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THE INFLUENCE OF RAINFALL AND GRAZING ON THE POPULATION AND COMPOSITIONAL RESPONSE OF SOME SAVANNA GRASSLANDS

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A thesis submitted to the Faculty of Science,
University of the Witwatersrand, Johannesburg,
in fulfilment of the requirements for the degree
of Doctor of Philosophy

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ABSTRACT

The study aimed to differentiate the effect of rainfall and grazing on the compositional change of savanna grasslands, and to explain responses in terms of the life history patterns of the main species. An extinction prone perennial grass under heavy grazing was identified as a palatable, obligate seed reproducer with low seed production and poor dispersal (e.g. *Themeda triandra* and *Heteropogon contortus*), which could become extinct if the established population and the seed bank were eliminated. *Aristida* species were expected to show the converse pattern. Grazing was manipulated for three or five years, and rainfall for one year, on a sandveld site, and two clay soil sites which supported the same species in different amounts, respectively.

The prevailing trend of increasing aridity had a greater effect on composition than the imposed treatments. On the sandveld, the community changed fundamentally because of extensive mortality of the initially dominant *Pogonarthria squarrosa*, an explosion of forbs, and a marked increase of *Digitaria eriantha* on the heavily grazed and of *Aristida* species on the lightly grazed treatment. The changes of *P. squarrosa* and of *Aristida* species were inconsistent with the increaser-decreaser classification of species. The composition of both clay soil sites showed small cumulative changes which are explained by the effects of mainly rainfall rather than grazing on the seed output, recruitment, growth and mortality of the main species, namely *T. triandra*, *Bothriochloa insculpta*, *H. contortus*, *Setaria incrassata* and *Aristida bipartita*, and patterns of grazing selectivity.

S. incrassata and *T. triandra* were the most and *B. insculpta* the least heavily grazed species. There was up to 50% turnover in basal area (70% in number) of all species except *S. incrassata* (<2%). Tuft size of all

species decreased due to recruitment and tuft fragmentation, and basal area decreased, but density increased. Recruitment varied with rainfall, and declined under heavy grazing for *B. insculpta*, *H. contortus* and *T. triandra*. Mortality increased with time and was restricted to smaller individuals. Grazing increased the mortality of *A. bipartita*, *D. eriantha*, *H. contortus* and *S. incrassata*.

Population growth rates, determined from matrix modelling, varied in accordance with rainfall, with little effect of grazing. The survival of the smallest size class was important for declining populations. The proportion remaining in a size class or increasing in size was important for stable or growing populations.

Seed output ha^{-1} ($X10^6$) ranged between <4 for *T. triandra* and *H. contortus* and >100 for *A. bipartita*. Intra-seasonal drought and grazing decreased seed production, but *A. bipartita* maintained high levels, which enabled it to successfully colonize available patches and increase its population under heavy grazing. *A. bipartita* (Thlavekisa) and *S. incrassata* (both sites) were well represented, and *T. triandra* and *H. contortus* poorly represented, in the seed bank, which ranged from 430 to 4320 seeds m^{-2}. Sustained grazing could eliminate the seed bank of *T. triandra* and *H. contortus*. Stoloniferous growth enabled *D. eriantha* to successfully colonize available patches and to increase its population under heavy grazing. *S. incrassata* and *T. triandra* had poor colonizing ability. *S. incrassata* was not protected from grazing by rhizomatous growth and was susceptible to low rainfall, but the longevity of clones may buffer the species.

Findings were consistent with a model of local extinction. The life history patterns and population dynamics of the main species can serve as a basis for the prediction of response of these communities to environmental variation.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted for any degree in any other University.

_____

_____ day of _____, 1991.

For Jo-Anne

PREFACE

The pursuit of a theory adequate to explain the change of vegetation with time has been one of the central themes of plant ecology this century. The discipline of range management owes its existence to this pursuit, but the development of both theoretical concepts and applied ecological thinking has not been without contention. There are currently a number of conceptual models of vegetation change competing for recognition, some of which attempt to provide universal generalisations, others more mechanistic explanations. Specifically, the influence of grazing, and to a lesser extent rainfall, on the vegetation dynamics of southern African savannas have been studied mainly at the community and the individual plant level, with a near dearth of inquiry into the population processes which link the two. Conflicting theories of community change may well be resolved at the population level, or at least an enhanced perspective may be gained. My motivation for undertaking this study was to develop further an interest in population dynamics nurtured as a student, and to see if ideas of plant demography could be useful in improving understanding of our savanna grasslands from both a theoretical viewpoint and for practical application. Although the coming of age of plant population ecology is relatively recent, marked by the advent of Harper's (1977) now classic tome, a population approach to rangeland problems has borne dividend in Europe, the Americas and Australia, but has all but been ignored in southern Africa. My wish is that this contribution will convince some that a population approach is of value for the future utilisation of southern African vegetation.

Only the examiners are ever liable to read a thesis, and to make it more palatable I have restricted the content to mainly that material which I hope to publish, bar some background. In this regard the literature review entitled "Local extinction in perennial grasslands: a life history

approach" has been published in *The American Naturalist*, "Patch colonisation in a savanna grassland" in the *Journal of Vegetation Science*. "The influence of rainfall and grazing on the seed production and seed banks of some savanna grasslands" has been accepted by *The Journal of Applied Ecology*, and the chapter entiled "The influence of rainfall and grazing on the compositional change of the herbaceous layer of a sandveld savanna" has been accepted by the *Journal of the Grassland Society of southern Africa*. The chapter on matrix modelling of population change has been submitted to *The Journal of Applied Ecology*. Valuable comment which improved the content of these manuscripts was received from A. Bailey, R. Cowling, D. Grossman, M. Mentis, N. Owen-Smith, S. Pierce, R. Pyke, K. Rogers, W. Teague and B. Walker.

No scientific journey is undertaken alone, but I can only single out a few of the many who have contributed to the eventual completion of this one. Brian Walker originally suggested and motivated for a study of this type. His departure early in the study left his successor, Mike Mentis, to become supervisor for the long haul to the end. The Directorate of Nature Conservation of the Transvaal Provincial Administration provided a logistical base at the Hans Hoheisen Research Station. The local authorities of the farm Clare and the Department of Agriculture of Gazankulu allowed the work to be undertaken in areas under their jurisdiction. The staff of the Computer Centre of the University of the Witwatersrand, particularly Ana Ferreira, and members of the Department of Statistics, were always helpful when assistance was required. The SASOL laboratory undertook most of the soil analyses free of charge. Financial support was obtained from the Savanna Biome Programme of the FRD, and the Special Programme on Disturbance Ecology of M.T. Mentis.

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CHAPTER 1

INTRODUCTION

The objective of this study was to work toward an improved predictive capability of the compositional response of savanna grasslands to grazing and rainfall variability. A literature review (O'Connor 1985) identified that the influence of grazing on the compositional dynamics of savanna grasslands is dependent on the climatic regime and on trends of above or below average rainfall. Previously grazing had been considered as the primary determinant of successional changes in rangeland, in accordance with Clementsian concepts of plant succession (Clements 1916; Weaver & Clements 1938). Rainfall variability was thought to merely depress or accelerate the the rate of unidirectional change (Westoby *et al*. 1989). The results of long-term experiments from southern Africa (O'Connor 1985) implied that grazing alone had a weak effect on compositional change, and that changes depended on the contingency of events (McNaughton 1983) such as drought and heavy grazing, or a sequence of wet years with no grazing. Unfortunately, most of the long-term experiments had been poorly designed or sampled too infrequently to yield firm conclusions. The primary goal of this study was therefore to differentiate the effect of rainfall and grazing on the compositional change of the herbaceous stratum of a savanna.

An implication of the Clementsian approach to range management is that vegetation changes are unidirectional and reversible. In recent years this has been challenged as an appropriate paradigm for range management, especially for semi-arid areas (Noble 1986; Westoby *et al*. 1989; Mentis *et al*. 1989). A second goal was therefore to assess whether the changes,

if any, resulting from the combination of, for example, extreme drought and severe grazing, were irreversible.

A life history approach was chosen to accomplish this. Previous southern African research has been of a phenomelogical nature, in common with most studies pertaining to ecological theory (Tilman 1988), without consideration of the mechanisms underlying responses. A third goal was therefore to investigate the population processes of individual species which determine the compositional response of savanna grasslands (Jones & Mott 1980). In order to focus research effort, evidence was sought for those life history attributes of savanna grasses which might influence their population dynamics (e.g. Noble & Slatyer 1980). A key concept developed was the local extinction of an "extinction prone" species (Chapter 2). The population dynamics of such a species under sustained grazing in conjunction with drought is determined by its life history attributes. Similarly, the success of certain species under heavy grazing is determined by their life history patterns. The study sought to test these predictions, and to identify other life history attributes, and define how they responded to grazing and rainfall.

