term, however, grazing mismanagement may result in reduced cattle gains, and therefore a farmer has long-term rather than short term control over cattle performance.

There was an interaction between stocking rate and rainfall at Dordrecht but not at Llanwarne (table's 6.1 & 6.2), indicating that stocking rate had a consistent effect on gain animal^{-1} at Llanwarne but not at Dordrecht. At 800mm rainfall high stocking rates did out perform low stocking rates, but not at 900mm rainfall (fig 6.1 C). The interaction although present is weak and not entirely convincing.

There was some indication of an interaction between stocking rate and grass biomass at Llanwarne (table 6.1) but not at Dordrecht (table 6.2). This is surprising, because fodder shortages are expected to be greater at high stocking rates in low rainfall years than low stocking rates, and therefore this interaction is expected to be ubiquitous.

Table 6.1 Estimates of the regression coefficients for factors hypothesized to affect gain per animal at Llanwarne.

Model (r^2 = 64.8)	Coefficient	t-prob
Constant	-0.27	0.853
biom	0.885	0.002
sr	5.64	0.080
accum	0.000084	0.564
biomsq	-0.03373	0.003
Biom_sr	-0.549	0.099
Model (r^2 =83.8)	**Coefficient**	**t prob**
Constant	3.182	<.001
rain	0.007615	<.001
sr	-0.99	0.389
accum	0.0000455	0.630
Rainsq	-0.62E-05	<.001
Rain_sr	0.00027	0.889

Key to variables: biom: peak grass biomass, biomsq: quadratic function for peak grass biomass
sr: stocking rate, accum: accumulated grazing days/ha,
Biom_sr: interaction between peak grass biomass and stocking rate,
rain: annual rainfall, Rainsq: quadratic function for annual rainfall,
Rain_sr: interaction between annual rainfall and stocking rate.

Table 6.2 Estimates of the regression coefficients for factors hypothesized to affect gain per animal of cattle at Dordrecht.

Model (r^2 =33.8)	Coefficient	t prob
Constant	1.28	0.535
biom	0.704	0.053
sr	5.72	0.292
accum	0.000077	0.702
biomsq	-0.0277	0.058
Biom_sr	-0.666	0.284
Model (r^2 = 70.7)	**Coefficient**	**t prob**
Constant	4.807	<.001
rain	0.00368	0.002
sr	-5.92	0.005
accum	0.000270	0.056
Rainsq	-0.37E-05	<.001
Rain_sr	0.00619	0.053

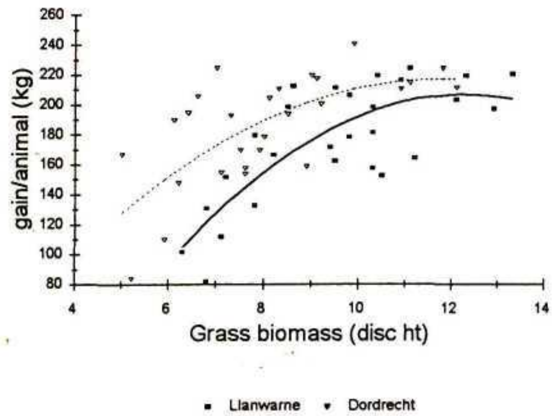
Key to variables: biom: peak grass biomass, biomsq: quadratic function for peak grass biomass
sr: stocking rate, accum: accumulated grazing days/ha,
Biom_sr: interaction between peak grass biomass and stocking rate,
rain: annual rainfall, Rainsq: quadratic function for annual rainfall,
Rain_sr: interaction between annual rainfall and stocking rate.

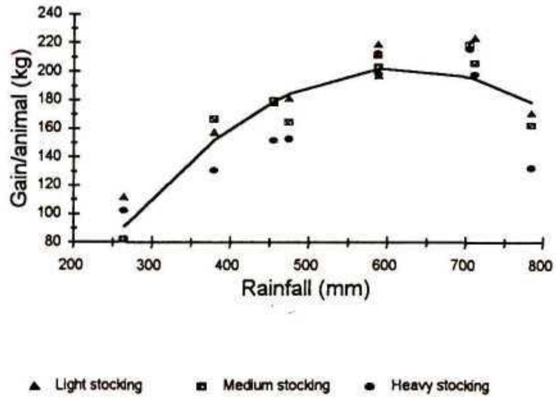
Table 6.3 Analysis of variance showing the percentage of the variance accounted for by the various factors in the regression model.

Llanwarne			
Change	d.f.	s.s.	% Variance
+ rain	1	0.76943	45.36
+ sr	1	0.06575	3.88
+ accum	1	0.00000	0.00
+ Rainsq	1	0.63871	37.66
+ Rain_sr	1	0.00021	0.01
Residual	21	0.22187	
Total	26	1.69598	

Dordrecht			
Change	d.f.	s.s.	% Variance
+ rain	1	0.47567	28.85
+ sr	1	0.18950	11.49
+ accum	1	0.03252	1.97
+ Rainsq	1	0.48261	29.27
+ Rain_sr	1	0.07805	4.74
Residual	21	0.38993	
Total	26	1.64829	

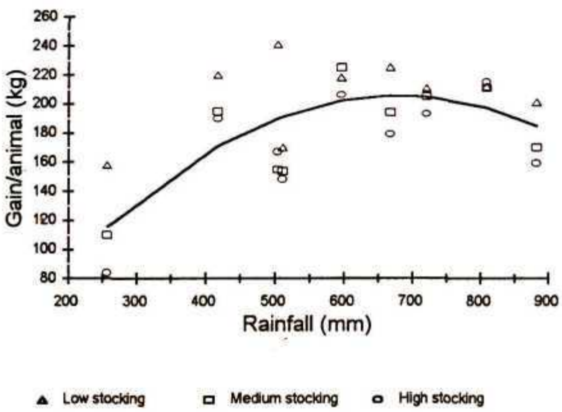
Key to variables:sr: stocking rate, accum: accumulated grazing days/ha, rain: annual rainfall, Rainsq: quadratic function for annual rainfall, Rain_sr: interaction between annual rainfall and stocking rate.

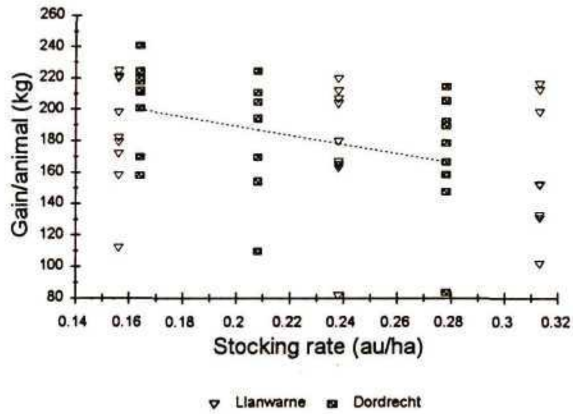




A

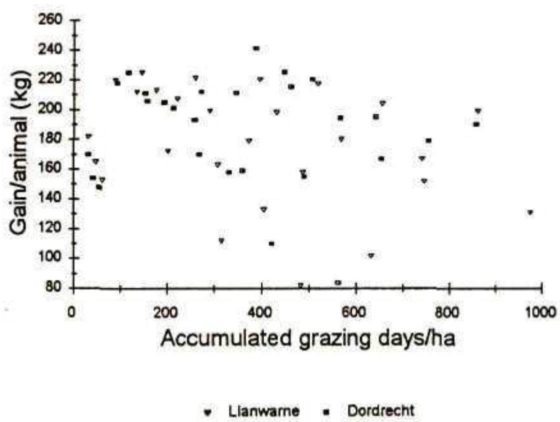
B





C

D



E

Figure 6.1 Relationship between peak grass biomass (A), rainfall at Llanwarne (B) & Dordrecht (C), stocking rate (D), accumulated grazing (E) and gain animal^{-1}. When two lines fitted, broken line = Dordrecht

Gain ha^{-1} analysis

It was suspected that there may be some sort of curvilinear relationship between peak grass biomass and gain ha^{-1} of cattle (fig 6.2 A), thus a quadratic function for peak grass biomass was included in the regression model. The quadratic function for peak grass biomass was significant with the Llanwarne data but not with the Dordrecht data, though the *t* probability suggests that a quadratic effect may be present (table 6.4 & 6.5).

For the model using rainfall instead of peak grass biomass, a quadratic function for rainfall was included due to a suspected strong curvilinear relationship between rainfall and gain ha^{-1} of cattle (fig 6.2 B & C). Both the linear and quadratic functions of rainfall at Llanwarne and Dordrecht were significant (table 6.4 & 6.5). The relationship between gain/ha and rainfall at Llanwarne can be described by the equation: gain $ha^{-1} = -32.6 + 0.2579(\text{rain}) - 0.0002088(\text{rain})^2$ and at Dordrecht by the equation: gain $ha^{-1} = -8.3 + 0.1537(\text{rain}) - 0.0001127(\text{rain})^2$. Differentiation of these equations and solving for rain shows that one can expect optimal gain/ha in a rainfall season of 618 mm at Llanwarne and 682 mm at Dordrecht. These values are in agreement with the optimal values calculated for gain $animal^{-1}$. Thus for cattle farmers in the Zululand lowveld, one could say that a rainfall season of between 600 and 700 mm is ideal for cattle production.

Stocking rate had a significant positive effect on gain ha^{-1} at Llanwarne but not at Dordrecht (table 6.4 & 6.5). This is surprising seeing that, with an increase in stocking rate one would expect an increase in gain ha^{-1}, because there are more and more animals contributing to gain per unit area. However after a certain stocking rate competition for forage is so high and gain $animal^{-1}$ so low that gain ha^{-1} no longer increases but rather declines (Jones & Sandland 1974). This effect was not observed in the range of stocking rates applied at Llanwarne and Dordrect (fig 6.2 D). The stocking rates are obviously not high enough for these negative feedback effects to take effect. There was no significant effect of accumulated grazing on gain ha^{-1} at Llanwarne (table 6.4), but as with gain ha^{-1} at Dordrecht, there was an indication that gain ha^{-1} had increased slightly over time, though this result is only supported by the rainfall model (table 6.5). There is perhaps an indication of this trend in fig 6.2 E. These results indicate that there has almost certainly been no decline in cattle performance with heavy stocking rates over time, at either Llanwarne or Dordrecht.

The interaction between rainfall and stocking rate was significant at Dordrecht, as it was with gain $animal^{-1}$ at Dordrecht. It is likely that some feature of the vegetation at Llanwarne does not allow this interaction to develop. At very low rainfall there was lower gain ha^{-1} at high stocking rates than at medium stocking rates (fig 6.2 C), while at Llanwarne this inconsistency was not present (fig 6.2 B), and this may explain why this interaction was significant at Dordrecht only.

The accumulated analysis of variance showed that at Llanwarne stocking rate accounted for 47% and rainfall 45% of the variance in gain ha^{-1} of cattle (table 6.6). This is in contrast to gain animal^{-1}, where rainfall accounted for a significantly greater amount of the variance than stocking rate. At Dordrecht, however, rainfall accounted for 50% and stocking rate 23.9% of the variance in gain ha^{-1} (table 6.6). Although rainfall accounted for more of the variance in gain ha^{-1} than stocking rate at Dordrecht, stocking rate did account for more than double the variance in gain ha^{-1} than it did with gain animal^{-1}. These results indicate that a farmer is able to exert significant control on the amount of cattle products produced in a season, by varying the stocking rate.

Table 6.4 Estimates of the regression coefficients for factors hypothesized to affect gain ha^{-1} of cattle at Llanwarne

Model (r^2 = 80.0)	Coefficient	t-prob
Constant	-2.57	0.096
biom	0.856	0.002
sr	9.27	0.007
accum	0.000101	0.492
biomsq	-0.0331	0.004
Biom_sr	-0.474	0.155
Model (r^2 = 90.1)	**Coefficient**	**t-prob**
Constant	0.657	0.078
rain	0.00763	<.001
sr	3.37	0.010
accum	0.0000560	0.573
Rainsq	-0.62E-05	<.001
Rain_sr	0.00023	0.910

Key to variables: biom: peak grass biomass, biomsq: quadratic function for peak grass biomass
sr: stocking rate, accum: accumulated grazing days/ha,
Biom_sr: interaction between peak grass biomass and stocking rate,
rain: annual rainfall, Rainsq: quadratic function for annual rainfall,
Rain_sr: interaction between annual rainfall and stocking rate.

Table 6.5 Estimates of the regression coefficients for factors hypothesized to affect gain ha^{-1} of cattle at Dordrecht

Model (r^2 = 40.6)	Coefficient	t-prob
Constant	-0.81	0.694
biom	0.641	0.078
sr	8.88	0.111
accum	0.000076	0.710
biomsq	-0.0262	0.074
Biom_sr	-0.513	0.411
Model (r^2 = 75.7)	Coefficient	t-prob
Constant	2.294	<.001
rain	0.00363	0.002
sr	-1.43	0.449
accum	0.000265	0.053
Rainsq	-0.36E-05	<.001
Rain_sr	0.00627	0.044

Key to variables: biom: peak grass biomass, biomsq: quadratic function for peak grass biomass
sr: stocking rate, accum: accumulated grazing days/ha,
Biom_sr: interaction between peak grass biomass and stocking rate,
rain: annual rainfall, Rainsq: quadratic function for annual rainfall,
Rain_sr: interaction between annual rainfall and stocking rate.

Table 6.6 Analysis of variance showing the percentage of the variance accounted for by the various factors in the regression model

Llanwarne			
Change	d.f.	s.s.	% variance
+ rain	1	0.74498	24.32
+ sr	1	1.43051	46.71
+ accum	1	0.00013	0.004
+ Rainsq	1	0.64198	20.96
+ Rain_sr	1	0.00015	0.004
Residual	21	0.24439	
Total	26	3.06214	
Dordrecht			
Change	d.f.	s.s.	% variance
+ rain	1	0.47147	25.16
+ sr	1	0.44774	23.90
+ accum	1	0.03081	1.64
+ Rainsq	1	0.47624	25.42
+ Rain_sr	1	0.08011	4.28
Residual	21	0.36700	
Total	26	1.87337	

Key to variables:sr: stocking rate, accum: accumulated grazing days/ha,
rain: annual rainfall, Rainsq: quadratic function for annual rainfall,
Rain_sr: interaction between annual rainfall and stocking rate.

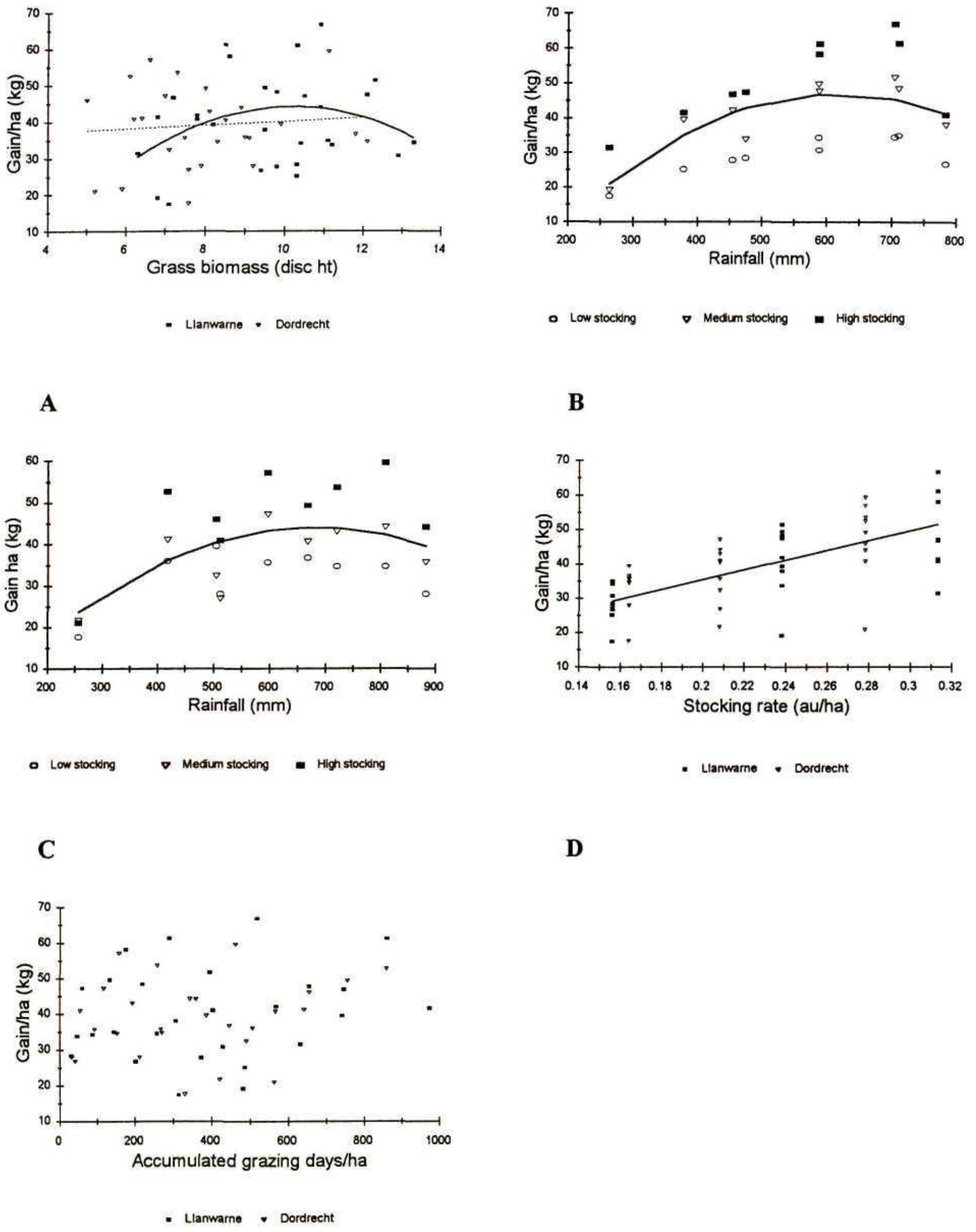


Figure 6.2 The relationship between peak grass biomass (A), rainfall at Llanwarne (B) & Dordrecht (C), stocking rate (D), accumulated grazing (E) and Gain/ha. When two lines fitted, broken line = Dordrecht

Discussion

The fact that no decline in cattle production at high stocking rates was detected in the regression analyses despite observed compositional changes (chapter 4), and declines in grass production in some of the high stocking rate camps (chapter 5), may have significant implications for our understanding of factors governing secondary production, and suggests that the spatial scale of management plays an important role in determining the sustainability of secondary productivity. Only one of the high stocking rate camps at Dordrecht (H 1) and at Llanwarne (H 2) exhibited compositional change and a decline in peak grass production. The cattle were not limited to these camps but were rotated between the two replications of the high stocking rate camps, according to the availability of forage. If the cattle had been limited to a particular camp then one might expect to see reduced performance of those cattle that were in the degraded camps. This illustrates the role that spatial scale plays in determining secondary production. In addition this result may be support for the 'key resource' hypothesis of Scoones (1992). He proposed that top land areas may erode and decline in productivity, while other areas may receive soil and water as a result of erosion processes and thereby increase in productivity, enabling sustained cattle numbers in dry periods. The H 2 camp at Dordrecht may function as a 'key resource' area because it has shown signs of increased productivity (chapter 5) and should therefore, be better able to sustain cattle in dry periods. These processes may occur widely in Africa's rangelands, and it is proposed on the strength of these results, has allowed long term stable cattle numbers in the communal regions of Zimbabwe (Scoones 1992) and Zululand (Tapson 1991).

A large amount of caution should be exercised, however, because as admitted by Scoones (1992), degradation of these 'Key resource' areas may result in a crash in the overall carrying capacity of the system. It is possible that in the future, with continued heavy stocking, this will occur. Even if it happens in several centuries time, which is outside the time scale of contemporary decision making processes, it is an unsatisfactory situation.

Some interesting results arising from this section of the study, was the strong quadratic relationship between rainfall and gain animal^{-1} and rainfall and gain ha^{-1} of cattle, and less conspicuously with grass biomass and gain animal^{-1} and gain ha^{-1}. `t Mannetje (1982) has demonstrated a similar, strongly quadratic relationship between gain animal^{-1} and rainfall from a *Cenchrus ciliarus, Macroptilium atropurpureum* pasture grazed by steers. Thus in exceptional rainfall seasons (above 700 mm for this region) farmers can expect lower cattle performance and may need to use supplements to counter such drop offs in performance. Another option that could improve gain animal^{-1} in high rainfall seasons would be to stock at high levels when excessive rain has fallen during the first few months of the growing season. The reason behind this is that there may be an interaction between rainfall and stocking rate, in its effect on animal performance. Evidence for this interaction was found in this analysis (table 6.2), and is predicted on an empirical and theoretical basis. In general there is a negative relationship between stocking rate and gain animal^{-1} (Cowlishaw 1969, Jones & Sandland 1974, Bransby *et al.* 1988) and was observed in this study (fig 6.1 D). Under certain circumstances, however, this may not always be the case. Denny *et al.* (1974) found that cattle had higher gains at high stocking rates in a four paddock system, than cattle at low stocking rates in an eight paddock system with longer periods of absence. The most likely explanation for this is that with longer periods of absence, especially at low stocking rates, the grass was able to 'grow out' and was therefore of lower quality and digestibility than for the cattle at heavier stocking rates. The voluntary intake of forage has been positively related to the digestibility of the dry matter and energy (Minson 1982). Hacker (1982) noted that most studies indicate a negative correlation between digestibility and yield of grasses, although the correlation is usually weak. With increased grass growth there is a dilution of nutrients (Jarrell & Beverly 1981), and an increase in lignification and decreased cell wall digestibility (Wilson 1982). Pate & Snyder (1979) cited by Wilson (1982) found that high water table levels resulted in reduced crude protein in grasses and increased cell wall content. A change in the structure of the sward (i.e. decreased leaf/stem ratios) with increased growth has been observed by (Stobbs 1975). Stobbs (1973, 1975) found that bite size of cattle on tropical pastures of the same species but different structure, was larger from those pastures with higher leaf/stem ratios and that this can affect intake by the cattle. Thus in very high rainfall years, exceptional grass growth and resultant changes in sward structure are expected to have a negative impact on gain animal^{-1}. This may explain why gain animal^{-1} declined during high rainfall seasons at Llanwarne and Dordrecht (fig 6.1 B & C). Another factor that may contribute to declining animal performance, is scouring by the cattle, which occurs early in the season when the grass is exceptionally green and of high water content. As the season progresses and the grass 'grows out', this factor will become less important and poor forage quality and changes in the structure of the sward will start to have an effect. Thus these two factors may work in combination with each other, one early in the season and the other later in the season.

The result of Denny *et al.* (1974) and evidence for lower forage quality, digestibility and intake, with higher grass growth/rainfall demonstrates how stocking rate may interact with rainfall in affecting animal performance. At high rainfall and low stocking rates, cattle may not be able to keep grass growth in check, with resultant deteriation in forage quality and changes in sward structure, and thereby poor animal performance. At high stocking rates and high rainfall excessive growing out of grass may not occur, resulting in better forage quality and animal performance. Therefore, by stocking heavily during periods of rapid grass growth (induced by high rainfall combined with favourable growing conditions), farmers may be able to overcome this decline in animal performance at high rainfall levels, and thereby significantly improve the productivity of their operations. It should be noted, however, that the evidence from Llanwarne and Dordrecht does not entirely support these predictions of better gain animal^{-1} with high stocking rates and high rainfall (fig 6.1 B & C). There is sufficient evidence, however, to warrant further investigation of this strategy, especially under a range of bioclimatic types. Even if individual animal performance does not improve with heavy stocking rates in high rainfall seasons, the resultant increase in gain ha^{-1} with increased stocking rate (fig 6.2 D), will compensate for the decline in individual animal performance under these conditions.

There is evidence that heavy stocking rates do not degrade the vegetation during high rainfall years (Ash *et al.* 1991). Rather range degradation is most likely with heavy grazing in drought periods (Livingstone 1991), and therefore farmers, within reasonable bounds, can afford to stock heavily during these high rainfall periods.

The above reasoning together with the problem of determining carrying capacity in semi-arid environments (Stoddart 1960, McLeod 1997), suggests that farmers should employ an opportunistic and flexible management strategy, to optimise the productivity and sustainability of their operations.

Another interesting result was that rainfall was found to be a better predictor of cattle performance than grass biomass. The fact that the rainfall model accounts for a significantly greater amount of the variance than the peak grass biomass model is of importance for those interested in modelling these systems. Rainfall rather than grass biomass is obviously the best variable to use when modelling cattle performance, because not only is it a better predictor of cattle performance, but is also easier data to collect than grass biomass data.

The relationship between stocking rate and gain animal^{-1} appears to be linear (fig 6.1 D), which is in agreement with the model of Jones & Sandland (1974), however this model predicts that the relationship between gain ha^{-1} and stocking rate will be quadratic. In the trials at Llanwarne and Dordrecht the relationship was linear, but it is expected that at higher stocking rates gain ha^{-1} would decline, because the availability of forage would be so low, that individual animal gain would be negligible, and therefore the addition of extra animals could not compensate for the poor performance of the individual animals. There is an indication of this effect at Dordrecht during low rainfall seasons when forage is limiting, where the medium stocking rate treatment gave better gain ha^{-1} than the high stocking rate treatment (fig 6.2 C).

CHAPTER 7

A FENCE LINE CONTRAST STUDY AT LLANWARNE: PLANT AND SOIL RESPONSES TO STOCKING RATES

Introduction

Rangeland degradation will generally be manifest in compositional changes and reduced primary and secondary productivity. The mechanisms that result in reduced productivity are of primary concern to rangeland scientists, because elucidation of these is needed to provide a sound theoretical base from which sustainable management strategies for rangelands may be determined.

Accelerated soil loss through overstocking is the most severe mechanism of range degradation because it results in a lack of suitable growing media, moisture and nutrients for the plants, that cannot be replaced in a time frame relevant to mankind. However more subtle and less severe mechanisms of degradation may be through a reduction in soil nutrient levels without the loss of the soil itself, though this has yet to be confirmed. This may occur by means of nutrients being relocated in the landscape through dung and urine deposits at popular sites such as at water holes or under trees, or nutrient export during animal off take.

In an environment where water is limiting a reduction in the amount of rainfall captured as soil moisture, will most likely reduce grass production because there is less water available for use by plants. It is emerging in the literature as one of the most important mechanisms leading to range degradation and alternate vegetation states. Heavy stocking rates have been shown to result in soil compaction and reduced infiltration (Rhoades *et al.* 1964, Rauzi & Hanson 1966, Warren *et al.* 1986, Pluhar *et al.* 1987).The mechanism by which soil compaction occurs, may be in part due to compaction by cattle, but is more likely to occur through the reduced canopy cover of the grass layer, exposing the soil to compaction and surface sealing by raindrop impacts. Grazing has been strongly linked to a reduction in soil moisture levels (Milchunas & Lauenroth 1993). The increase in runoff and a decrease in infiltration and soil moisture levels, translates into a reduction in rain-use efficiency for the rangeland (Le Houerou 1989) and possibly alternate vegetation states (Rietkerk & Van de Koppel 1997).