I now provide an overview of the thesis. The concept of local extinction is developed, and the predictions of these defined life history attributes on the population dynamics of such a species are made. The generality of an empirical study can only be judged with an understanding of the context within which the information was collected. A comprehensive description is therefore given of the study area (climate, geology, soils), the composition of the woody component, the structure, composition and spatial patterning of the herbaceous layer, and the attributes of the key grass species. The study design is described. The following sections describe the vegetation dynamics of the herbaceous stratum of the communities studied. Firstly, the overall compositional and structural dynamics are summarised, followed by an associated

analysis of the population processes of the key grass species. The patterns of grazing selectivity by cattle are described, which facilitates interpretation of the population and community changes. Matrix modelling techniques are then used to assess the overall behaviour of the population which results from the integration of the various population processes. The dynamics of seed banks are given special consideration. The short-term colonisation pattern of cleared patches is similarly discussed in detail. The concept of local extinction is evaluated with the empirical findings, and the life history patterns of the other species are defined. These are contrasted with some current conceptual models of the dynamics of plant communities. Finally, I identify the almost practical impossibility of pursuing an experimental approach for the investigation of compositional change of the herbaceous layer of southern African savannas. An alternative approach, termed tactical modelling, is offered (and contrasted with similar current approaches), which can provide a rigorous pursuit of this field, and serve as a real world predictive aid.

In summary, this thesis offers what I consider to be an original mechanistic approach to the phenomenon of compositional change. The empirical component of the study lends support to an original and universal concept of the dynamics of perennial grasslands.

CHAPTER 2

LOCAL EXTINCTION IN PERENNIAL GRASSLANDS: A LIFE HISTORY APPROACH

The possibility that multiple stable states exist within natural ecosystems was first proposed by Lewontin (1969). In the subsequent two decades there have been many mathematically based theoretical efforts which have addressed this issue (e.g. Holling 1973; Noy-Meir 1975; May 1977; Ludwig *et al*. 1978; Walker *et al*. 1981). The development of an empirical basis for the concepts of stability and of multiple stable states has not been as fruitful (Connell & Sousa 1983). They conclude that "ideas of population or community stability based upon the existence of equilibrium states have seldom if ever been tested adequately because of the difficulty of defining the equilibria, measuring the strength of the disturbing forces and measuring the rate or degree of recovery in natural communities." A compounding problem has been confusion regarding the concept of stability (Connell & Sousa 1983; Lewin 1986). A conceptual shift is apparent in which the relevance of questions of equilibrium in communities or populations is rejected (e.g., Holling 1973), with the alternative proposal (Connell & Sousa 1983) "to study the broader class of mechanisms which ensure population persistence regardless of whether equilibria can be identified. These mechanisms include both those which reduce the likelihood of extinction or irruption and those which result in the reestablishment of communities if populations of some of the component species become extinct locally." In particular, the value of notions of equilibria in many rangelands has been discounted (Noble 1986; Westoby *et al*. 1989).

This chapter therefore adopts the alternative proposal of Connell and Sousa, and focuses on the population processes which can influence the extinction or persistence of perennial grass populations. Specifically, the present purpose is to define a conceptual model of the local extinction of perennial grass species with certain life history attributes, commonly found in many of the world's rangelands.

Local extinction is defined as the disappearance of the existing population and the seed bank of a species for at least a time period (following Connell & Sousa 1983) that it would take for a complete turnover of all individuals, including the seed bank. The model is based on the truism that any population would become locally extinct if, in combination, the established population together with the seed bank was eliminated and new seed could not be introduced and individuals successfully recruited. An appropriate spatial framework for this process is from the regional (an area that potentially encompasses more than one colonizable patch - Sousa 1984) to the landscape level.

The approach has been to compile a wide array of empirical evidence into a general model, but I first define the environment and type of species the model is applicable to, and describe the model in its entirety without any literature citation. Three sections follow which collate the evidence on the elimination of an established population, the elimination of the seed bank, and the constraints of dispersal on recolonisation. Brief contrasts are then made with species with differing life history attributes. The man-influenced changes in the spatial and temporal scales of ecosystem processes that have created the possibility of local extinction are discussed. Finally, some alternative hypotheses and the implications of the model for secondary succession are considered. This evidence, when taken together, is considered to provide a convincing argument that local extinction has been, and will more so be in the future

with increased human pressures and global climate change, a significant occurrence in perennial grasslands.

A MODEL OF THE LOCAL EXTINCTION OF A PERENNIAL GRASS SPECIES

The Environment

The environments focused on are the perennial (especially savanna) grasslands of southern Africa, which are readily identifiable with grasslands of a similar structure and a comparable climate (such as savannas worldwide and the North American prairies). The perennial grasslands of southern Africa occur within a range of climates from semi-arid (400 mm mean annual precipitation (MAP)) to moist (1000 mm MAP). The coefficient of variation of MAP of semi-arid regions is 40% and of moist regions is less than 10% (Tyson 1986). A similar relationship exists in North America (MacMahon 1979). The summer rainfall region of southern Africa is postulated to exhibit a cyclical pattern of rainfall of nine wet years followed by nine dry years (Tyson 1986). Whether or not a true rainfall cycle exists, the summer rainfall region of southern Africa experiences sequences of years of above and below average rainfall. Thus a succession of years of above or below (drought) average rainfall occur with a higher than expected tendency, also common for North American (e.g., Albertson & Weaver 1942) and for Australian grasslands (Nix 1983). The general importance of soil moisture is illustrated by the close reflection the floristic structure of perennial grasslands show to available soil moisture on a continental (e.g., Australia - Johnson &

Tothill 1985) and regional scale (e.g., North American prairies - Bazzaz & Parrish 1982).

The Species and the Plant Community

The comparison of the population dynamics of species in different environments requires the formulation of a functional species described on the basis of life history characteristics, which include mortality patterns, reproductive effort, dispersal mechanisms, dormancy mechanisms, requirements for germination and establishment, and modes and rates of vegetative growth. Individual species express a correlated set of these characteristics, as is evidenced by the distinction between pioneer and climax species (Weaver & Clements 1938), *r*- (short life expectancy and a large proportion of energy and other resources devoted to many, small propagules) versus K-selected (long life expectancy and a small reproductive effort in a few, large propagules) species (MacArthur & Wilson 1967), and ruderal, stress-tolerant and competitive strategies (Grime 1979). Coexisting grass species differ markedly in life history characteristics, including longevity (Canfield 1957; Williams & Roe 1975; Wright & van Dyne 1976; West et al. 1979), reproductive effort (Salisbury 1942; Jones 1968; Rabinowitz & Rapp 1980; Silva & Ataroff 1985; Dye & Walker 1987), dispersal ability (Rabinowitz & Rapp 1981), and modes and patterns of vegetative growth (Brown 1985; Dye & Walker 1987). Most coexisting grass species differ in their palatability, and in their susceptibility to grazing, implicit in the widely adopted definition of increaser and decreaser species (Ellison 1960; Foran *et al.* 1978). The susceptibility of a species to grazing depends on its morphometric and physiological attributes (Caldwell *et al.* 1981; Coughenour *et al.* 1985b).

A species common to most grasslands has the following characteristics; long-lived established plants, obligate seed reproduction (i.e. an absence of stoloniferous or rhizomatous growth), a low seed crop size of larger bodied diaspores (and usually seeds), seeds posses longevity of only two to three years, diaspores (usually single seeds) display attenuated dispersal patterns (and are minimally transported by secondary agents), and established plants are found palatable by grazers. I define this as an "extinction prone perennial grass". This species would match many of the species of sub-climax or climax grasslands (commonly recognised as possessing K-selected characteristics - McIntosh 1980). Two examples examined in detail include the well known bunchgrasses *Andropogon scoparius* (now *Schizachyrium scoparium*) and *Themeda triandra*. The former contrasts with the latter in that it has lighter seeds, but is also poorly dispersed. (Original sources must be referred to for the authorities of species - these two species quoted below). The longevity of *T. triandra* is approximately 10 yr (Mott *et al.* 1985), and because seeds last no longer than a few years, the appropriate timespan for local extinction is of this order. The exact life-history attributes of an extinction prone grass species would vary along the climatic gradient under consideration, and these attributes are defined partly in relation to coexisting species. Thus an extinction prone species of a semi-arid grassland may behave like an invasive species (possessing *r*-type characteristics) in a moist grassland. Many of the "increaser" species (Foran *et al.* 1978) posses K-selected characteristics, but because they are unpalatable to grazers they would not be susceptible to extinction.

Table 2.1. The influence of sequences of years of above or below average rainfall, together with sustained heavy or light grazing, on the population processes of an extinction prone species (defined in the text).

	RAIN	
	High	Low
Light Grazing	Phase of population growth. Increase in seed bank through prolific seed production, relatively low predation. Successful germination and establishment.	Moderate mortality of established population. Seed bank declines because of reduced inputs, increased predation, and seedling mortality. Minimal establishment.
Heavy Grazing	Low mortality of established population. Seed bank declines because of reduced inputs and high predation. Successful germination but low establishment because of trampling.	Heavy mortality of established population, eventually eliminated. Seed input eliminated. Rapid attrition of seed bank from severe predation and seedling mortality. Poor establishment, which is negated by trampling.