Thus the aim of this study was to determine if after nine years of grazing, there were any statistically detectable differences between low and high stocking rates in the concentrations of selected soil chemical and physical factors, plant nitrogen and phosphorus concentration and standing crop and grass biomass. The reason being that these are variables known to have a direct or indirect influence on the productivity of the system and would provide insights into the pathways and mechanisms of range degradation if degradation has taken place. It was also intended to elucidate whether factors such as species composition and grass biomass affect the concentration and standing crop of plant nitrogen and phosphorus.

Methods

This study was conducted at Llanwarne using fence line contrasts between the high (0.313 au ha^{-1}) and low (0.156 au ha^{-1}) stocking rate treatments. No high vs low stocking rate treatment contrasts were present at the Dordrecht trial, and therefore it was not included in the study. The reason a fence line contrast approach was used, was an attempt to reduce noise in the form of environmentally induced spatial variability of ecological components that tend to mask treatment effects. To adopt a random sampling strategy with any success in a spatially variable environment such as at Llanwarne, would mean that a large number of samples would have to be taken. It was hoped that by using a fence line contrast strategy the effects of environmental variability on the ecological components measured would be minimised. The reasoning behind this is that samples close together are more likely to have similar environmental influences than samples far apart. Thus a pairwise sampling strategy across fence lines with analysis by paired *t*-tests, allows a sample to be compared against its partner across the fence where environmental conditions are likely to be similar, rather than being compared against a sample taken further away where environmental conditions are likely to be dissimilar.

Pairwise sampling was done along the fence lines where, a 0.25 m^2 quadrat was placed systematically along the fence and five metres each side of the fence (fig 7.1). Fifteen pairwise samples were collected per fence line (i.e. 30 quadrats per fence line).

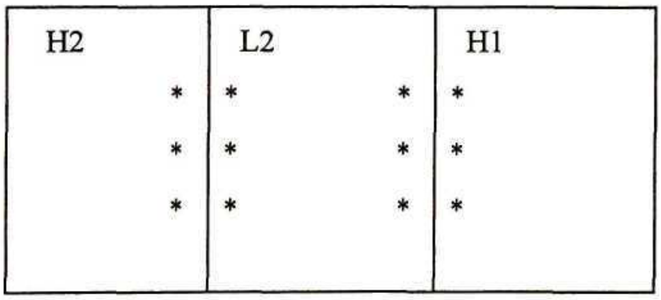


Figure 7.1 A sketch showing the pairwise sampling strategy along fence lines at Llanwarne (* = quadrat).

Due to the variability in soil nutrients from beneath and between trees in savannas (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Belsky *et al.* 1989) samples were stratified (i.e. only placed between tree canopies in an attempt to reduce the number of samples needed to adequately test treatment effects).

The parameters sampled in each quadrat were: grass species for biomass determination and nutrient analysis, a 30cm soil core for root biomass determination, a 10 cm soil core for bulk density determination and a soil sample for soil analysis.

Grass species in a quadrat were clipped and bagged individually, dried at 60° C for 48 hours, weighed and milled for nutrient analysis. The 30 cm soil core was dispersed in a bucket of water on a reciprocal shaker and washed through a graduated series of sieves of 3.35 mm, 1.5 mm, 0.7 mm and 0.5 mm to separate the roots into various size classes, which were dried at 60 °C for 48 hours and weighed.

The 10 cm soil core was dried at 105 °C for 48 hours and weighed to determine soil bulk density. The soil sample was obtained by taking five 10 cm deep soil samples from the quadrat using a 5 cm diameter soil auger. These were bulked, thoroughly mixed and a subsample taken for analysis.

Nutrient analysis

To obtain an estimate of plant nitrogen and phosphorus for a quadrat, the proportion by mass of each grass species that occurred in a quadrat was calculated. The 0.5 g sample to be analysed for a particular quadrat, was weighed out according to the proportion that each species occurred in that quadrat (i.e. if *Urochloa mosambicensis* made up 86% of the biomass of a quadrat and *Sporobolus ioclados* the remaining 14%, 0.43 g of the former and 0.07 g of the latter would be weighed out to make up the required sample mass of 0.5 g for analysis). Thus a representative estimate of the N and P status of a quadrat could be obtained.

Plant phosphorus was determined by ashing 0.5g of sample at 500° C for two hours, then digesting the ash with 4M $HCl\backslash HNO_3$ on a sandbath. The extracts were made up to 100ml, and the phosphorus content was determined colorimetrically with a Spectronic 20D spectrophotometer using the vandomolydate yellow method at a wavelength of 440 nm.

Plant nitrogen was determined according to the method of Hambleton (1975). Forage quality analysis was done using the method of van Soest and Wine (1967) where neutral detergent and acid detergent fibre are determined *in vitro*. This analysis was done on one species only (*Urochloa mosambicensis*) rather than the mix of species from a quadrat such as with N and P analyses, so that one could test whether stocking rate is affecting the forage quality of individual species.

Soil organic carbon was determined by the wet oxidation method of Walkley & Black (Walkley 1947).

Soil phosphorus was fractionated into three main components, the object of which was to investigate how stocking rate affected these three forms. The three forms were: A) Ammonium Bicarbonate (Ambic) extractable phosphorus, which represents (to a degree) that portion of the phosphorus that is available to plants. B) NaOH extractable phosphorus which represents the fixed or unavailable phosphorus. C) Organic phosphorus, which will be an important component of the phosphorus cycle and should be affected by stocking rate. To obtain the Ambic and NaOH extracts 2.5 gms of soil (ground to pass through a 0.5 mm sieve), was first extracted overnight on a reciprocal shaker with 25 ml of Ambic solution. This was centrifuged and the supernatant liquid filtered into glass vials. After carefully draining the Ambic from the soil, more Ambic was added and allowed to soak for a couple of hours to remove any remaining phosphorus that was not drained with the supernatant liquid. After centrifuging, the second supernatant was carefully drained from the sample and discarded. Then 25 ml of 0.5 M NaOH was added to the sample and shaken overnight on a reciprocal shaker. This was centrifuged and filtered into glass vials for storage. To determine the concentration of phosphorus in these extracts they were read colorimetrically on a Spectronic 20D spectrophotometer at a wavelength of 670 nm using the molybdate blue method. However it has been observed that organic matter in the extracts contributes to the absorbence read on the spectrophotometer, and thus gives inflated estimates of phosphorus concentration. This is particularly severe when there is a high organic matter content in the extract. The relationship between organic matter content and absorbence is linear, as determined by a dilution series (fig 7.2).

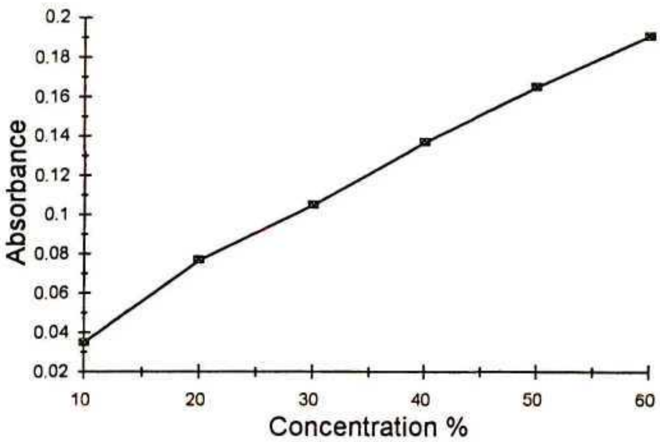


Figure 7.2 The relation between the concentration of organic matter in the supernatant liquid and absorbence on a spectrophotometer.

To account for the extra absorbence, the absorbence due to organic matter was determined by pipetting out two ml of extract and instead of adding eight ml distilled water and 10 ml colour reagent, 18 ml of distilled water was added without colour reagent. The absorbence was set to zero on the spectrophotometer and the absorbence of these samples was then read at 670 nm. This value was subtracted from the value obtained when using colour reagent (i.e. the absorbence due to the organic matter and phosphorus).

In order to obtain an estimate of organic phosphorus, a value for total phosphorus had to first be obtained from which the value for inorganic phosphorus could be subtracted. To determine total phosphorus four ml of extract was pipetted into a crucible and evaporated. This was then ashed at 500° C overnight, to convert all organic phosphorus to inorganic phosphorus. This was dissolved in 1 M HCl and the phosphorus concentration determined using the same method as for inorganic phosphorus above.

Analysis of data

To test for the effect of stocking rate on grass biomass (above and below ground), plant phosphorus and nitrogen (concentration and standing crop), forage quality, soil bulk density, soil phosphorus and soil organic carbon, pairwise *t*-tests were used. In this test the null hypothesis is that the differences between paired samples across the fence line is zero. The rejection of the null hypothesis means that the differences are not zero and this implies a stocking rate effect.

To elucidate which factors affect plant nutrients four separate regression analyses were done on nitrogen and phosphorus concentration and nitrogen and phosphorus total standing crop as the response variables, and stocking rate, species composition, biomass and interactions between stocking rate and species composition as the independent variables. In this way the relative influence of each of these variables on the response variable in question could be determined.

The reason for using species composition as a variable in the model is that species differ in their concentrations of nitrogen and phosphorus and should therefore influence the nutrient status of each quadrat. Owing to the large number of species, however, it is not possible to fit each species as separate variables of species composition. Therefore correspondence analysis (CA) was used to analyse the data to reduce species composition down to a few orthogonal variables, incorporating the essence of any features of composition that may be of importance. These variables are the first few axes of the analysis, and their site scores were used in the regression analysis.

Grass biomass was also expected to affect the concentration and standing crop of nutrients by means of a dilution effect with increasing biomass (Jarrell & Beverly 1981), and was therefore considered an important variable to include in the analysis.

A further ordination was done on the grass species from each quadrat and the plant nitrogen and phosphorus values for those quadrats using CA with environmental variables included. This is useful for graphically illustrating which species give rise to the range of values for nitrogen and phosphorus in quadrats.

Results

Contrasts

Table 7.1 Paired *t*-tests on various plant and soil parameters at high and low stocking rates.

(H1/L2 FENCE LINE)	Units	t prob	Mean	
Variable			H1	L2
Soil bulk density	gms/cm^3	**0.02**	1.55	1.46
Organic Carbon	%	**0.057**	1.95	2.17
Soil P (Ambic)	mg/kg	0.37	14.49	12.66
Soil P (NaOH)	mg/kg	0.73	37.74	38.75
Soil P (Organic)				
Ambic extracted	mg/kg	0.15	2.66	4.95
NaOH extracted	mg/kg	0.79	313.3	319.73
Plant N	%	**0.07**	1.27	1.11
Plant P	%	**0.03**	0.44	0.35
Standing crop N	gms/1m^2	**0.056**	1.88	2.60
Standing crop P	gms/1m^2	0.31	0.64	0.72
Forage Quality				
NDF	%	0.67	31.95	31.50
ADF	%	**0.01**	38.96	40.65
Grass Biomass				
Above ground	gms/1m^2	**0.03**	154.24	250.60
Below ground				
Total	gms/1000cm^3	0.59	3.39	3.19
Fine	gms/1000cm^3	0.64	0.66	0.63
(L2/H2 FENCE LINE)			L2	H2
Soil bulk density	gms/cm^3	0.64	1.54	1.55
Organic Carbon	%	0.62	1.85	1.76
Soil P (Ambic)	mg/kg	**0.057**	10.70	9.47
Soil P (NaOH)	mg/kg	0.36	32.31	33.66
Soil P (Organic)				
Ambic extracted	mg/kg	0.80	2.27	2.49
NaOH extracted	mg/kg	0.36	268.95	278.13
Plant N	%	0.14	0.97	1.05
Plant P	%	**0.01**	0.29	0.40
Standing crop N	gms/1m^2	**0.085**	2.56	2.00
Standing crop P	gms/1m^2	0.72	0.76	0.72
Forage Quality				
NDF	%	0.87	30.93	30.68
ADF	%	0.11	41.66	40.51
Grass Biomass				
Above ground	gms/1m^2	**0.04**	270.6	198.0
Below ground				
Total	gms/1000cm^3	0.38	3.65	3.32
Fine	gms/1000cm^3	0.53	0.90	0.83

Soil bulk density was significantly higher at high stocking rates on the H1/L2 fence line (table 7.1) indicating possible soil compaction by cattle at high stocking rates, although this is not supported by the L2/H2 fence line (table 7.1). Soil organic carbon was reduced on the H1/L2 fence line but as for bulk density there was no difference on the L2/H2 fence line. A reduction of organic carbon may be brought about by reduced reincorporation of organic material, as a result of lower grass biomass. Soil phosphorus (Ambic extracted) showed a reduction on the L2/H2 fence line at high stocking rates. However there was no difference on any fence line with NaOH extracted phosphorus or organic phosphorus. Thus there is a suggestion that stocking rate may affect phosphorus levels in the soil, but only plant available phosphorus. Plant phosphorus showed increased concentrations at high stocking rates on both fence lines. Seeing that there was reduced grass biomass at high stocking rates on both fence lines (table 7.1) increased concentrations of plant phosphorus is most likely a function of phosphorus being concentrated with poor growth (Jarrell & Beverly 1981). Also soil phosphorus was reduced at high stocking rates, so increased plant phosphorus cannot be attributed to the availability of phosphorus in the soil. Surprisingly there was no statistically significant effect on plant nitrogen concentration although the t-values suggest a real effect, especially on the H1/L2 fence line. There was no difference in the standing crop of plant phosphorus but there was a lower standing crop of plant nitrogen at high stocking rates on the H1/L2 fence line, and tending that way on the H2/L2 fence line, implying a loss of nitrogen bound in the organic component of the system.

Although there was an effect on above ground grass biomass there was no effect on below ground biomass (grass roots) on either fence line. Seeing that a reduction in leaf mass usually means a reduction in root mass (Youngner 1972), this result is most likely due to the high variability of the samples. Milchunas & Lauenroth (1993), however, found no effect of grazing on root biomass, which supports these results.

From the forage quality analyses on *Urochloa mosambicensis* there were no differences in the NDF percentage (which represents the cell contents). However on the H1/L2 fence line *Urochloa mosambicensis* had a lower ADF percentage (% of cellulose and lignin) at high stocking rates. The fact that there was no significant difference in the ADF % on the H2/L2 fence line may be due to a very small sample size. Thus there is the possibility that high stocking rates may improve the digestibility of grasses.

Ordination of species composition data

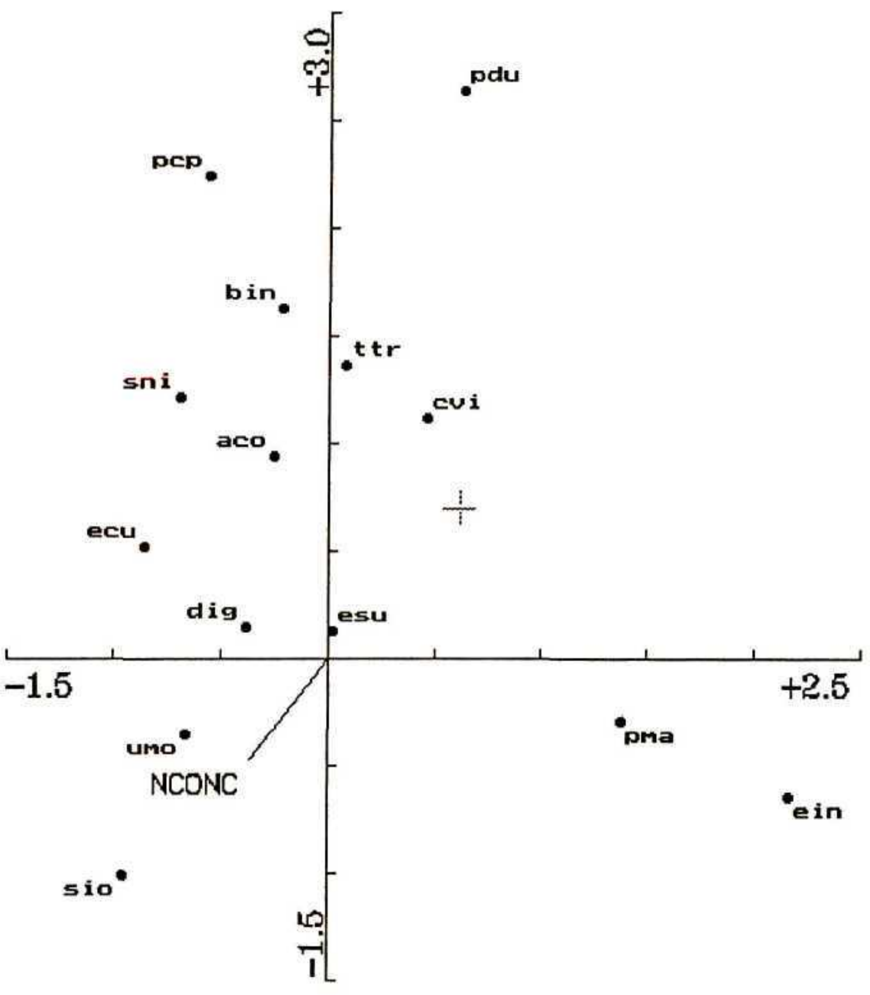


Figure 7.3 Ordination diagram of species showing direction of gradient in grass N & P concentration. The P concentration gradient is the same as the N gradient and therefore is not shown.

Key to species: ACO: Aristida congesta, BIN: Bothriochloa insculpta, CVI: Chloris virgata, DIG: Digitaria argyrograpta, ECU: Eragrostis curvula, ESU: Eragrostis superba, SIO: Sporobolus ioclados, SNI: Sporobolus nitens, TGR: Trichoneura grandiglumis, TRA: Tragus racemosus, TTR: Themeda triandra, UMO: Urochloa mosambicensis, PCP: Panicum coloratum, PMA: Panicum maximum, PDU: Panicum deustum, EIN: Eleusine indica

Panicum maximum is very important on axis 1, with most of its variance being accounted for (94%). *Urochloa mosambicensis* and *Sporobolus ioclados* have a large proportion of their variance accounted for by this axis (45% and 22% respectively) and have large negative scores. Quadrats dominated by *Panicum maximum* have high site scores, and quadrats dominated by *Urochloa mosambicensis* and *Sporobolus ioclados* have low site scores. Thus axis 1 is contrasting the presence or absence and abundance of these two groups of species (fig 7.3). There is no distinct phosphorus gradient along this axis (fig 7.3), and this is reflected in the regression analysis (table 7.2).

There are two particular suites of species that are important on axis 2. They include *Panicum deustum, Panicum coloratum, Bothriochloa insculpta and Themeda triandra* with positive scores, and *Sporobolus ioclados* and *Urochloa mosambicensis* with negative scores (fig 7.3). *Sporobolus ioclados* had the greatest negative score, and *Panicum coloratum* and *Panicum deustum* had the highest positive scores for this axis.

When *Sporobolus ioclados* or *Urochloa mosambicensis* dominated a quadrat there is a low site score on axis two, and a high phosphorus concentration for that quadrat. When the species above, that have positive scores dominated a quadrat, there is a high site score and a low phosphorus concentration for that quadrat. Thus axis two is contrasting the presence or absence and abundance of these two suites of species which in turn influence the phosphorus concentration of a particular quadrat. Thus the phosphorus gradient is well related to axis 2 and therefore was important in the regression analysis (table 7.2).

Regression analysis

Stocking rate has an effect on the concentration of plant phosphorus, by increasing the concentration with increased stocking rate (positive coefficient), but has not affected plant nitrogen concentration (table 7.2). This is not entirely consistent with the *t*-test results in table 7.1, where on the H 1/L 2 fence line there is a strong suggestion of an increase in the plant nitrogen concentration at high stocking rates. Grass biomass affects the plant phosphorus and nitrogen concentration by decreasing the concentration with increased grass biomass (negative coefficient) (table 7.2). This confirms that the increased plant phosphorus and to a lesser extent plant nitrogen concentration at high stocking rates (table 7.1) is the result of reduced grass biomass at high stocking rates (Jarrell & Beverly 1981).

No main effects of species composition were significant for plant phosphorus and nitrogen concentration, however the axis 2 by stocking rate interaction was significant for plant phosphorus concentration. This is probably because that although there is a general phosphorus and nitrogen gradient along axis 2 (fig 7.3), it is not consistent across stocking rates, as revealed by an examination of the data. The nitrogen gradient was obviously weaker along axis 2, and was therefore non-significant.

As expected the standing crop of nitrogen and phosphorus was directly related to grass biomass (table 7.2). Grass biomass would be expected to affect total standing crop of nutrients, seeing that standing crop is a multiple of biomass.

Table 7.2 Estimates of the regression coefficients for plant phosphorus and nitrogen concentration and standing crop.

Phosphorus concentration (R^2 = 43.8)		
Variable	Estimate	t prob
Constant	0.3189	<.001
Axis 1	0.000653	0.281
Axis 2	0.000177	0.134
Axis 3	-0.000305	0.278
Axis 4	-0.001180	0.119
Biomass	-0.001180	0.047
Stocking rate	0.440	0.018
Axis1*SR	-0.00230	0.372
Axis2*SR	-0.00697	0.008
Nitrogen concentration (R^2 = 44.8)		
Constant	1.211	<.001
Axis 1	0.00114	0.327
Axis 2	-0.00018	0.864
Axis 3	0.000394	0.209
Axis 4	0.000063	0.865
Biomass	-0.00237	0.038
Stocking rate	-0.014	0.969
Axis1*SR	-0.00767	0.124
Axis2*SR	-0.00568	0.244
Phosphorus standing crop (R^2 = 72.5)		
Constant	-0.0050	0.870
Axis 1	0.000370	0.276
Axis 2	0.000094	0.763
Axis 3	0.0001358	0.141
Axis 4	-0.000118	0.278
Biomass	0.002703	<.001
Stocking rate	0.169	0.102
Axis1*SR	-0.00132	0.363
Axis2*SR	-0.00162	0.258
Nitrogen standing crop (R^2 = 88.1)		
Constant	0.084	0.140
Axis 1	0.000492	0.428
Axis 2	-0.000294	0.606
Axis 3	0.000131	0.435
Axis 4	0.000038	0.848
Biomass	0.008649	<.001
Stocking rate	0.013	0.945
Axis1*SR	-0.00274	0.302
Axis2*SR	-0.00149	0.566

It is surprising that the regression analysis has shown that neither stocking rate nor any species composition effect has influenced the total standing crop of phosphorus and nitrogen, especially seeing that the *t*-tests did show an effect of stocking rate on the standing crop of nitrogen. This is most likely a function of the lower efficiency of the regression analysis, in that paired *t*-tests reduce the noise effect by only making comparisons between paired samples which are likely to have less influence of environmental variation. The species composition differences were obviously not strong enough to have a significant influence on the standing crop of nutrients.

Discussion

Tongway & Ludwig (1997a) consider a degraded or dysfunctional system to be a 'leaky' system, i.e. leaks water, soil and nutrients from the system, where in the past they would have been captured, utilised and recycled within the system. This leads to a downward spiral of the system, because reduced growth pulses as a result of lost water and nutrients, mean reduced ability to capture nutrients, thus intensifying the feedback. According to them there is overwhelming evidence from Australian rangelands that dysfunctional systems have reduced moisture and nutrients. A large body of literature exists relating vegetation shifts in semi-arid grasslands to soil degradation (Van de Koppel *et al.* 1997). In contrast to this Milchunas & Lauenroth (1993) found no significant effect of grazing on soil organic carbon, soil nitrogen, soil phosphorus and soil pH. A conspicuous feature of the results from this study is the lack of any consistent trends between low and high stocking rates, in soil parameters. Although there may have been a reduction in soil phosphorus and organic carbon and an increase in soil bulk density on one fence line at high stocking rates, there was no difference on the other fence line. Thus there is only weak evidence that heavy stocking rates have had some effect on the various soil nutrients. In a semi-arid system, however, reductions in primary productivity need not be related to reductions in soil nutrients. Soil moisture in an environment where moisture is limiting is a major component of system productivity. Any factor reducing the availability of soil moisture to plants will have a significant negative impact on primary production. It should be noted that soil moisture was not measured in this study, which may be an important omission, considering that Milchunas & Lauenroth (1993) found a grazing induced reduction in soil water in 13 out of 15 sites.

Heavy stocking rates indirectly increase the concentration of phosphorus and nitrogen in grasses by reducing the amount of grass growth, which results in an increased concentration of these nutrients in the plant (table 7.2) (Jarrell & Beverly 1981). This effect was not as strong for nitrogen as it was for phosphorus (table 7.1) which explains why a decrease in grass biomass at high stocking rates, decreased the standing crop of plant nitrogen but not the standing crop of plant phosphorus. The reduction in grass biomass was compensated for by an increase in the concentration of plant phosphorus to a large enough extent to maintain the overall standing crop of phosphorus. The weaker increase in nitrogen concentration at high stocking rates (table 7.1), was insufficient to sustain a constant level of nitrogen standing crop with reduced grass biomass.

Kelly & Walker (1976) working in SE Zimbabwe did not detect any clear trend in the concentration of nitrogen and phosphorus between heavy and lightly utilized areas, although crude protein percentage was higher in the heavily utilized areas in March. The latter result is what would be predicted from the concentration effect and supports the results of this study. They observed that areas under heavy utilization had, on average, less than one third the available protein, carbohydrates and fat, than the lightly utilized areas. This was also the case in this study where the total standing crop of nitrogen was reduced at heavy stocking rates. Thus it appears that although the forage quality at high stocking rates is higher than at low stocking rates, there is a reduction in the overall amount of protein available to animals. This may have a negative effect on animal production, especially at higher stocking rates if the amount of forage becomes limiting.

In conclusion there was no convincing evidence in this study that soil nutrient changes were the primary mechanisms leading to compositional change and reduced grass biomass, although the fence line contrasts were probably too limited in spatial distribution and sample size to adequately test this hypothesis and were only done at Llanwarne. Also there was no measure of the trends in soil moisture, which is more likely to change than soil nutrients, and therefore no conclusions can be drawn on the effects of stocking rate on this aspect of the system. Many more studies will be needed in the future to provide a clearer picture of the mechanisms of range degradation.

Future investigations should focus on long term trends in soil nutrients and especially soil moisture budgets under heavy grazing, as well as rates of soil loss under various grazing intensities, and how this interacts with slope. There is an indication that with low stocking rates there may be no difference in runoff rates on slopes and flat land, but significantly greater runoff on slopes compared with flat land at high stocking rates (Swanepoel 1998). Emphasis should be placed on high replication in sampling, which is necessary to overcome the problems of high spatial variability in soil parameters.

CHAPTER 8

CONCLUSION

In general the results of the various analyses in this study complemented each other very well, enabling certain conclusions to be drawn with a greater degree of confidence. Most of the results support traditional ideas about semi-arid rangeland functioning, with regard to the reaction of the various growth forms or strategies of species to rainfall and grazing, and that on an annual scale rainfall has the major effect on species composition dynamics, seasonal peak grass biomass and cattle production. Stocking rate has a more subtle but important long term effect on compositional change and long term heavy grazing leads to a decline in grass production.