The Proposal

I define here how a perennial grass with the above life history attributes can, and has, become locally extinct, without reestablishment, in grasslands with variable rainfall and subject to sustained heavy grazing by large mammalian grazers. The major processess determining persistence or extinction are summarised in Figure 2.1 and Table 2.1.

Under light grazing, an extinction prone species experiences a degree of population turnover in a temporally varying rainfall environment principally as a result of periods of sustained drought. Neither drought nor grazing on their own, although capable of inducing high levels of mortality, are likely to eliminate an established population. But the combination of drought and sustained grazing, particularly for a successive number of years, is capable of eliminating an established population. As a consequence, an established population can disappear more readily in semi-arid rather than moist regions, because semi-arid regions experience a greater frequency and duration of droughts. Successful recruitment is a function of seed availability, seed germination, and seedling survival. During drought years, most seed is likely to perish as a result of successful germination but failure to establish because of intra-seasonal drought. Sustained grazing further diminishes successful seedling establishment mainly due to trampling.

An adequate seed supply, when conditions are amenable for establishment, is critical for population maintenance. But these species have a transient seed bank of small size, and when seed input is curtailed the seed bank is rapidly extinguished. These species do not form a persistent seed bank because innate dormancy, although common, is relatively shortlived, induced dormancy is absent, and the seeds have a limited intrinsic capacity for survival (2-3 yr). Therefore the size of the seed

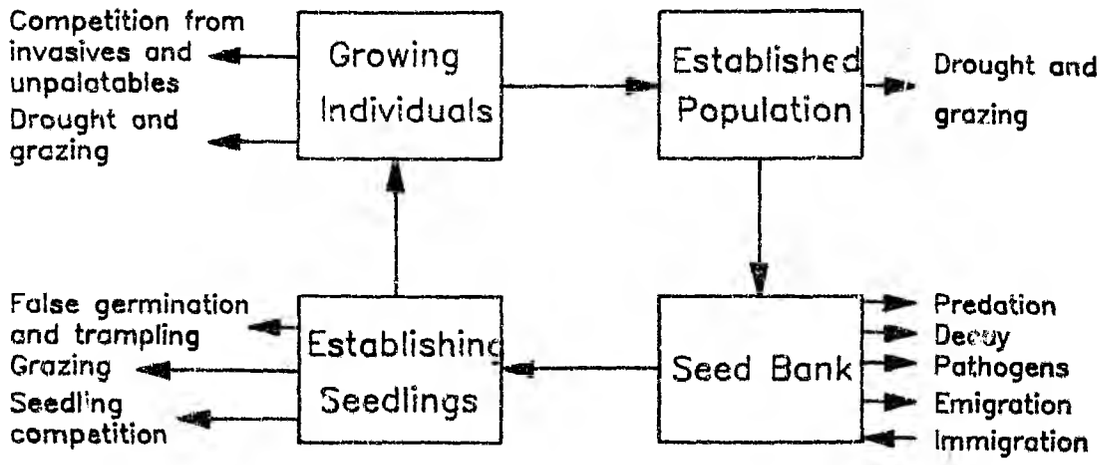


Figure 2.1. The life cycle of an extinction prone perennial grass (defined in the text) illustrating the major agents which cause losses from the established population, the seed bank, establishing seedlings, and established plants growing to maturity. The diagram represents conditions of light or moderate grazing. The text defines a conceptual model of how sustained heavy grazing in man-influenced systems can result in the elimination of each of the above components of the population.

bank is determined primarily by the annual input of seed. The "persistence" of the seed bank is therefore ensured by the longevity of established plants. Even under conditions of favourable rainfall and low grazing, these species do not have abundant seed production, because up to 100% of the seed can be consumed by pathogens, and pre- and post-dispersal predators. Seed production is curtailed during drought, and seedling mortality can rapidly deplete seed banks. Heavy grazing can eliminate seed inputs through direct ingestion of inflorescences. If drought and sustained severe grazing persist for longer than the intrinsic capacity for survival of the seeds, the seed bank is eliminated. If the

established population has been eliminated, the occurrence of the species within the seed bank then becomes a function of its dispersal capabilities. An extinction prone species is essentially self-dispersed, hence dispersal distances are limited. These species mostly colonize gaps in close proximity of the parent vegetation, although incidental animal agents will facilitate dispersal at a range of distances. Incidental long-range dispersal would be ineffective in maintaining a population because of the low probability of survival of germinated seedlings.

The observed persistence of these species indicates that their life history attributes are adapted to drought and moderate defoliation. The recolonisation of gaps by these species depends primarily on the presence of an established population which can provide an annual rain of seed onto these gaps. The longevity of the species is important to ensure that a proportion of tufts will live through an extended drought and be able to provide a source of seeds. Consistently high levels of grazing sustained over a sufficient number of rainfall cycles will eventually result in the elimination of the established population, which is effectively also elimination of the seed bank, and hence local extinction. It is suggested that the man-influenced changes in the temporal and spatial patterns of grazing in these systems have rendered the established population and seed bank vulnerable to local extinction.

THE ELIMINATION OF THE ESTABLISHED POPULATION OF A PERENNIAL GRASS SPECIES

What is the evidence that local extinction of an "extinction prone perennial grass" has occurred, and what are the circumstances which can lead to this? There are clear anecdotal references to the local

extinction of individual species as a result of "overgrazing". *Themeda australis* (now *T. triandra*) grassland has given way to *Heteropogon contortus* grassland over a period of 40 yr in Queensland (Mott *et al.* 1985), and *Themeda triandra* and other perennial grasses have disappeared from the False Upper Karoo in South Africa (Acocks 1975). *Agropyron spicatum* has disappeared from much of its former range in North America (Mack & Thompson 1982). The species is not physiologically capable of compensating for severe defoliation, interpreted as the result of the lack of evolutionary pressure on the species since the Pleistocene extinction of large mammals some 10000 yr ago (Caldwell *et al.* 1981; Mack & Thompson 1982).

However, most empirical examples provide only indirect support of local extinction. For example, longer term compositional changes in the savanna grasslands of southern Africa reveal no conclusive evidence of local extinction of individual species subject to drought, heavy grazing and sustained burning (O' Connor 1985), partly the result of the few data sets which covered a sufficient length of time, or were sampled at an appropriate temporal scale. These and other data sets clearly indicate that drought and severe grazing, each significant mortality factors of established individuals, but on their own insufficient to eliminate an established population, can, when in conjunction for a successive number of years, effect the extinction of an established population. As a consequence, elimination of an established population is most easily realised in semi-arid and mesic rather than moist regions, because of the greater frequency and duration of years of drought. Two main examples illustrate this.

Compositional responses to 15 years of severe grazing at five sites in Zimbabwe varied according to climate and soil type (Kennan 1969). A moist site (940 mm pa) and a mesic site with sandy soils (615 mm pa) maintained relatively stable composition. In mesic savannas on heavy textured soils,

rainfall variation with or without moderate grazing resulted in the pronounced variation of the abundance of individual species, but not their elimination, whereas severe grazing associated with a number of drought years eliminated six species. For example *Themeda triandra* disappeared within seven years of heavy grazing, and required eight years of rest to reappear. At the most arid site (425 mm pa), a series of dry years eliminated ungrazed perennial grasses, but they reestablished under protection during a series of wet years. Only two years of heavy grazing reduced the sward to annuals, and some of the perennials did not reestablish after 10 yr of rest. A review of 58 longer term (> 5 yr) studies concerning the influence of rainfall and grazing on compositional change revealed similar patterns (O'Connor 1985).

A striking effect of the seven year drought of the 1930's in the tall-grass and mixed prairie of North America was the extinction or great depletion of what had been the regional dominant, *Andropogon scoparius* (Weaver & Albertson 1936, 1939; Albertson & Weaver 1942, 1944), and the depletion of other major perennial species. The replacement of true prairie by mixed prairie dominated by *Agropyron smithii* over a belt 200 to 300 km in width (Weaver 1943; Albertson & Weaver 1944) strongly suggests local extinction, although subsequent changes were not published. *A. scoparius* was also replaced by *Bouteloua gracilis* and *B. curtipendula* in the drier mixed prairie (Albertson & Weaver 1944). In the xeric *Buchloe dactyloides - B. gracilis* vegetation type, these two species declined markedly irrespective of grazing, with increases shown by *Sporobolus cryptandrus* (Albertson & Weaver 1942). This drought was followed by a number of years of high rainfall, but *A. scoparius* made little recovery in areas which had been formerly heavily grazed (Albertson & Weaver 1944). Even in the absence of grazing, 13 years of favourable rainfall were required for *A. scoparius* and *A. gerardii* to attain their pre-drought dominance (Weaver 1954). *Astrebla* spp. and *Dicanthium*

sericeum responded similarly to climatic variability in Australia (Williams & Roe 1975; Orr 1981; Orr & Evenson 1985).