An important result was that vegetation on unstable landscapes such as steep slopes is more vulnerable to compositional change and declines in productivity than vegetation on flat land, and especially the vegetation of landscapes in depositional rather than erosional environments. Such landscapes exhibited relatively little compositional change that could be attributed to stocking rate, and showed no decline in grass production under the heavy stocking rates used in this study. These observations strongly support current techniques of taking slope angle into account when determining the carrying capacity of a region, although the highly variable year-to-year grass production due to variable rainfall, suggests that there is no single value for the carrying capacity of this region.

Farmers should use an opportunistic management strategy in semi-arid environments, rather than fixed stocking rates. Unpredictable rainfall and highly variable grass production make a mockery of the concept of a single carrying capacity in semi-arid regions. Freudenberger *et al.* (1997) have shown that grazing pressure (number of animals/unit of feed) is poorly related to stocking rate in semi-arid regions, owing to highly variable forage availability. Farmers should attempt to prevent the grazing pressure rather than stocking rate, exceeding certain critical levels, as this is more ecologically meaningful. For example, a recommended stocking rate is still likely to result in overgrazing during a severe drought, and it is in these drought window periods that degradation is likely to occur (Livingstone 1991).

Heavier stocking in high rainfall seasons should be encouraged to at least compensate for the expected reduction in animal performance under these conditions (chapter 6). Farmers must be careful, however, to leave sufficient reserves of forage for the winter, in the light of the observations of reduced seasonal grass production at heavy stocking rates, even during high rainfall seasons (fig 5.2 & 5.5 chapter 5).

The fact that only sites that are in a more erodible landscape have shown signs of degradation, suggests that an important mechanism leading to range degradation is through some soil related process. Hatch (pers comm) noticed that over the duration of the trial, soil had washed out of the high 1 camp at Dordrecht and had built up against the lower fence of the camp. Not much soil is needed to be lost to have a significant effect on the availability of nutrients in the system. Tongway & Ludwig (1997a) note that soil nutrients are concentrated in the upper few cm of soil, this being the reason why even modest levels of soil erosion can quickly drive a landscape into dysfunction. The fence line contrast study, however, does not lend strong support to the hypothesis that there have been large soil nutrient changes which have brought about the observed vegetation changes at Llanwarne, although the problems of high spatial variation and small sample size have to be taken into account when considering this result, and the fact that the fence line contrast study was limited to Llanwarne. Soil loss is likely to have played a part in degradation, especially at Dordrecht where erosion was observed during the trial. It is also likely that an increase in runoff and a reduction in infiltration rates has been an important mechanism affecting changes in productivity on steeper slopes. Slopes are well drained and therefore have less soil moisture than flat land, meaning that reduced water capture on slopes has a cumulatively larger effect on plant growth. Reductions in soil moisture with grazing were observed at 13 out of 15 sites by Milchunas & Lauenroth (1993), and therefore it is likely that this been an important mechanism leading to declining productivity on the steeper slopes at Llanwarne and Dordrecht.

The other mechanism by which degradation can occur is through compositional changes that are unrelated to soil changes, but are rather the result of perennial grass species being replaced by lower producing annuals and short lived perennials under heavy grazing. The reason that this may be restricted to steeper slopes, is the possibility that perennial grasses are less resistant to heavy grazing under low soil moisture conditions, which is generally the situation on slopes. This hypothesis is supported by observations of increased rates of grass mortality during drought, in landscape positions of low soil moisture (Freudenberger *et al.* 1997). The fact that there is a general declining trend in seasonal grass production with increasingly positive axis 1 and axis 2 compositional scores (fig's 5.3, 5.4, 5.6 & 5.7, chapter 5) shows that species composition has an important effect on grass production.

The fact that cattle performance did not decline in the heavy stocking rate camps, was probably due to them being rotated between camps that had degraded, and those that had not (i.e. the H1 camp at Dordrecht had degraded but not the H2 camp). This lends support to the key resource hypothesis of Scoones (1992), that cattle were able to maintain their levels overtime in the communal regions of Zimbabwe by use of key resource areas that provide fodder in dry periods. The lower parts of the H 2 camp at Dordrecht occurred on deep bottom land soils that had very high yields of *Panicum maximum* which could provide fodder late into the dry season and thus functioned as a key resource area. Trees played an important role in this system by providing areas of improved grass production, through a micro-climate that is favourable for good yields of *Panicum maximum* and *Panicum coloratum*, even in those high stocking rate camps that had degraded to an annual and weakly tufted perennial dominated sward. Thus trees gave rise to a form of key resource area in this region.

Further research on degradation in semi-arid environments should focus on the role that slope angle plays in affecting increases in water runoff and reductions in soil moisture with heavy stocking rates. The reason being that the rate at which water is able to infiltrate the soil on steep slopes may decline on an order of magnitude greater with heavy stocking rates, than the rate at which it may infiltrate soil on flatter land at heavy stocking rates, due to there being a longer retention time of that water on flatland where there is less potential for runoff. It would also be useful to test whether perennial grasses are less resistant to high levels of defoliation at lower soil moisture levels. If this is the case then this could be a mechanism by which perennial grasses decline on steeper slopes without any noticeable soil changes, because there is generally expected to be a lower soil moisture status on steeper slopes as a result of better drainage.

Research is also needed to be done on the interaction between stocking rate and rainfall and its effect on cattle performance. If it can be shown that in certain regions cattle perform better at high stocking rates than at low stocking rates during high rainfall seasons, then this could be an important strategy for farmers in improving the productivity of their farming operations.

It is also important to establish whether heavy stocking rates during high rainfall seasons result in range degradation. If it can be shown that rangeland is only vulnerable to degradation with heavy stocking rates during low rainfall periods, then farmers can afford (within reasonable limits) to apply heavier stocking rates during high rainfall seasons, and thereby improve the output of their operations.

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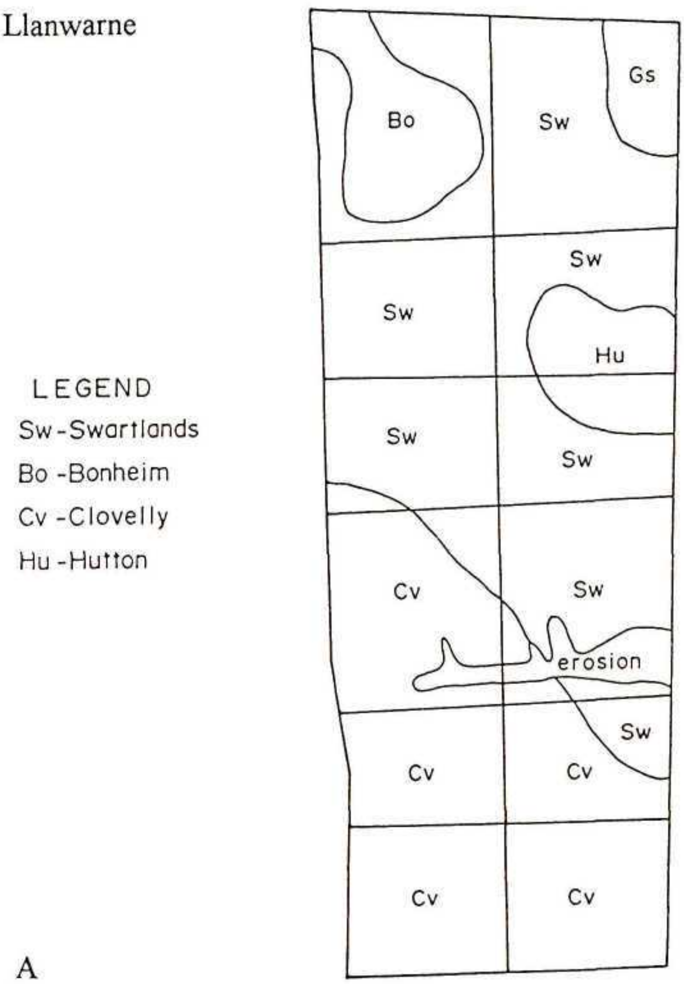
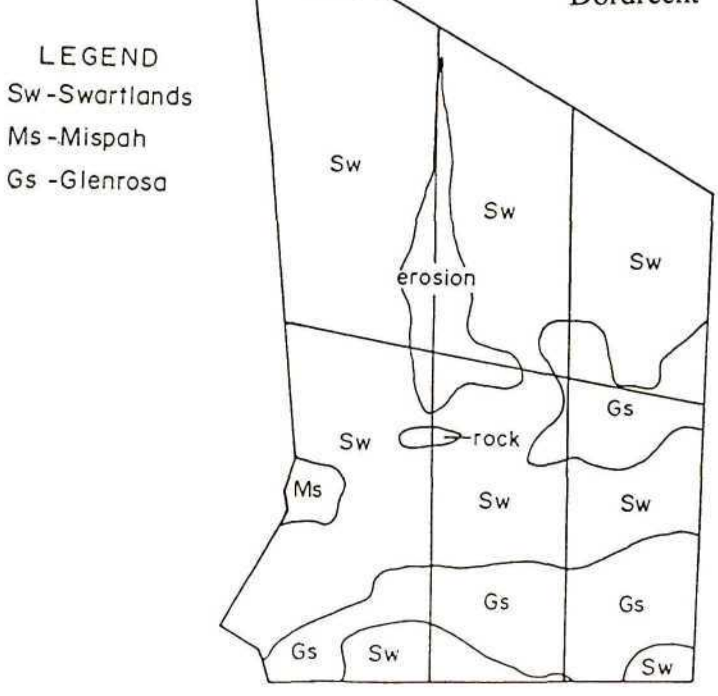
Appendix 1 Soil map of the Llanwarne and Dordrecht trials.

Llanwarne



A

Dordrecht



B

Appendix 2 Llanwarne seasonal peak grass biomass data

GRAZ	AXIS1	AXIS2	RAIN	ACCUM	SOIL	PREV	BIOM	CAMP
26.2	-0.6125	-0.3050	475	0.0	53.1	*	10.00	L186/87
40.0	-0.2113	-0.4113	475	0.0	80.0	*	10.90	M186/87
52.5	-0.1606	-0.4295	475	0.0	80.0	*	9.25	H186/87
0.0	-0.3886	-0.3297	475	0.0	40.7	*	10.51	L286/87
0.0	-0.9260	0.0581	475	0.0	61.3	*	11.40	M286/87
0.0	-0.4463	-0.7672	475	0.0	47.5	*	11.79	H286/87
45.9	-0.5239	-0.3310	588	25.9	53.1	10.00	10.65	L187/88
70.0	-0.1843	-0.2650	588	39.5	80.0	10.90	9.61	M187/88
65.6	-0.2342	-0.4541	588	51.9	80.0	9.25	8.45	H187/88
0.0	-0.5810	-0.2744	588	34.9	40.7	10.51	10.12	L287/88
0.0	-0.6687	-0.3164	588	53.3	61.3	11.40	9.38	M287/88
0.0	-0.5671	-0.9075	588	70.0	47.5	11.79	8.74	H287/88
26.2	-0.4353	-0.3570	711	84.9	53.1	10.65	12.60	L188/89
40.0	-0.1572	-0.1186	711	129.5	80.0	9.61	12.25	M188/89
52.5	-0.3077	-0.4786	711	170.0	80.0	8.45	10.11	H188/89
13.1	-0.7733	-0.2190	711	90.2	40.7	10.12	9.50	L288/89
10.0	-0.4114	-0.6909	711	137.6	61.3	9.38	7.26	M288/89
13.1	-0.6879	-1.0477	711	180.6	47.5	8.74	6.98	H288/89
32.8	-0.3496	-0.1626	784	144.5	53.1	12.60	9.48	L189/90
50.0	-0.2169	-0.2148	784	220.4	80.0	12.25	10.78	M189/90
52.5	-0.2853	-0.1781	784	289.4	80.0	10.11	8.17	H189/90
13.4	-0.2972	0.0475	784	144.5	40.7	9.50	9.34	L289/90
20.5	-0.4375	-0.4350	784	220.4	61.3	7.26	8.16	M289/90
26.9	-0.4086	-0.3985	784	289.4	47.5	6.98	7.52	H289/90
13.4	-0.2639	0.0318	705	205.9	53.1	9.48	14.76	L190/91
20.5	-0.2765	-0.3110	705	314.2	80.0	10.78	12.70	M190/91
39.4	-0.2628	0.1224	705	412.5	80.0	8.17	11.44	H190/91
23.4	0.1880	0.3139	705	196.9	40.7	9.34	11.86	L290/91
35.7	-0.4636	-0.1791	705	300.4	61.3	8.16	11.88	M290/91
46.9	-0.1292	0.2507	705	394.4	47.5	7.52	10.40	H290/91
0.0	0.3279	0.1328	264	255.2	53.1	14.76	7.88	L191/92
0.0	0.2616	0.0730	264	389.4	80.0	12.70	8.96	M191/92
0.0	0.2886	0.2549	264	511.3	80.0	11.44	8.00	H191/92
32.4	0.4515	0.1606	264	261.5	40.7	11.86	6.24	L291/92
49.5	0.2708	0.0335	264	398.9	61.3	11.88	4.58	M291/92
65.0	0.6041	0.2151	264	523.8	47.5	10.40	4.68	H291/92
32.8	0.3279	0.1328	455	332.3	53.1	7.88	8.20	L192/93
50.0	0.2616	0.0730	455	506.9	80.0	8.96	7.14	M192/93
65.6	0.2886	0.2549	455	665.6	80.0	8.00	7.22	H192/93
13.1	0.4515	0.1606	455	298.6	40.7	6.24	11.30	L292/93
0.0	0.2708	0.0335	455	455.5	61.3	4.58	8.54	M292/93
26.3	0.6041	0.2151	455	598.1	47.5	4.68	7.12	H292/93
33.1	0.9196	0.2337	589	412.8	53.1	8.20	11.50	L193/94
50.5	0.7996	0.4569	589	629.7	80.0	7.14	10.16	M193/94
66.3	0.8399	0.3874	589	828.1	80.0	7.22	8.72	H193/94
0.0	0.7149	0.0072	589	332.0	40.7	11.30	14.34	L293/94
0.0	1.0051	0.2460	589	506.5	61.3	8.54	14.00	M293/94
0.0	1.3373	0.1794	589	665.0	47.5	7.12	11.83	H293/94
30.0	0.3963	-0.1992	379	452.1	53.1	11.50	9.22	L194/95
45.7	0.3645	-0.1563	379	689.7	80.0	10.16	6.08	M194/95
60.0	0.5403	-0.1428	379	905.6	80.0	8.72	4.96	H194/95
0.0	0.5055	-0.0921	379	406.5	40.7	14.34	11.38	L294/95
0.0	0.6218	0.0296	379	620.2	61.3	14.00	10.40	M294/95
0.0	0.8253	-0.0266	379	814.4	47.5	11.83	8.72	H294/95
0.0	0.0009	0.6034	680	517.6	53.1	9.22	13.64	L195/96
0.0	-0.5276	0.5458	680	789.7	80.0	6.08	13.09	M195/96
0.0	-0.6636	0.5448	680	1036.9	80.0	4.96	9.47	H195/96
0.0	-0.2503	0.3252	680	454.9	40.7	11.38	12.12	L195/96
0.0	0.1539	0.5358	680	694.0	61.3	10.40	12.97	M295/96
0.0	-0.8953	1.4293	680	911.3	47.5	8.72	9.74	H295/96

Appendix 3 Dordrecht seasonal peak grass biomass data

GRAZ	AXIS1	AXIS2	RAIN	ACCUM	SOIL	PREV	POS	BIOM	CAMP
27.2	-0.2032	-0.5250	511	0.0	45.9	*	u	7.53	L186/87
34.5	-0.3951	0.8824	511	0.0	58.3	*	u	6.31	M186/87
46.1	0.3271	1.5459	511	0.0	62.9	*	u	5.33	H186/87
0.0	-0.5946	-0.4089	511	0.0	56.2	*	l	8.22	L286/87
0.0	-0.8474	-0.2652	511	0.0	47.7	*	l	8.79	M286/87
28.9	-0.0372	0.1126	511	0.0	47.1	*	l	7.06	H286/87
48.2	-0.3494	-0.6956	596	27.2	45.9	7.53	u	8.71	L187/88
43.7	-0.3747	0.2176	596	34.5	58.3	6.31	u	5.85	M187/88
12.2	-0.0987	0.0624	596	46.1	62.9	5.33	u	5.03	H187/88
20.7	-0.4553	-0.4974	596	36.7	56.2	8.22	l	9.58	L287/88
26.2	-0.5703	-0.0026	596	46.6	47.7	8.79	l	8.13	M287/88
0.0	-0.1454	-0.0961	596	62.3	47.1	7.06	l	8.24	H287/88
6.9	-0.4964	-0.8661	720	89.2	45.9	8.71	u	8.46	L188/89
8.7	-0.3543	-0.4472	720	113.2	58.3	5.85	u	6.34	M188/89
11.7	-0.5244	-1.4212	720	151.2	62.9	5.03	u	6.56	H188/89
20.3	-0.3160	-0.5858	720	94.8	56.2	9.58	l	8.11	L288/89
69.9	-0.2932	0.2600	720	120.2	47.7	8.13	l	9.86	M288/89
93.4	-0.2535	-0.3048	720	160.7	47.1	8.24	l	7.98	H288/89
6.9	-0.3097	-0.0490	882	141.5	45.9	8.46	u	9.36	L189/90
17.5	-0.3392	-0.3358	882	179.5	58.3	6.34	u	7.88	M189/90
0.0	-0.3022	-0.9664	882	239.9	62.9	6.56	u	7.40	H189/90
34.4	-0.1779	-0.1800	882	162.2	56.2	8.11	l	9.00	L289/90
52.8	-0.1084	0.0900	882	205.7	47.7	9.86	l	7.08	M289/90
70.6	-0.1665	-0.2711	882	274.9	47.1	7.98	l	10.32	H289/90
13.8	-0.1229	0.7682	808	192.5	45.9	9.36	u	11.44	L190/91
17.5	-0.3241	-0.2244	808	244.2	58.3	7.88	u	10.86	M190/91
23.4	-0.0800	-0.5116	808	326.4	62.9	7.40	u	9.62	H190/91
24.6	-0.0397	0.2259	808	230.9	56.2	9.00	l	12.78	L290/91
31.2	0.0765	-0.0800	808	292.9	47.7	7.08	l	10.90	M290/91
41.7	-0.0795	-0.2374	808	391.4	47.1	10.32	l	12.60	H290/91
0.0	0.1923	0.3700	257	254.5	45.9	11.44	u	8.34	L191/92
0.0	0.1776	-0.3825	257	322.8	58.3	10.86	u	5.58	M191/92
0.0	0.4284	-0.4462	257	431.5	62.9	9.62	u	4.48	H191/92
34.4	0.5809	0.1404	257	288.6	56.2	12.78	l	6.90	L291/92
43.7	0.6051	-0.3406	257	366.1	47.7	10.90	l	6.18	M291/92
58.4	0.5099	-0.2822	257	489.3	47.1	12.60	l	5.98	H291/92
41.7	0.1923	0.3700	504	274.2	45.9	8.34	u	9.38	L192/93
26.7	0.1776	-0.3825	504	347.8	58.3	5.58	u	5.68	M192/93
70.7	0.4284	-0.4462	504	464.8	62.9	4.48	u	4.00	H192/93
13.8	0.5809	0.1404	504	388.7	56.2	6.90	l	10.44	L292/93
17.5	0.6051	-0.3406	504	493.0	47.7	6.18	l	8.44	M292/93
23.4	0.5099	-0.2822	504	658.9	47.1	5.98	l	5.94	H292/93
27.9	0.5074	-0.0283	667	340.6	45.9	9.38	u	11.04	L193/94
35.4	0.6792	-0.5406	667	432.0	58.3	5.68	u	6.05	M193/94
47.3	0.9368	-0.3808	667	577.4	62.9	4.00	u	5.32	H193/94
0.0	1.2015	0.0548	667	431.3	56.2	10.44	l	12.52	L293/94
0.0	1.1336	-0.6011	667	547.0	47.7	8.44	l	11.02	M293/94
0.0	1.0993	-0.3269	667	731.1	47.1	5.94	l	10.70	H293/94
13.9	0.3690	-0.2419	418	421.2	45.9	11.04	u	9.30	L194/95
8.9	0.7085	-0.2747	418	534.1	58.3	6.05	u	4.88	M194/95
29.5	0.4425	-0.0757	418	713.9	62.9	5.32	u	3.80	H194/95
13.9	0.1076	-0.1179	418	470.5	56.2	12.52	l	8.72	L294/95
17.7	0.0761	-0.0311	418	596.8	47.7	11.02	l	7.82	M294/95
23.6	-0.0642	0.3095	418	797.6	47.1	10.70	l	8.30	H294/95
27.6	-0.0525	0.9159	687	481.0	58.3	9.30	u	8.77	L195/96
52.0	-0.3136	0.6078	687	610.1	58.3	4.88	u	5.08	M195/96
69.5	-1.1135	0.7975	687	815.4	62.9	3.80	u	4.22	H195/96
0.0	-0.3556	0.8522	687	530.4	56.2	8.72	l	14.47	L295/96
0.0	-0.1516	0.7582	687	672.7	47.7	7.82	l	12.46	M295/96
0.0	-0.6774	0.4521	687	899.1	47.1	8.30	l	15.11	H295/96

KEY TO VARIABLE HEADINGS (SEASONAL PEAK GRASS BIOMASS DATA)

GRAZ = Number of grazing days ha^{-1} from initiation of grass growth until attainment of peak grass biomass.

AXIS1 & AXIS2 = Site scores from correspondence analysis of compositional data.

RAIN = Rainfall in season in which corresponding observations were made.

ACCUM = Accumulated grazing days ha^{-1}, calculated as sum of grazing days ha^{-1} from start of trial up to season in which corresponding observations were made.

SOIL = Average soil depth of camp.

PREV = Previous years seasonal peak grass biomass.

POS = Up-slope camps or Down-slope camps

BIOM = Seasonal peak grass biomass (represented by disc meter height in cm).

CAMP = Treatment camp and relevant year.

Appendix 4 Cattle gain animal^{-1} data at Llanwarne

GAIN	SR	BIOM	ACCUM	RAIN	SEASON
182	0.156	10.3	30.4	475	1986/87
173	0.238	11.2	46.4	475	1986/87
153	0.313	10.5	61	475	1986/87
220	0.156	10.4	87.6	588	1987/88
212	0.238	9.5	133.6	588	1987/88
206	0.313	8.6	175.3	588	1987/88
225	0.156	11.1	144.5	711	1988/89
207	0.238	9.8	220.4	711	1988/89
199	0.313	8.5	289.4	711	1988/89
172	0.156	9.4	201.4	784	1989/90
163	0.238	9.5	307.3	784	1989/90
133	0.313	7.8	403.5	784	1989/90
221	0.156	13.3	258.4	705	1990/91
220	0.238	12.3	394.2	705	1990/91
217	0.313	10.9	517.6	705	1990/91
113	0.156	7.1	315.5	264	1991/92
82	0.238	6.8	481.2	264	1991/92
102	0.313	6.3	631.9	264	1991/92
179	0.156	9.8	372.4	455	1992/93
180	0.238	7.8	568.1	455	1992/93
152	0.313	7.2	746.6	455	1992/93
198	0.156	12.9	429.3	589	1993/94
204	0.238	12.1	655	589	1993/94
198	0.313	10.3	860	589	1993/94
158	0.156	10.3	486.3	379	1994/95
167	0.238	8.2	741.9	379	1994/95
131	0.313	6.8	974.1	379	1994/95

Appendix 5 Cattle gain animal^{-1} data at Dordrecht

GAIN	SR	BIOM	ACCUM	RAIN	SEASON
170	0.164	7.9	32	511	1986/87
149	0.208	7.6	40.6	511	1986/87
148	0.278	6.2	54.2	511	1986/87
218	0.164	9.1	92	596	1987/88
225	0.208	7	116.7	596	1987/88
206	0.278	6.6	156	596	1987/88
211	0.164	8.3	151.9	720	1988/89
205	0.208	8.1	192.6	720	1988/89
194	0.278	7.3	257.4	720	1988/89
201	0.164	9.2	211.7	882	1989/90
170	0.208	7.5	268.6	882	1989/90
159	0.278	8.9	358.9	882	1989/90
212	0.164	12.1	271.6	808	1990/91
211	0.208	10.9	344.5	808	1990/91
215	0.278	11.1	460.4	808	1990/91
151	0.164	7.6	331.5	257	1991/92
103	0.208	5.9	420.4	257	1991/92
76	0.278	5.2	561.9	257	1991/92
241	0.164	9.9	386	504	1992/93
155	0.208	7.1	489.5	504	1992/93
167	0.278	5	654.3	504	1992/93
225	0.164	11.8	445.9	667	1993/94
194	0.208	8.5	565.5	667	1993/94
179	0.278	8	755.8	667	1993/94
220	0.164	9	505.7	418	1994/95
195	0.208	6.4	641.4	418	1994/95
190	0.278	6.1	857.3	418	1994/95

Appendix 6 Cattle gain ha^{-1} data at Llanwarne

GAIN/HA	SR	BIOM	ACCUM	RAIN	SEASON
28.4	0.156	10.3	30.4	475	1986/87
40.4	0.238	11.2	46.4	475	1986/87
47.3	0.313	10.5	61	475	1986/87
34.3	0.156	10.4	87.6	588	1987/88
49.6	0.238	9.5	133.6	588	1987/88
63.5	0.313	8.6	175.3	588	1987/88
35	0.156	11.1	144.5	711	1988/89
48.4	0.238	9.8	220.4	711	1988/89
61.3	0.313	8.5	289.4	711	1988/89
26.8	0.156	9.4	201.4	784	1989/90
38	0.238	9.5	307.3	784	1989/90
40.9	0.313	7.8	403.5	784	1989/90
34.5	0.156	13.3	258.4	705	1990/91
51.6	0.238	12.3	394.2	705	1990/91
66.8	0.313	10.9	517.6	705	1990/91
17.6	0.156	7.1	315.5	264	1991/92
19.2	0.238	6.8	481.2	264	1991/92
31.5	0.313	6.3	631.9	264	1991/92
27.8	0.156	9.8	372.4	455	1992/93
42	0.238	7.8	568.1	455	1992/93
46.8	0.313	7.2	746.6	455	1992/93
30.8	0.156	12.9	429.3	589	1993/94
47.6	0.238	12.1	655	589	1993/94
61.1	0.313	10.3	860	589	1993/94
25.2	0.156	10.3	486.3	379	1994/95
39.4	0.238	8.2	741.9	379	1994/95
41.5	0.313	6.8	974.1	379	1994/95

Appendix 7 Cattle gain ha^{-1} data at Dordrecht

GAIN/HA	SR	BIOM	ACCUM	RAIN	SEASON
28	0.164	7.9	32	511	1986/87
31.3	0.208	7.6	40.6	511	1986/87
40.9	0.278	6.2	54.2	511	1986/87
35.7	0.164	9.1	92	596	1987/88
47.2	0.208	7	116.7	596	1987/88
57.1	0.278	6.6	156	596	1987/88
34.6	0.164	8.3	151.9	720	1988/89
43	0.208	8.1	192.6	720	1988/89
53.6	0.278	7.3	257.4	720	1988/89
32.9	0.164	9.2	211.7	882	1989/90
35.7	0.208	7.5	268.6	882	1989/90
44.1	0.278	8.9	358.9	882	1989/90
34.7	0.164	12.1	271.6	808	1990/91
44.2	0.208	10.9	344.5	808	1990/91
59.5	0.278	11.1	460.4	808	1990/91
24.8	0.164	7.6	331.5	257	1991/92
21.7	0.208	5.9	420.4	257	1991/92
21	0.278	5.2	561.9	257	1991/92
39.5	0.164	9.9	386	504	1992/93
32.4	0.208	7.1	489.5	504	1992/93
46	0.278	5	654.3	504	1992/93
36.7	0.164	11.8	445.9	667	1993/94
40.6	0.208	8.5	565.5	667	1993/94
49.3	0.278	8	755.8	667	1993/94
36	0.164	9	505.7	418	1994/95
41.1	0.208	6.4	641.4	418	1994/95
52.6	0.278	6.1	857.3	418	1994/95

KEY TO VARIABLE HEADINGS FOR CATTLE PERFORMANCE DATA

RAIN = Rainfall for relevant season.