Field based estimates of mortality in semi-arid grasslands corroborate this pattern. The availability of soil moisture, independently of grazing effects, was a major influence on the survival of perennial grasses on the Jornada range (Wright & van Dyne 1976), in *Astrebla* grasslands (Williams & Roe 1975), and for *Eragrostis lehmanniana* (Fourie & Roberts 1977). Clipping experiments, although possibly not very representative of grazing, have induced high levels of tuft mortality in many perennial species (Ndawula-Senyimba 1972; Hodgkinson 1976; McLean & Wikeem 1985a, 1985b). Two years of drought and severe grazing had catastrophic effects on the survival of the palatable perennial grasses of a southern African savanna, between 74% and 97% died (Scholes 1985).

Given that an adequate seed supply exists, successful recruitment will primarily be a function of seed germination and seedling survival. High juvenile mortality is expected in established vegetation, and drought is the most important influence on seedling recruitment (Cook 1979). A familiar pattern is for germination to occur in response to a favourable rainfall event, and for the seedlings to die during a subsequent period of no rainfall (Glendenning 1941; Albertson & Weaver 1942; Pratt 1963, 1964; Donaldson & Kelk 1970; Ndawula-Senyimba 1972; Silcock 1977; Harradine & Whalley 1980; Cox 1984; McKeon 1985; Frasier *et al.* 1987). Such events rapidly deplete seed banks.

The patterns of seedling mortality when climatic conditions are suitable and space is available are critical for population maintenance. Large mammals incur high seedling mortality through their trampling action (Wright & van Dyne 1976). For example, only 3 of 759 seedlings survived two intensive 3-day grazing periods over 10 mo as opposed to 97 of 839 seedlings which survived the same period under no grazing (Salihi & Norton

1987). A host of other agents also mitigate against seedling survival (e.g., rodents - Pyke 1986).

THE ELIMINATION OF THE SEED BANK

The size of the seed bank of a species at any given time is the summation of the set of processes influencing the input and output of seeds (Harper 1977). The input of seeds is a function of the abundance of a species, and of the resource factors influencing seed production. Seed produced may be lost to pre- or post-dispersal predation. The dormancy mechanisms and the intrinsic capacity of survival of the seeds of a species will determine the number of seeds remaining in the seed bank. Losses from the bank will occur to deep burial, decay, or germination. The key feature of an extinction prone perennial species is that the seeds have an intrinsic capacity for survival of only a few years, and hence the size of this transient seed bank is regulated primarily by inputs (Figure 2.2). Once inputs have been eliminated, there would be rapid attrition of the seed bank, unless there was net immigration of seed. This section illustrates how the processes portrayed in Figure 2.2 can interact to result in the elimination of the seed bank.

The annual seed production of perennial grasses at a semi-arid or mesic site is a function of population abundance and rainfall (Albertson & Weaver 1942; Brown 1943; Weaver & Mueller 1942; Cornelius 1950; Knapp 1984; Dye & Walker 1987). Seed set can fail in drought years. For example, no reproductive tillers were recorded for either *Andropogon gerardii* or *A. scoparius*, during a year of 295 mm of rainfall (MAP 820 mm) (Knapp 1984). Plots irrigated in this year (610 mm) achieved a

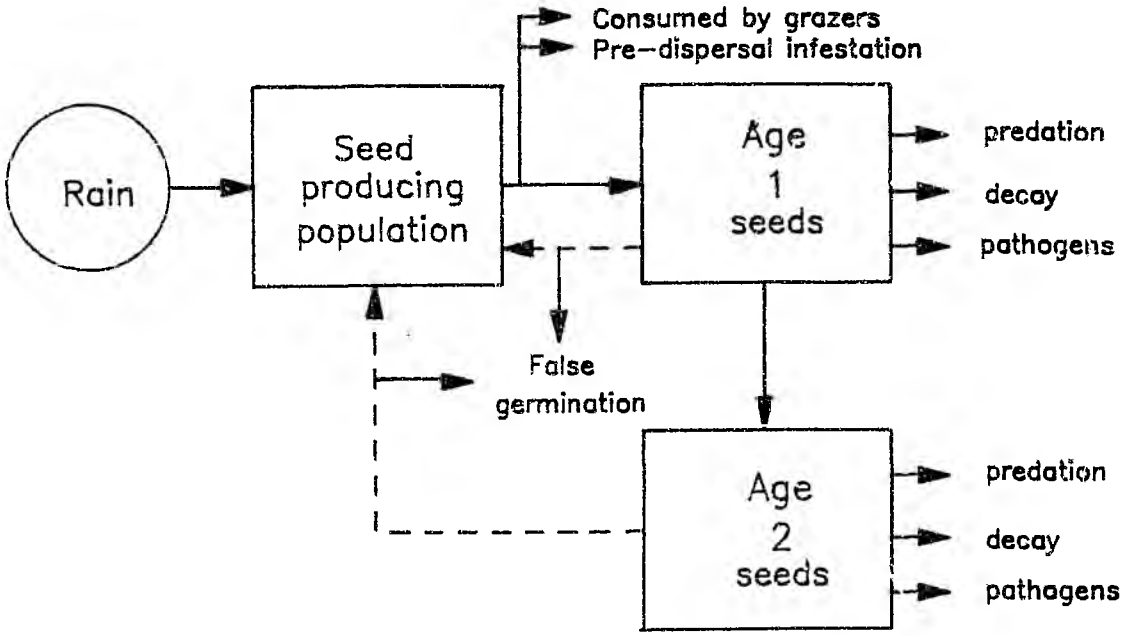


Figure 2.2. The processes determining the size of the seed bank of an extinction prone perennial grass (defined in the text). The seed bank has an age structure of only two (or a few) years because seeds are readily germinable and have a limited intrinsic capacity for survival if dormant. The size of the seed bank is therefore determined primarily by annual inputs (dependent on population abundance and rainfall). Under conditions of sustained drought and heavy grazing, seeds inputs are eliminated, and the seed bank survives for as long as the intrinsic capacity for survival of the seeds (2-3 yr).

reproductive tiller output comparable with the preceding high rainfall year (637 mm).

In general, defoliation decreases seed production (Jameson 1963), simply because sustained grazing pressure during the growing season can result in the total consumption of inflorescences (Brown 1943; Barnes 1960; Tainton & Booysen 1964, 1965; Ambasht & Maurya 1970). Defoliation can

indirectly depress the reproductive output in succeeding years if the plants vigour is affected (Mueggler 1975; McLean & Wikeem 1985b).

High levels of pre-dispersal infestation of seeds can occur (Jones 1964; Lock & Milburn 1970). For example, there was up to 80% direct ovule loss to orthopterid and planthopper consumption of the four major species of a salt marsh perennial grass community (Bertness *et al.* 1987). Although plants have a limited ability to compensate for reproductive tissue lost to herbivory or infestation (Islam & Crawley 1983; Solomon 1983), this depends in part on the level of infestation or predation (Woronecki *et al.* 1980).

Once diaspores fall to the ground, seeds become exposed to post-dispersal predation by ants, rodents and birds (Reynolds 1950, 1958; Sharp & Barr 1960; Campbell 1966; Russell *et al.* 1967; McGowan 1969; Berg 1975; Pulliam & Brand 1975; Fry 1983). For example, harvester ants foraging in an Australian range removed 100% of the seeds of *Themeda australis* and *Digitaria ciliaris* within 14 hr (Mott & McKeon 1977). The kangaroo rat *Dipodomys merriami* could consume all of the seed of the preferred grasses, *Aristida* spp., *Heteropogon contortus*, and *Trichachne californica*, produced in dry years (Reynolds 1950, 1958). The levels of predation by these agents has demonstrable effects on grassland dynamics. Experimental poisoning of ants revealed that ant predation of seed could prevent the recruitment of grass seedlings in pastures (Campbell 1966; McGowan 1969), which threatened the persistence of *Lolium rigidum* when grown in competition with annual grasses (McGowan 1969). Compositional changes in rodent exclosures over 15 years suggested that rodents could unfavourably affect the abundance of perennial grasses during periods of low seed production (Reynolds 1950).

The fate of a seed which escapes predation is to germinate or to remain dormant, depending on the dormancy mechanisms the seed possesses and the

environmental milieu the seed is exposed to. The three primary dormancy mechanisms displayed by seeds, innate, induced and enforced (Harper 1977), determine if a species can form a persistent or a transient seed bank (*sensu* Thompson & Grime 1979). Although innate dormancy is commonplace among grasses, it is unlikely to result in a persistent seed bank, because it is an adaptation that ensures that a seed will not germinate during the dry winter periods when successful establishment is unlikely, but will germinate at the onset of the rainy season (Angevine & Chabot 1979). Innate dormancy does not persist for much longer than eight months in these grasses (Coukos 1944; Lock & Milburn 1970; Brown 1982; Hacker 1984), after which the seeds germinate readily. There is no evidence of induced dormancy in tropical and sub-tropical grasses. For the formation of a persistent seed bank, the intrinsic capacity for survival while in a state of enforced dormancy would be most important for imbibed seeds buried in the soil (Roberts 1981).

Seed burial experiments reveal the astonishing intrinsic capacity of survival of the seeds of small seeded herbaceous dicotyledons whilst in a state of induced or enforced dormancy (Madsen 1962; Kivilaan & Bandurski 1981). Perennial grasses display no evidence of this ability (Coukos 1944; Madsen 1962; Winkworth 1963; Lock and Milburn 1970; Williams 1983). For example, no viable seeds of *Lolium perenne*, *Dactylis glomerata*, *Poa pratensis*, *Festuca arudinacea*, or *Festuca rubra* were retrieved after 29 mo of burial (Rampton & Ching 1966). The mortality of buried grass seeds is principally due to the breakdown of dormancy mechanisms and deep germination resulting in death (85% of the buried seeds of *Lolium perenne* succumbed in this fashion - Schafer & Chilcote 1969) and pathogen attack (Janzen 1977).

An extinction prone species is unlikely to form a persistent seed bank of appreciable size. Because the seeds have a limited intrinsic capacity for survival, the seed bank is comprised of seeds only a few years old.

Hence the size of the seed bank is determined primarily by the seed production of that year (Figure 2.2). But even during periods of high seed production, pre-dispersal predation, intense post-dispersal predation, and readiness to germinate, would result in a seed bank of poor stature in relation to the representation of the species in the vegetation. A host of studies corroborate this prediction (Chippendale & Milton 1934; Lippert & Hopkins 1950; Major & Pyott 1966; Thompson & Grime 1979; Hodgkinson *et al.* 1980; Howe & Chancellor 1983; Belsky 1986b; Johnson & Anderson 1986). For example, *Andropogon gerardii* and *A. scoparius* were abundant species in the seed rain of an ungrazed tall grass prairie (600 and 1200 seeds m^{-2} respectively), but were not recorded in the seed bank (Rabinowitz 1981).

A. scoparius illustrates the pattern found during periods of drought and heavy grazing. During the drought seed production was minimal, germination followed by seedling mortality was widespread (Albertson & Weaver 1942, 1944), and the seed bank was eliminated from the mixed prairie and depleted in the true prairie (Weaver & Mueller 1942). The seed bank was dominated by "r-selected" species such as *Sporobolus cryptandrus*, *Bouteloua gracilis*, and *Buchloe dactyloides*, and 37% of the area sampled had no seed bank of grasses at all (Weaver & Mueller 1942). Many of the species of British grasslands rapidly decline in the seed bank once input of seed is eliminated (Williams 1984).

THE CONSTRAINTS OF DISPERSAL

The potential for a species to reinvade an area following local extinction, depends on the dispersal mechanisms of the species and the distance that the diaspore has to traverse. The dispersal mechanisms

include self-dispersal (autochory), wind dispersal, dispersal on the outside of an animal (epizoochory) or through the gut of an animal (endozoochory). Autochory, characteristic of an extinction prone species, operates on a restricted spatial scale. The effectiveness of wind dispersal depends on diaspore shape and weight but is restricted to a regional scale for all but the lightest of diaspores. Animal dispersal has the potential for long distance transport of propagules. Perennial grass species without wind or animal dispersal mechanisms exhibit little lateral displacement from the parent plant. In awned species such as *Andropogon scoparius* (the awn serves to slow the fall and act as a guide parachute - Rabinowitz & Rapp 1981) seeds are not dispersed more than 2 m (Rice *et al.* 1960). Wind dispersal was an effective agent in the invasion of abandoned fields by *Aristida* species, because the triple-awned structure of the diaspore facilitates its being rolled by the wind (Rice *et al.* 1960), but the dispersal of *Elymus elydoides*, a species adapted for wind dispersal, did not exceed 40 m in natural vegetation (Marlette & Anderson 1986).

Animal dispersal is therefore the major potential means of seed dispersal at a landscape scale, and the distances involved depend on whether or not the animal is spatially restricted in its movements. For what spectrum of seed types can animal dispersal be effective, and specifically can the diaspores of an extinction prone species be transported over landscape scales? The Merriam kangaroo rat selects seeds of large seeded perennial grasses, and in cacheing these seeds transports them for distances of 0.5 to 30 m (Reynolds 1950, 1958). A small proportion (2%) of these caches are not rediscovered, and seedlings germinate from them. Endozoochory is a potential mechanism for long distance dispersal amongst the Gramineae (Janzen 1984), but is restricted to small seeded graminoids (Heady 1954). For example, the "early successional" species *Cynodon dactylon* was essentially the only species germinating from the dung of cattle on the Transvaal highveld, where the seeds of a wide array of species were

available, with an individual beast transmitting up to 4000 seeds per day (Jones 1964).

Epizoochory can possibly effect long distance dispersal of heavier diaspores, but not if they are rounded and smooth. However, *Themeda triandra*, which has awned diaspores, a character most often interpreted as an adaptation for burrowing into soil, was one of the six most common species found lodged in the fur of hares in East Africa (Agnew & Flux 1970). In the chapparal of Israel, awned diaspores of Gramineae were significantly higher in abundance on animals relative to their abundance in the area, and showed significantly longer retention times on sheep and goats than species without awns (Shmida & Ellner 1983). Data are lacking for the indigenous large mammals and cattle. These are potential dispersal agents over landscapes, but the majority of these species have smooth fur and therefore may not function well as epizoochorous agents. It is contentious whether the above examples concerning awned seeds reflect true or incidental epizoochory. Experimental evidence suggests that the primary function of awns is to locate the individual seed in an appropriate microsite which will enhance the probability of seedling survival following germination (Peart 1979, 1981, 1984), by maintaining the growing coleorrhiza within a zone of soil moisture (McKeon 1985), or protection of the seed from fire (Lock & Milburn 1970).

It is concluded that a proportion of these seeds, greater for regional as opposed to landscape scales, will be transported by animal vectors. Diaspores transported by animal agents are likely to be continuously lost during animal movement (Bullock & Primack 1977, Shmida & Ellner 1983), and therefore with a ubiquitous species, such as *Themeda triandra* or *Andropogon scoparius*, a proportion of these diaspores will probably find themselves in "safe sites" or deposited on an inappropriate substrate. Is the rate of propagule dissemination by animal vectors sufficient to ensure a probability of successful establishment in an environment which

has been inimicable to the persistence of the formerly established population ? The poor results of range reseeding experiments (e.g. Pratt 1963, 1964), in which the rate and amount of seed supply probably far exceeds that effected by animal vectors, suggests not, even with amelioraced grazing pressure.

In the Matopos experiment (Kennan 1969), the eight years taken for *Themeda triandra* to reappear once rested from grazing suggests that no residual seed bank had persisted, and illustrates the poor dispersal ability of *Themeda*, as the species was abundant in adjacent vegetation.

INTERACTIONS WITH OTHER SPECIES

Heavy grazing promotes the increase of invasive species and species which share the life history attributes of an extinction prone species but which are unpalatable. Invasive species are capable of maintaining prolific seed production even under heavy grazing, and thereby dominate the pool of seed available for recolonisation, a major factor promoting their invasiveness (Harradine & Whalley 1980; Brown 1985). The seeds of annual and short lived perennial grasses also tend to have a slightly greater intrinsic capacity for survival than the seeds of longer lived perennial grasses (e.g., Rampton & Ching 1966). Most invasive species have good dispersal capabilities because they are wind dispersed (e.g., Rice *et al.* 1960) or animal dispersed (Janzen 1984), and thereby preempt extinction prone species in the occupation of available gaps. The disparity in the numbers of seeds and therefore seedlings of invasive species and an extinction prone species mitigates against the successful establishment of the latter. Unpalatable climax and sub-climax grasses have similar low levels of seed production of large seeds, and inefficient

dispersal of seeds, as do extinction prone species. But grazing can promote increases of unpalatable species through its effects on the seed bank, because inflorescences are not consumed to the same extent, but the increase of unpalatable species will be far slower than that of invasive species. Furthermore, grazing can alter the competitive relationships of these species during the growth phase of established plants and thereby favour the growth of an unpalatable or invasive species at the expense of the palatable species (Norman 1960; Jones & Cross 1971), resulting in their domination of those areas where they do occur. For example, the demise of *Agropyron spicatum* has been associated with the competitive influence of an invasive alien *Bromus tectorum* (Mack 1981).