ACCUM = Accumulated grazing days ha^{-1}, calculated as sum of grazing days ha^{-1} from start of trial up to season in which corresponding observations were made.

BIOM = Seasonal peak grass biomass (represented by disc meter height in cm).

SR = Stocking rate

Season = Season in which corresponding observations were made.

Appendix 8 Compositional data (nearest plant method)

LLANWARNE 1986

	L1	M1	H1	L2	M2	H2
ABA	0.3	0.3	0.0	0.3	1.0	0.3
BIN	0.3	0.3	2.7	4.0	0.3	6.7
CCI	1.7	2.3	0.3	0.3	0.7	0.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	5.0	2.7	0.0	0.0	0.0	0.3
DAR	24.7	25.3	23.0	17.7	15.3	22.3
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	1.0	1.7	1.7	0.3	0.7	1.3
ESP	1.0	0.0	0.3	1.0	0.0	0.7
EPA	2.3	1.0	1.0	1.7	2.0	3.3
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	1.0	0.7	1.0	0.3	0.3	0.3
PAN	46.3	30.7	42.6	36.4	38.0	37.7
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	0.0	0.0	0.0	0.0	0.0	0.0
SIO	1.0	8.3	6.0	9.3	6.0	10.3
TTR	6.0	5.0	6.7	5.3	4.7	2.0
TRA	0.7	1.0	1.0	0.0	2.0	2.3
UMO	1.3	17.7	8.6	12.0	5.3	3.7
FOR	7.3	3.0	5.0	10.0	17.7	8.7
SED	0.0	0.0	0.0	0.0	0.0	0.0
UNA	0.0	0.0	0.0	1.3	6.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

DORDRECHT 1986

	L1	M1	H1	L2	M2	H2
ABA	0.3	0.0	1.7	0.0	0.0	0.0
BIN	1.0	0.3	0.3	0.7	0.3	1.0
CCI	0.0	0.3	0.0	0.0	0.0	0.0
CEX	0.0	0.3	0.0	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	0.0	0.0	1.3	0.3	0.3	2.7
DAR	24.0	7.3	10.3	12.0	2.0	2.7
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	0.0	0.0	2.0	6.7	15.3	9.7
ESP	4.7	1.0	4.3	0.3	0.3	0.7
EPA	3.3	0.0	0.3	1.0	1.7	1.3
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	0.0	0.0	0.3	0.0	0.0	0.0
PAN	34.7	28.4	11.6	31.7	26.0	38.7
MRE	0.0	0.0	0.3	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	0.0	9.7	35.0	0.0	0.0	5.7
SIO	11.0	6.0	4.0	22.7	15.3	0.7
TTR	0.3	0.7	3.3	1.7	11.0	8.3
TRA	2.3	1.0	2.3	1.7	0.0	2.3
UMO	12.3	14.3	9.0	7.3	5.0	14.7
FOR	5.7	25.7	10.0	13.0	20.7	11.7
SED	0.0	0.0	0.0	0.0	0.0	0.0
UNA	0.3	5.0	3.7	1.0	2.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

LLANWARNE 1988

	L1	M1	H1	L2	M2	H2
ABA	0.3	0.3	1.0	1.3	1.7	0.3
BIN	0.7	2.3	2.3	8.3	2.3	2.3
CCI	1.0	2.3	0.0	0.0	0.3	1.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	0.0	0.0	0.0	0.0	0.0	0.0
DAR	22.0	15.3	25.0	13.0	17.7	34.0
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	2.7	2.0	3.3	6.0	1.3	1.7
ESP	1.0	0.0	1.3	0.7	0.0	0.3
EPA	2.3	0.7	0.3	3.7	0.7	4.7
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	1.0	0.3	0.7	1.3	0.0	0.0
PAN	51.3	43.7	30.0	28.3	42.2	35.4
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	0.7	2.0	2.7	0.0	0.3	0.0
SIO	1.7	7.3	13.3	6.0	15.7	5.0
TTR	3.7	9.0	4.3	11.0	2.7	3.7
TRA	0.0	0.0	0.0	0.0	1.7	0.0
UMO	4.0	9.7	10.3	3.7	6.0	4.7
FOR	7.3	5.0	5.0	12.7	7.0	7.0
SED	0.0	0.0	0.0	0.0	0.0	0.0
UNA	0.3	0.0	0.3	4.0	0.3	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

DORDRECHT 1988

	L1	M1	H1	L2	M2	H2
ABA	0.7	0.0	2.0	0.0	2.0	0.7
BIN	0.3	1.3	0.0	0.3	0.0	0.7
CCI	0.0	0.0	0.0	0.0	0.0	0.0
CEX	0.0	0.0	0.3	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	0.0	0.0	0.3	0.0	0.3	5.3
DAR	29.0	13.3	18.7	18.7	7.3	3.0
ECU	0.0	0.0	2.7	0.0	0.0	1.7
ESU	2.0	0.0	0.7	3.3	8.3	13.0
ESP	4.0	1.0	3.7	1.0	0.3	8.7
EPA	4.0	0.3	7.7	0.0	0.7	1.3
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	0.3	0.0	0.7	0.0	0.3	0.3
PAN	26.7	18.0	15.0	28.3	31.3	28.0
MRE	0.0	0.0	1.7	0.0	0.3	0.3
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	1.0	7.7	4.3	2.0	6.3	5.3
SIO	17.0	25.7	22.3	23.7	8.3	9.3
TTR	0.0	0.3	0.0	0.7	0.7	1.3
TRA	1.0	0.7	1.0	4.7	0.0	1.7
UMO	9.0	15.3	12.3	8.0	11.0	11.7
FOR	4.0	9.3	5.3	8.0	15.7	7.7
SED	0.0	0.0	0.3	0.0	0.0	0.0
UNA	1.0	7.0	1.0	1.3	7.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

LLANWARNE 1990

	L1	M1	H1	L2	M2	H2
ABA	1.3	0.3	3.0	5.3	2.0	1.0
BIN	1.3	1.7	2.0	3.0	4.0	11.3
CCI	4.3	3.7	0.7	0.0	1.3	0.3
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	2.0	1.0	2.0	2.0	0.0	6.0
DER	4.0	0.7	2.0	0.7	2.0	0.3
DAR	13.0	17.3	13.0	6.0	15.3	10.7
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	1.3	0.7	0.7	0.3	1.7	0.0
ESP	1.3	1.7	3.3	1.3	0.0	2.0
EPA	0.0	0.0	0.0	0.0	0.0	0.0
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	0.3	0.0	0.0	0.7	0.3	1.6
PAN	40.7	43.7	35.7	47.0	35.7	31.7
MRE	0.3	0.0	0.0	0.3	0.0	0.0
SFI	0.0	0.0	1.3	0.7	0.3	0.0
SNI	0.0	0.0	0.3	0.0	0.0	1.3
SIO	1.7	8.0	7.3	5.0	5.3	5.0
TTR	15.0	13.3	11.7	5.3	10.3	4.3
TRA	0.0	0.0	0.0	1.0	0.3	0.3
UMO	8.7	5.3	8.3	11.3	10.7	12.3
FOR	3.3	2.0	5.3	8.3	7.7	6.3
SED	1.0	0.3	0.3	0.7	0.3	0.7
UNA	0.3	0.3	3.0	1.0	2.7	4.7
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

DORDRECHT 1990

L1	M1	H1	L2	M2	H2
0.3	0.3	1.3	0.7	2.3	2.7
1.0	1.3	6.7	1.7	2.3	1.7
1.0	0.0	0.0	0.3	0.3	0.0
1.0	0.0	1.3	0.3	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
6.3	0.0	0.0	3.3	0.0	0.7
3.0	17.7	12.3	14.0	5.0	1.3
0.0	0.0	0.0	1.0	0.3	0.0
4.3	1.7	5.0	1.7	1.7	6.7
0.0	1.7	7.0	1.0	15.3	17.3
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.7	0.0	1.7	2.0	0.7	0.0
50.4	38.6	24.3	40.6	37.7	47.7
0.0	0.0	1.7	0.0	0.0	0.3
4.0	0.3	0.7	2.0	2.7	0.3
0.0	2.0	2.7	2.0	2.0	0.3
0.7	5.3	6.3	2.7	4.7	0.0
13.3	1.3	11.3	5.3	0.7	2.7
0.0	0.0	0.0	0.0	1.3	0.0
5.3	11.3	13.0	12.7	10.0	9.3
8.7	8.7	3.0	8.3	7.7	6.3
0.0	0.7	1.0	0.0	0.0	0.3
0.0	9.0	0.7	0.3	5.3	2.3
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0

LLANWARNE 1993

	L1	M1	H1	L2	M2	H2
ABA	2.4	1.7	3.0	3.0	4.0	8.0
BIN	2.7	2.4	3.7	3.0	1.7	6.4
CCI	1.7	2.7	0.7	0.4	0.7	1.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.7	1.4	0.0	0.7	0.7
DER	0.4	0.0	1.4	0.0	0.7	0.4
DAR	5.0	6.0	4.4	6.0	3.4	4.0
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	0.7	1.7	1.4	0.7	4.0	0.7
ESP	0.0	0.0	0.0	0.0	0.0	0.0
EPA	0.0	0.0	0.0	0.4	0.4	0.0
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	1.4	2.0	0.4	1.7	1.4	1.0
PAN	44.1	48.1	53.4	58.8	48.0	36.3
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	2.3	5.0	4.0	2.4	7.7	3.7
SIO	1.7	1.4	2.7	2.7	1.7	3.4
TTR	1.3	2.3	3.0	5.4	2.0	0.7
TRA	4.3	2.0	1.7	1.7	9.4	8.7
UMO	30.0	23.4	19.1	14.1	16.0	24.5
FOR	1.0	1.0	0.4	0.4	0.0	0.0
SED	0.0	0.0	0.0	0.0	0.0	0.0
UNA	0.0	0.0	0.0	0.0	0.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

DORDRECHT 1993

L1	M1	H1	L2	M2	H2
1.7	2.3	2.0	6.3	6.0	4.3
2.0	2.7	0.0	0.0	3.0	1.3
0.3	0.3	0.0	0.0	0.0	0.3
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.7	0.3
0.7	0.7	0.0	0.0	0.7	0.3
9.7	8.3	10.0	2.0	8.0	4.3
0.0	0.0	0.0	0.0	0.0	0.0
1.3	3.3	0.7	0.3	2.3	0.7
0.0	0.0	0.0	3.7	0.3	0.7
1.7	0.3	0.3	0.0	0.3	0.0
0.0	0.0	0.3	1.0	0.3	0.3
4.0	0.3	0.0	0.3	2.0	0.7
46.4	53.7	45.4	38.3	18.4	49.7
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
3.0	1.3	2.7	5.0	5.7	2.0
9.0	3.7	6.7	13.3	17.7	2.3
5.0	6.0	1.3	1.0	3.7	1.0
1.3	0.7	7.0	10.7	10.7	5.6
13.7	16.3	23.0	17.7	20.3	26.0
0.3	0.3	0.7	0.3	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0

LLANWARNE 1994

	L1	M1	H1	L2	M2	H2
ABA	3.3	1.6	2.3	3.7	5.3	7.3
BIN	1.0	0.7	1.0	4.6	2.3	2.3
CCI	1.0	3.0	0.7	0.3	1.0	0.3
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	0.0	0.0	0.0	0.0	0.0	0.0
DAR	9.6	8.0	14.0	7.0	2.0	7.6
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	1.0	1.0	1.3	3.0	0.7	3.3
ESP	0.0	0.0	0.0	0.0	0.0	0.0
EPA	0.7	0.3	0.3	1.3	1.0	0.3
FAF	0.0	0.0	0.0	0.0	0.0	0.0
HCO	0.3	0.3	0.3	1.0	0.7	0.0
PAN	53.2	50.0	49.9	67.9	58.6	46.6
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	0.0	0.3	0.3	0.7	0.0	1.3
SIO	6.3	11.7	5.3	0.0	2.3	2.7
TTR	2.3	2.3	1.0	2.3	0.0	1.3
TRA	0.0	0.3	0.3	0.0	0.0	1.3
UMO	20.7	18.7	22.3	6.0	23.0	24.0
FOR	1.0	1.0	1.0	1.7	3.6	1.0
SED	0.0	0.0	0.0	0.0	0.0	0.0
UNA	0.0	0.0	0.0	0.0	0.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