CHANGES IN THE SPATIAL AND TEMPORAL PATTERNS OF SYSTEMS

Why should species which have a history of selection for the environmental vicissitudes discussed suddenly become candidates for local extinction, particularly at a landscape level? I speculate that the answer is related to the influence of human intervention on the spatial and temporal scales of processes within these systems. In the selective milieu prior to extensive human influences the palatability of a species such as *Themeda triandra* was dependent on the growth stage of the plant. The species is selected by a diversity of grazers when fresh growth commences at the beginning of the season, but as the growing season advances an increased proportion of material is invested in structural components (principally reproductive culms), and the plant is generally only selected by bulk grazers, such as buffalo (*Syncerus caffer*) (Sinclair & Gwynne 1972; Page & Walker 1978). Similarly, cattle and deer in British Columbia select for recently burnt or heavily grazed individuals of *Agropyron spicatum* but avoid ungrazed individuals which have accumulated moribund material

(Willms *et al.* 1980). Heavy defoliation of an extinction prone species therefore only occurred on a pulse basis, and these species experienced light defoliation when inflorescences were being produced and seeds shed. I suggest that one of the primary effects of human influence on rangelands today, including wildlife systems in which migration has been curtailed (Walker *et al.* 1987), has been the alteration of heavy grazing from an intermittent seasonal pulse to a sustained grazing pressure throughout the growing season. A possible scenario of impending global climate change for southern African grasslands is a general decrease of MAP, together with an increased variability of MAP (Wilson & Mitchell 1987; Washington & Meehl 1989), with the implication from this thesis of an increased probability of the extinction of these grasses over wide areas.

ALTERNATIVE HYPOTHESES

The population approach of this essay does not intend that these are the sole, or in some circumstances the most likely, processes which might result in the local extinction of certain perennial grasses. Peterson (1984) contends that the criterion of Connell & Sousa (1983), that the physical environment must not be different for two alternative states to be differentiated, is arbitrarily strict, and focuses attention on biotically induced physical conditions as one of the most likely mechanisms involved in maintaining alternative states. To evaluate the role of the physical environment in local extinction, evidence for the strength of abiotic variables as determinants of herbaceous composition, and evidence for biotically induced changes in these variables is required. Ideally it should further be demonstrated that the modified environment should have properties that both result in self replacement of the resident population, and reduce the likelihood of invasion of the

alternative population from another site (Sousa & Connell 1985). The importance of soil moisture in determining herbaceous composition has been discussed. The influence of soil physico-chemical properties on herbaceous composition in savannas is illustrated by the differences between fertile and infertile savanna soils experiencing the same rainfall regime (e.g., Johnson & Tothill 1985), and by the dramatic transformation of the species composition of sites fertilised with nitrogenous compounds (Mills 1964; Donaldson *et al.* 1984). A classic example of a system change mediated by soil properties is the demise of the *Acacia xanthophloea* woodlands in Amboseli due to changing soil salinity levels (Western & van Praet 1973), but this was an extrinsically induced change. However, examples of biotically induced and irreversible changes of composition are rare. Otterman (1974) postulates for the Gaza region, that high albedo soils denuded by overgrazing are cooler than regions covered by natural vegetation, and this thermal depression effect results in a decreased lifting of air necessary for cloud formation and precipitation, thus leading to climatic desertification. Biotic influences on soil chemical factors are well recognised. Grazers can influence the botanical composition of pastures at a patch scale by dunging (Norman & Green 1978), but the persistence of this effect is unknown. The decreased proportion of late successional species and the increased proportion of early successional species on grazed Transvaal grasslands may be a consequence of the increased amounts of plant available (but not of total) nitrogen made available by the rapid cycling of nitrogen by dunging (Roux 1969), but these effects are unlikely to persist with the amelioration of grazing. Former iron-age sites of human settlement are one example of a biotically induced and apparently irreversible change in composition (e.g , Feely 1980). In the Nylsvley region of the Transvaal these sites are islands of fertile soils supporting a dissimilar vegetation to the surrounding matrix of dystrophic soils (Huntley & Morris 1982). The available evidence therefore suggests that biotically induced changes in the soil

physico-chemical environment may result in local extinction in some circumstances.

IMPLICATIONS OF THE MODEL FOR SECONDARY SUCCESSION

Characteristically the reestablishment of perennial grasses following cultivation is an extremely slow process, it did not occur within 40 yr in Kansas (Booth 1941) or within 70 yr in the Transvaal highveld (Roux 1969). The established population of perennial grasses is rapidly eliminated by sustained cultivation, although perennating organs can survive a few years of cultivation (Rice & Penfound 1954). The residual seed population of an extinction prone species at the time of abandonment of the field depends on the intrinsic capacity of survival of buried seeds, as immigration can be discounted and surface seed is likely to germinate and rapidly perish, and therefore a field cultivated for a consecutive number of years would not contain a residual seed population. The reestablishment of these species therefore depends on the quantity of available seed of the species in the surrounding vegetation and the dispersal ability of the species. The conventional explanation for the slow rate of successional change of fields has been an autogenic (Clementsian) model of succession, in which a species (or community) induces a change in the edaphic environment inimical to itself but beneficial to another species (or community), thereby facilitating a compositional change (Connell & Slatyer 1977 give a review).

Successional studies of the American prairies (Rice *et al.* (1960) and the Transvaal highveld (Roux & Warren 1963; Roux 1969) provide support for this model, but the role of the availability of disseminules has also been recognised. The annual *Aristida oligantha* rapidly invades abandoned

fields because the diaspore is rolled by wind, whereas the diaspores of *Andropogon scoparius* are not blown more than 2 m (Rice *et al.* 1960). Consequently the latter species advances slowly from the periphery, requiring 9-13 yr to become established. Jones (1964) rejected the autogenic model of succession for the Transvaal highveld, and postulated that the failure of climax perennial grasses to reestablish was principally due to the lack of available seeds. These climax species had a low reproductive output compared with the prolific reproductive output of the early successional species (Jones 1968). Seeds of some of the early successional species were also readily disseminated by wind and animal vectors. Unfortunately these conflicting theories were never subjected to the simple test of providing a seed source of these climax perennial grasses in recently abandoned fields.

The failure of the climax grasses of the Transvaal highveld to reestablish within 70 yr is in accordance with the present model. This length of time is well in excess of the generation length of these species, which raises the question of what are the implications of local extinction for the climax vegetation of an area. The differential ability of different species to recolonise disturbed areas would depend on the size of the area. The vegetation recolonising an abandoned road resembled the surrounding climax vegetation (Jones 1964), but large fields did not attain their former composition. Hence the climax is not a single end-point - there are a number of different possible endpoints determined by the history of extinction and the size of disturbance.

SUMMARY

A common element of many perennial grasslands, defined as an extinction prone perennial grass, is a palatable obligate seed reproducer, producing low numbers of larger diaspores, which are poorly dispersed. Such a species can become locally extinct on a regional or landscape scale in grasslands which experience both a variable rainfall, in which drought is characteristic, and sustained heavy grazing. The changes in the temporal and spatial patterns of grazing in man-influenced systems has created the possibility of local extinction. Catastrophic mortality of established populations occurs as a consequence of droughts in combination with sustained grazing, eventually leading to the elimination of the population. Elimination of the established population is more likely to occur in semi-arid than moist areas because of the greater frequency and duration of droughts. The maintenance or reestablishment of the population depends on successful recruitment, but seedling mortality is high because of intra-seasonal drought and trampling.

The seed bank of an extinction prone species is rapidly eliminated if the input of seed is curtailed. These species do not form persistent seed banks, because the seeds have a limited (2-3 yr) intrinsic capacity for survival when in a state of induced or enforced dormancy. Innate dormancy only lasts for a few months. Therefore the size of the seed bank is determined primarily by the annual input of seed. But even under favourable rainfall and light grazing, 100% of seed produced can be lost to predation. Seed production can fail from drought and from the direct consumption of inflorescences. An extinction prone species is self-dispersed, and therefore poorly dispersed. The rate and scale of incidental animal dispersal is unlikely to assist in the maintenance or reestablishment of a population, because of the low probability of seedling survival. The decline of an extinction prone species under heavy

grazing is compounded by the concomitant competitive influences of invasive species and unpalatable species which both benefit from heavy grazing. Irreversible changes in the physico-chemical environment may also result in local extinction, but these processes are not mutually exclusive. The autogenic model of secondary succession is inadequate for these grasslands if the present concept of local extinction is upheld.

CHAPTER 3

STUDY DESIGN

To achieve the primary objective of differentiating the effect of rainfall and grazing on compositional change (Chapter 1), an experiment which manipulated rainfall and grazing was established on both a heavy-textured and a sandy soil, and for the heavy-textured soil on two areas which initially differed in composition because of grazing history. Rainfall and grazing were chosen for manipulation because they appeared to be the driving variables most likely to elicit the greatest compositional response (O'Connor 1985). Soil type, specifically the contrast between nutrient-rich clay soils and relatively infertile sandy soils, is a major determinant of savanna structure and dynamics (Frost *et al*. 1986), and therefore comparisons were sought between heavy-textured and sandy soils.

Our present understanding of the dynamics of southern African savanna grasslands is not based on a rigorous experimental approach so popularly espoused by community ecologists (e.g. Hairston 1989), but much of it has been derived from descriptive and comparative work. For example, few of the 126 experiments concerning savanna grassland dynamics reviewed in O'Connor (1985) would qualify as experiments by Connell's (1983) definition.

Similarly, in establishing this study the choice was between a sound statistical design with adequate replication of treatments, which would have restricted the study to only one site with the given resources, or no replication of treatments but more sites with defined environmental contrasts (e.g. Kelly & Walker 1976) from which a broadened ecological

perspective could be gained. Because this was an exploratory study of the influence of rainfall and grazing on the mechanisms of compositional change of southern African savanna grasslands, the latter approach was considered likely to yield greater insight, and point the way to areas which should receive the rigorous approach.

The one specific objective of the manipulation was to create extreme levels of rainfall and grazing, and to measure the resulting changes in both the composition and the population dynamics of the main species. It was expected from long-term studies (O'Connor 1985) that there would be more pronounced compositional changes on the heavier textured rather than on the sandy soils per unit of annual rainfall change (O'Connor 1985). It was also expected that the sites with a history of heavy utilisation would improve primarily in response to high rainfall, while sites with a history of lenient utilisation would deteriorate in response to a combination of drought and heavy grazing, not heavy grazing alone.

The second goal (Chapter 1) was to assess if the compositional changes were potentially irreversible. This was to be indirectly evaluated from the population dynamics of the extinction prone species identified in the study, in accordance with the expected responses defined in Chapter 2. This in part achieved the third goal (Chapter 1) which was to define the population responses of the main species as a basis for the explanation of overall compositional change. A specific objective was therefore to measure in detail the changes in the population abundance of the main species as well as their seed production, seed bank dynamics, recruitment, changes in individual size, mortality, and colonising ability, and to model the longer term population responses using matrix models.

An ideal would have been to repeat the two by two arrangement of soil type by grazing history across the gradient of climatic regimes (semi-arid, mesic, moist) of southern African savannas, but the logistics required

meant that only one area could be studied. A mesic region was chosen. Logistic requirements also restricted the study to three of the four contrasts, the sandy soil environment with a history of light utilisation was not investigated.

Details of sites

The study was conducted at three approximately 1.5-ha sites in Gazankulu, eastern Transvaal, a mesic region receiving c. 650 mm per annum, falling mainly between October and April. The average daily maximum temperature for nearby Skukuza from October to March is >30°C (maximum=32.3°C in December and January) while the absolute maximum for this period is greater than 40°C (maximum=44.5°C in November). The region is underlain by Makhutswi gneiss (SACS 1980). There has been a later intrusion of Timbavati gabbro dykes (Walraven 1986). The region is a dissected Post African I surface of the early Miocene, with the original surface preserved on interfluves (Partridge & Maud 1987). The elevation of the region is approximately 500 m. The terrain is gently undulating, and all three sites were sited on the flanks of gentle (<5°) slopes.

The sandveld site (24°38'S;31°23'E) was sited on gneiss, while the Utha (24°43'S;31°25'E) and the Thlavekisa (24°38'S;31°24'E) sites were sited on gabbro. Prior to the 1920's, the region was a wildlife system with scattered subsistence farming, although none of the sites appear to have ever been ploughed. The region was gazetted for commercial cattle ranching in the 1920's, and consolidated into the southern Gazankulu "homeland" in the early 1960's. The sandveld and Thlavekisa sites were on Clare (220KU), Utha was on Athol (238KU). Clare included the town of Hluvukani, and supported one of the higher human densities in the region.

The farm was communally grazed by cattle and goats, and stock densities were high because of the number of people, although figures are not available. The sandveld site was particularly heavily utilised because of its proximity (<0.5 km) to a major livestock watering point. Athol had less settlement than Clare, and the Utha site was further removed from settlement than the other two sites. The Utha site has been fenced and managed as a controlled cattle grazing scheme since 1980. The human population on Clare has close to doubled since 1986 because of an influx of Mozambican refugees, but this did not occur on Athol. Refugees established new villages directly adjacent to the Thlavekisa site and in close proximity (<1km) of the sandveld site. The refugee influx increased grazing pressure because a significant proportion of former pastoral land was settled or tilled.

The conclusions of any empirical study are to some extent location specific, and therefore the soil properties of all three sites and the composition and structure of the woody vegetation of the two clay soil sites have been detailed in Appendices 1 and 2 to allow comparison with other southern African savannas.

Experimental procedure

Three ≈1.5-ha sites were selected and fenced in 1984, and each was divided into two approximately equal portions, one of which was subjected to heavy cattle grazing over the next three (sandveld) or five years, the other to light grazing (Table 3.1). Grazing occurred as discrete events at regular intervals throughout the growing season, with up to 50 head of cattle per event (of one or two days). Grazing was restricted to the

Table 3.1. The number of cattle grazing days and the number of grazing events (in parenthesis) per growing season for the Utha and Thlavekisa sites, and the annual (July to June) rainfall.

	Grazing days (events)				Rainfall (mm)	
	Thlavekisa		Utha		Thlavekisa	Utha
Season	Heavily grazed (0.81 ha)	Lightly grazed (0.64 ha)	Heavily grazed (0.95 ha)	Lightly grazed (0.85 ha)		
1983/84	Communal grazing		Controlled grazing		714	n.r.
1984/85	134 (3)	(2)	224 (4)	85 (3)	821	665
1985/86	196 (9)	72 (4)	196 (7)	47 (3)	550	768
1986/87	168 (7)	0	168 (5)	35 (1)	425	438
1987/88	Communal	0	255 (6)	24 (1)	n.r.	663
1988/89	Sustained, heavy		n.r.	0	n.r.	400

n.r. - not recorded.

growing season because long-term trials indicated winter grazing had little effect (O'Connor 1985).

Some preliminary work on the distribution of species within a site was undertaken to guide the sampling strategy. The influence of tree canopies and termite mounds on the herbaceous composition of the Thlavekisa site was described (Griffioen & O'Connor 1990). Four sub-habitats were studied; mounds in the open, mounds under canopies, flat areas in the open and flat areas under canopies. A correspondence analysis of the eight most common perennial grasses demonstrated that each of the four

sub-habitats supported a distinct herbaceous flora. *Cenchrus ciliaris* was associated only with mounds in the open, while *Heteropogon contortus* and *Aristida bipartita* were restricted to flat areas in the open. *Panicum maximum* and *Setaria incrassata* were associated with shaded environments, and the former was the most prolific species on shaded mounds. Although *Setaria* was most prolific in shaded flat areas it was also common in the open. *Themeda triandra* was associated with flat areas. the woody vegetation. Similarly it was found at Utha that the woody canopy influenced the local distribution of the main herbaceous species, and these results are more fully described in the subsequent chapter. Although no detailed measurements were taken on the sandveld site, a strong influence of the woody canopy on herbaceous composition was readily evident. This study was therefore restricted to between the tree canopies.

Within each grazing regime, three rainfall interception plots were constructed in 1984 at randomly located positions. These were restricted to between tree canopies. An interception plot consisted of wooden poles and heavy fencing wire upon which heavy duty plastic could be spread. When spread, the plastic was 2 m high at the apex and < 1 m high at the sides, and covered an area of 6 by 15 m. The plastic was only spread for individual storms, and retrieved once the storm had passed, hence plants were not physically disturbed. Ditches on the upslope and side-slope sides of each plot ensured that neither the water running off the plastic nor run-off from upslope entered the plot. Rainfall was reduced by 14% (75 mm) and 17% (129 mm) on the rainfall interception treatment at Thlavekisa and Utha respectively in the 1985/86 season. The Sandveld results are given in Chapter 5.

Rainfall was intercepted in the 1985/86 season only, as an influx of refugees into the area and their quest for building materials rendered it impractical to continue. The intention had been for at least two, and

preferably three years of rainfall manipulation. The implication of the disturbance was that extreme levels of rainfall could not be created, and comparisons were therefore limited to the natural variation in rainfall which occurred. Although this weakened the study, I decided to continue in the belief that the detailed data on population processes would meet the requirements of the degree, and decided to concentrate only on the clay soil sites in the final two years. For similar reasons, grazing treatments could not be maintained at the Thlavekisa site during the 1988/89 season. Fences had been removed the previous dry season, and both former grazing treatments were subjected to extremely intense grazing pressure throughout the growing season. The light grazing treatments had also been opened to grazing during the 1987 winter. An unplanned fire passed through the lightly grazed treatment at Thlavekisa during winter 1986.

Key species

Nomenclature for monocotyledons follows Gibbs-Russell *et al.* (1985), and for dicotyledons Gibbs Russell *et al.* (1987). The prominent perennial grasses of the clay soil sites were *Aristida bipartita*, *Bothriochloa insculpta*, *Digitaria eriantha*, *Heteropogon contortus*, *Setaria incrassata*, *Themeda triandra*, with small amounts of *Eragrostis superba* and *Urochloa mosambicensis*. Hereafter generic names only are used for convenience. *Themeda* and *Heteropogon* are longer-lived, palatable, obligate seed-reproducing species, while *Aristida* is a shorter-lived, wiry and unpalatable, obligate seed-reproducer. *Bothriochloa* reproduces mainly from seed but is occassionally stoloniferous. Two variants of *Digitaria* occurred. *Digitaria eriantha* var *pentzii* is a stoloniferous form and was

found at Utha, *D. eriantha* var *eriantha* grows by short compact rhizomes and was found at Thlavekisa.