DORDRECHT 1994

	L1	M1	H1	L2	M2	H2
ABA	1.6	4.0	0.3	0.3	1.3	3.8
BIN	2.6	0.6	0.0	2.6	1.0	2.1
CCI	0.3	0.0	0.0	1.6	1.6	0.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.0	0.0	0.0	0.0	0.0
DER	0.0	0.0	0.0	0.0	0.0	1.7
DAR	14.6	5.0	14.6	10.3	1.0	0.0
ECU	1.3	0.0	1.0	0.0	0.0	0.0
ESU	4.3	2.0	0.3	6.0	0.3	6.9
ESP	0.0	0.3	0.0	3.0	16.0	11.1
EPA	2.6	0.0	0.0	0.6	0.6	0.7
FAF	0.3	0.6	0.0	0.0	0.0	0.0
HCO	0.6	0.0	0.0	0.3	0.0	0.7
PAN	39.3	70.6	20.9	44.9	27.9	32.5
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.0	0.0	0.0	0.0	0.0
SNI	0.6	1.6	6.0	1.0	1.3	3.5
SIO	4.0	3.3	9.3	3.6	9.3	0.3
TTR	5.0	0.0	0.0	4.6	0.6	0.7
TRA	0.3	0.6	1.3	0.3	2.6	0.0
UMO	21.3	6.6	38.0	12.3	18.3	19.4
FOR	0.6	4.0	8.0	5.3	16.0	15.9
SED	0.0	0.3	0.0	0.0	0.0	0.0
UNA	0.0	0.0	0.0	0.0	0.0	0.0
DAU	0.0	0.0	0.0	0.0	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

LLANWARNE 1996

	L1	M1	H1	L2	M2	H2
ABA	2.7	3.3	1.7	0.7	3.7	1.3
BIN	0.7	0.7	1.0	5.3	1.7	1.7
CCI	0.0	0.0	0.0	0.0	0.0	0.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.7	0.3	2.0	1.7	2.0	1.0
DER	0.0	0.0	0.0	0.0	0.3	4.3
DAR	8.0	14.7	17.7	11.0	2.7	4.0
ECU	0.3	0.3	0.3	0.0	0.3	0.0
ESU	0.3	2.0	1.7	2.0	1.0	0.3
ESP	0.3	1.0	0.0	0.7	0.0	0.0
EPA	0.0	0.0	0.0	0.0	0.0	0.0
FAF	0.0	0.0	0.3	0.0	0.0	0.0
HCO	0.0	0.7	0.7	0.7	1.3	0.0
PAN	52.7	29.3	30.0	37.7	42.7	22.7
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.0	0.3	0.0	0.0	0.0	0.3
SNI	0.7	0.0	0.7	0.0	0.0	0.3
SIO	0.3	8.3	7.7	2.3	2.7	4.0
TTR	1.0	1.7	1.0	9.0	2.0	1.7
TRA	1.7	2.3	1.0	1.3	2.3	1.3
UMO	14.7	12.7	10.0	11.7	21.7	19.0
FOR	14.3	19.7	20.3	13.7	10.0	35.3
SED	0.7	1.0	0.3	0.3	2.0	0.3
UNA	0.3	0.0	3.0	0.7	3.0	1.7
DAU	0.3	1.7	0.7	1.3	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.7	0.7
TGR	0.0	0.0	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.0	0.0	0.0

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	L1	M1	H1	L2	M2	H2
ABA	2.3	1.0	2.3	1.0	5.0	3.0
BIN	1.3	0.0	0.0	1.3	0.0	0.3
CCI	0.0	0.0	0.0	0.0	0.0	0.0
CEX	0.0	0.0	0.0	0.0	0.0	0.0
CVI	0.0	0.0	1.0	1.3	0.3	0.0
DER	2.0	0.0	1.0	0.3	0.0	0.0
DAR	6.3	10.3	9.7	7.0	2.7	2.7
ECU	0.0	0.0	0.0	0.0	0.0	0.0
ESU	2.3	1.3	1.3	2.0	0.7	1.3
ESP	2.0	0.3	0.0	0.0	0.7	12.3
EPA	0.0	0.0	0.0	0.0	0.0	0.0
FAF	0.0	0.0	0.0	0.0	0.3	0.0
HCO	2.0	0.3	0.3	0.0	0.0	0.0
PAN	39.6	30.7	19.7	37.3	41.7	41.6
MRE	0.0	0.0	0.0	0.0	0.0	0.0
SFI	0.3	0.7	0.0	0.0	0.3	0.3
SNI	1.3	3.7	4.7	1.0	3.3	1.0
SIO	3.7	3.0	14.7	4.3	3.7	2.0
TTR	3.3	0.0	0.0	1.7	0.3	0.7
TRA	1.7	0.7	0.7	1.0	1.7	0.0
UMO	13.3	19.3	7.3	15.3	6.0	6.3
FOR	17.3	24.0	32.0	21.3	23.3	26.3
SED	0.7	0.7	0.7	1.0	0.0	0.0
UNA	0.0	3.7	4.7	2.0	4.7	0.3
DAU	0.0	0.0	0.0	0.3	0.0	0.0
AAD	0.0	0.0	0.0	0.0	0.0	0.0
TGR	0.3	0.3	0.0	0.0	0.0	0.0
ECE	0.0	0.0	0.0	0.3	0.0	0.3

Key to species:

AAD: *Aristida adscensionis*
ABA: *Aristida congesta*
BIN: *Bothriochloa insculpta*
CEX: *Cymbopogon excavatus*
CCI: *Cenchrus ciliaris*
CVI: *Chloris virgata*
DAU: *Dactyloctenium australe*
DAR: *Digitaria argyrograpta*
DER: *Digitaria eriantha*
ECE: *Enneapogon cenchroides*
ECH: *Eragrostis chloromelas*
ECU: *Eragrostis curvula*
ESU: *Eragrostis superba*
ESP: *Eragrostis sp*
EPA: *Eustachys paspaloides*
FOR: Forbs
FAF: *Fingerhuthia africana*
HCO: *Heteropogon contortus*
MRE: *Melinis repens*
SFI: *Sporobolus fimbriatus*
SIO: *Sporobolus ioclados*
SNI: *Sporobolus nitens*
TGR: *Trichoneura grandiglumis*
TRA: *Tragus racemosus*
TTR: *Themeda triandra*
UMO: *Urochloa mosambicensis*
UPA: *Urochloa panicoides*
UNA: Unallocated bare ground

Appendix 9 Fenceline contrast data from the H1/l2 fenceline and the L2/H2 fenceline

SOIL BULK DENSITY gms/cm3

H1	L2	L2	H2
1.5	1.54	1.51	1.63
1.59	1.63	1.48	1.49
1.5	1.37	1.53	1.62
1.54	1.47	1.65	1.62
1.5	1.41	1.46	1.59
1.62	1.6	1.54	1.67
1.63	1.27	1.64	1.59
1.51	1.31	1.36	1.37
1.58	1.37	1.5	1.53
1.52	1.47	1.5	1.56
1.56	1.46	1.67	1.58
1.54	1.48	1.59	1.5
1.59	1.53	1.52	1.45
1.64	1.39	1.57	1.47
1.39	1.57	1.51	1.51

ROOT MASS gms/1089.5cm

H1	L2	L2	H2
4.72	3.27	4.04	3.22
4.15	2.59	4.12	4.17
4.9	5.25	3	2.67
3.45	5.15	1.56	3.61
3.98	4.56	4.86	3
3.33	2.24	4.4	3.61
2.53	2.56	2.93	4.42
2.27	4.22	5.72	4.63
2.67	4.89	3.63	4.02
4.49	2.89	2.31	2.86
3.24	3.3	6.36	3.72
4.75	2.29	5.99	2.56
3.59	2.73	3.75	3.3
3.71	2.83	3.39	4.2
		3.59	4.4

GRASS BIOMASS gms/0.25m

H1	L2	L2	H2
36.82	69.35	61.45	57.67
18.67	74.05	144.52	86.33
34.9	107.76	40.97	26.45
36.44	132.03	73.1	54.11
43.34	61.52	48.55	48.66
31.02	32.88	36.15	19.47
31.38	12.4	35.85	84.02
49.96	20.32	113.21	66.64
36.49	80.71	20.88	31.58
20.82	101.18	5.41	6.9
44.84	55.64	88.99	42
48.01	42.32	105.74	32.8
30.45	39.86	61.18	51.21
44.61	72.93	90.39	81.9
70.68	36.86	88.4	52.81

Appendix 9 cont

SOIL ORGANIC CARBON %

H1	L2	L2	H2
2.48	2.2	2.37	1.53
1.91	1.62	2.09	1.95
1.92	1.74	1.96	1.52
1.63	1.94	1.48	1.58
1.51	1.94	2.97	1.18
1.64	2.11	1.58	1.75
1.7	2.5	1.36	1.69
1.89	2.09	2.47	2.27
2.31	3.03	1.91	2.31
2.08	2.62	1.58	1.11
2.35	2.06	1.69	1.41
2.03	2.25	1.45	1.33
1.88	1.99	1.88	2.46
1.71	2.26	1.42	2.58
2.25	1.96	1.55	1.76

SOIL PHOSPHORUS AMBIC EXTRACTED mg/kg

H1	L2	L2	H2
13.87	14.18	12.44	7.56
12.83	12.94	9.74	8.29
12.44	13.77	8.09	7.05
11.82	9.08	9.43	9.02
11.81	12.44	14.2	6.95
12.13	19.51	8.81	7.05
11.52	11.41	11.51	10.99
33.22	12.84	11.3	10.99
13.26	13.26	10.67	11.3
33.22	13.88	11.3	11.5
10.5	11.31	11.81	8.6
10.59	11.32	10.78	11.3
9.99	10.6	10.88	10.88
9.28	10.8	10.78	12.13
10.8	12.54	8.81	8.5

SOIL PHOSPHORUS NAOH EXTRACTED mg/kg

H1	L2	L2	H2
46.52	41.2	37.04	29.07
23.28	35.19	33.64	31.68
25.65	35.38	33.24	35.34
37.02	31.84	32.4	34.68
31.28	25.18	31.77	25.45
37.95	20.99	30.97	32.5
34.8	36.38	29.44	31.54
46.52	27.94	30.97	36.21
55.95	59.9	33.82	38.76
44.24	70.54	40.96	35.05
40.32	48.05	31.62	32.59
36.51	41.38	27.92	40.59
36.04	38.99	30.87	31.54
34.61	33.18	29.64	30.49
35.37	35.08	30.32	39.43

Appendix 9 cont

SOIL PHOSPHORUS ORGANIC AMBIC EXTRACTED mg/kg

H1	L2	L2	H2
1.18	5.92	0	0.33
0	2.79	0.86	0.62
0.93	10.71	1.5	9.99
8.96	25.5	2.53	4.97
2.23	0	0	1.28
4.61	0.26	7.55	2.88
2.52	2.3	4.18	4.7
6.41	0	0	1.99
5.16	6.84	0	0
3.72	1.85	1.34	2.49
0.18	1.05	7.94	1.66
2.78	4.07	0	1.68
1.03	1.09	1.42	0
0	3.24	2.2	0
0.22	8.57	4.5	4.81

SOIL PHOSPHORUS ORGANIC NAOH EXTRACTED mg/kg

H1	L2	L2	H2
335.37	309.75	269.66	208.49
271.37	319.68	283.31	248.02
295.73	319.76	282.44	294.11
308.99	310.47	247.3	255.35
342.05	269.49	203.62	217.64
337.62	199.92	308.12	298.92
318.27	311.74	250.12	315.02
291.76	244.21	276.96	311.98
378.7	484.49	308.21	317.04
199.76	467.71	294.75	235.52
378.84	395.72	263.99	287.17
345.37	313.07	257.35	300.6
299.41	308.44	272.98	277.27
279.74	255.85	250.81	296.94
316.28	285.58	264.63	307.83

PLANT NITROGEN %

H1	L2	L2	H2
1.42	1.06	1.32	1.2
1.84	1.35	0.97	1.09
1.66	0.78	0.85	1.25
1.22	0.79	0.76	1.23
1.2	1.29	0.81	0.99
1.33	1.25	1.23	1.32
1.19	1.25	1.03	0.77
1.36	1.55	1.02	0.89
1.33	0.98	1	1.23
1.49	1.06	0.98	1.07
1.02	1.08	0.8	1.01
1.04	1.13	0.9	0.84
1.12	0.92	1.17	1.08
0.84	0.96	0.8	1.01
1.04	1.26	0.84	0.76

Appendix 9 cont

PLANT PHOSPHORUS %

H1	L2	L2	H2
0.52	0.37	0.34	0.58
0.54	0.44	0.35	0.45
0.44	0.41	0.24	0.57
0.46	0.2	0.26	0.44
0.39	0.33	0.22	0.31
0.46	0.4	0.25	0.32
0.54	0.36	0.36	0.28
0.5	0.44	0.21	0.33
0.46	0.33	0.39	0.37
0.84	0.4	0.3	0.53
0.29	0.4	0.34	0.29
0.29	0.32	0.27	0.63
0.29	0.24	0.34	0.3
0.31	0.25	0.26	0.24
0.24	0.36	0.21	0.29

NEUTRAL DETERGENT FIBRE %

H1	L2	L2	H2
24.3	31.25	30.65	30.05
34.4	34.9	28.8	27.75
33.7	33.85	31.1	31.3
32	29.8	32.9	34.18
34.7	31.25	32.35	26.9
30.95	26.2	29.75	33.9
32.4	32.35		
31.55	33.1		
30.95	33.2		
33.3	32.05		
33.2	28.6		

ACID DETERGENT FIBRE %

H1	L2	L2	H2
36.4	39.5	46.6	44
41.7	44.2	38	38.7
41.5	44.5	41.3	37.4
37.5	38.8	37.6	39.3
38.4	36.7	38.6	36.8
36.3	37.4	43.5	43.2
41.1	40.1	42.5	41.2
38.9	41.3	45.2	43.5
37.3	40.1		
40.4	45		
39.1	39.6		