Setaria has an unusual pattern of clonal growth. An electrophoretic investigation found that genets occupied about 0.25 m^2 (Carter 1987). Each genet could produce up to 5.7 ramets, where a ramet is defined as an aggregation of tillers which is spatially distinct from similar aggregations. Excavation of four rhizome networks revealed putative genet densities of 13, 16, 36 and 17 genets/m^2 (electrophoretic investigations could not be conducted on the excavated material). It was apparent that a genet could give rise to a number of physiologically independent ramets when the rhizome connection between them decayed. When monitoring *Setaria* there was therefore no way of discerning whether a ramet was either a different genet or physiologically independent without excavation or electrophoretic work.

Consideration of the sandveld site is deferred until Chapter 5, because all the results pertaining to this site are presented in one chapter.

Vegetation sampling

This section describes sampling procedures whose results are described in a number of chapters. The description of sampling procedures which appear in only one chapter are deferred until that chapter.

Twenty randomly located square 0.5 m quadrats were permanently located within each interception plot. Twenty similar quadrats were also permanently located in an area of 10 by 20 m adjacent to each interception plot, which received normal rainfall. All plots were restricted to the

between tree canopy habitat. The composition of each plot was assessed at the end of the growing season (April, May), commencing with the 1984/85 season. The density of each species in each quadrat was counted. An individual was defined as an apparently physiologically independent unit. Most of the grasses are tufted perennials, and their density was easily determined. For *Setaria*, each ramet (as defined above) was counted, although these might have been connected by rhizomes. Each rooted node of a stolon of *Digitaria eriantha* was counted, as these all separated from the parent plant in the same season that they established. The relative contribution of each species to biomass was ranked (Mannetje & Haydock 1967), and the height of the sward was measured, while projected cover, moribund material and litter cover were ranked (Walker 1976). The percentage cover of vegetation, litter and bare ground were estimated with a 10-point (over 1.8 m) Bruce-Levy frame, with 200 points per plot. All 20 quadrats of each plot were counted for the first three seasons for all sites. Thereafter monitoring of the sandveld site was discontinued.

On the two clay-soil sites, commencing in the 1985/86 season, a sub-sample of five quadrats per plot was randomly selected. All individuals were tagged and charted, and their circumference measured (cm). The basal cover of each species and of all species combined could be derived from these measurements. Basal cover was considered the most appropriate variable by which to assess the response of an individual species and for the comparison of species responses, although it is biased by growth form. In comparisons between species it was evident there was some upward bias of the basal area of *Setaria* because of its growth form, yet basal area was still considered the most consistent estimator for comparisons of species performance because the range in tuft sizes, and the differences between species, rendered density unsuitable. Biomass and cover are of little use in population based studies because they reflect seasonal conditions of growth. Detailed sampling of individual tillers was impractical.

The tufts closest to 52 randomly located points in each plot were tagged in the 1984/85 season. Those tufts on the clay soil sites were measured at regular intervals throughout the 1985/86 and 1986/87 growing seasons, usually preceding and following grazing events. The height of the highest leaf and the highest culm held vertical were measured, the number of reproductive culms (irrespective of stage of development) were counted, the proportion of biomass removed by grazing and the proportion of moribund material were ranked (Walker 1976). The basal circumference was measured at least once annually.

The distance to, and the basal circumference of, the four nearest neighbours was measured (in cm) on the Thlavekisa (1986/87 season) and Utha sites (1985/86 and 1986/87 seasons). The sampling procedure accommodated the angular dispersion of the neighbours, in that only one neighbour in each of four quadrants about the target individual was measured. The orientation of the quadrants was determined by the position of the first two or three nearest neighbours.

Data analysis

The grazing treatments of each site are an example of pseudo-replication (Hurlbert 1984), and inferences concerning the effects of grazing are therefore external to the statistical analyses. Details concerning data analysis are given in each chapter.

CHAPTER 4

COMPOSITION AND STRUCTURE OF THE COMMUNITIES

INTRODUCTION

Intra- and inter-specific interactions are a central theme of community ecology, whose purpose is ultimately to explain the structure of, and number of species within, a community. Yet knowledge of the effects of rainfall and grazing on the abundance of a species does not necessarily reveal anything of the nature of individu teractions. Species are rarely randomly distributed within a comm , and a large amount of descriptive and correlative study has been undertaken to define patterns and identify associated physical and biological factors (e.g. Turkington *et al*. 1977; Turkington & Harper 1979a; Fowler & Antonovics 1981; Belsky 1986; Yeaton *et al*. 1986; Mahdi & Law 1987). These descriptive efforts are an essential first step toward understanding how the component species of a community coexist. A related correlative approach for investigating competitive relationships between and within species has been to examine spacing patterns between individuals in relation to their size (e.g. Yeaton & Cody 1976; Waller 1981; Cody 1986; Smith & Goodman 1986), or the neighbourhood environment of an individual plant (Turkington & Harper 1979b; Fowler & Antonovics 1981; Weiner 1982, 1984), and only recently in plant ecology has an experimental approach been adopted to define interspecies interactions (e.g. Fowler 1981; Silander & Antonovics 1982; Tilman 1982, 1988). The mark[illegible] rainfall variability of savannas may differentially favour species from year to year (Dye & Walker 1987).

Because of the significance of competition for vegetation dynamics, an objective was to describe the relationship between species, and to develop some initial hypotheses on competition in these communities. Therefore the patterns of spatial dispersion, patterns of association between species, spacing patterns between individuals, and differences in growth patterns between species were examined.

METHODS

The counts of species within the 240 permanently located quadrats at the end of the 1984/85 season formed the data base for the analysis of spatial pattern. The relationship between quadrats and between species was examined with reciprocal averaging (Hill 1979), using the CANOCO package (ter Braak 1988). Rare species were deleted and herbaceous dicotyledons entered as one species. The association between pairs of species was investigated with Hurlbert's (1969) coefficient of association, which is based on presence or absence. The coefficient is not effective if the value of one of the species tends to unity or zero. The degree of contagion of each major species at the scale of quadrats was investigated with Morisita's index of dispersion (in Greig-Smith 1983).

Interference between individuals would be expected to be reflected in their spacing patterns, dependent on the size of the individuals. The relationship between the size of a focal tuft and the size of its neighbours, together with the distances between them, has been widely investigated in a variety of habitats to infer competition (Yeaton & Cody 1976; Mack & Harper 1977; Nobel 1981; Waller 1981; Weiner 1982, 1984; Cody 1986; Penridge & Walker 1986; Smith & Goodman 1986; Firbank & Watkinson 1987). Most commonly a relationship has been sought between the combined

sizes of a focal tuft and its nearest neighbour and the distance between them. Size hierarchies are the norm for plant populations (e.g. Weiner 1985), and the symmetry of competitive interaction between two individuals would be expected to become more uniform the more equivalent their sizes were. Hence the largest neighbour may be a better predictor than the nearest neighbour for the spacing between individuals. However, the most appropriate measure is to consider the total neighbourhood environment, which Mack & Harper (1977) described by taking into account the density and size of all plants, and their angular dispersion, within two concentric circles around the focal tuft. The measure suffers from the problem that the size of the circles is arbitrary, and the effect of some individuals may be blocked out by closer ones. Firbank & Watkinson (1987) resolve these problems with a measure of the competitive pressure on a focal plant, p, defined as

$$p = \Sigma c_j d^{-2} w_{ij} ,$$

where d is the distance between tufts, c_j a constant for species j, and w_{ij} the size (weight) of the ith individual of species j. Weiner (1984) found that the inverse of the distance was as good a predictor as the inverse of the distance squared. Correlations can be sought between p and the size of the individual. I assumed that the predominant effect of a neighbour occurred as a single vector toward the focal tuft, whose magnitude was determined by the size of the individual (tuft radius) divided by the distance between tufts. Hence

$$N = \Sigma\ r_i/d_i$$

where N is the neighbourhood interference. It was usually found that four neighbours, and in some instances only three, completely surrounded the focal tuft.

Correlations were sought between the combined basal areas of a tuft and both its nearest or largest neighbour, and between the area of a tuft and the index of neighbourhood interference, using Pearson's product moment correlation coefficient. It was tested if each species had the same

species as its nearest or largest neighbour in a different proportion to that which it occurred in the surrounding vegetation, using the normal probability distribution for the difference between two proportions (z statistic, for n>20).

The growth pattern of the most common species of the two clay soil sites was described for the 1985/86 and 1986/87 growing seasons. The index of growth used was the extended leaf height of the individually monitored tufts. Means and standard errors were obtained from a pooled sample of the three plots per rainfall treatment in 1985/86, and six plots in 1986/87. Because most sample sizes were reasonably large (>30) asymptotic normality was assumed.

RESULTS

Spatial pattern

All species at all sites showed contagion ($p<0.05$), and therefore an individual of a species is most likely to interact with individuals of the same species.

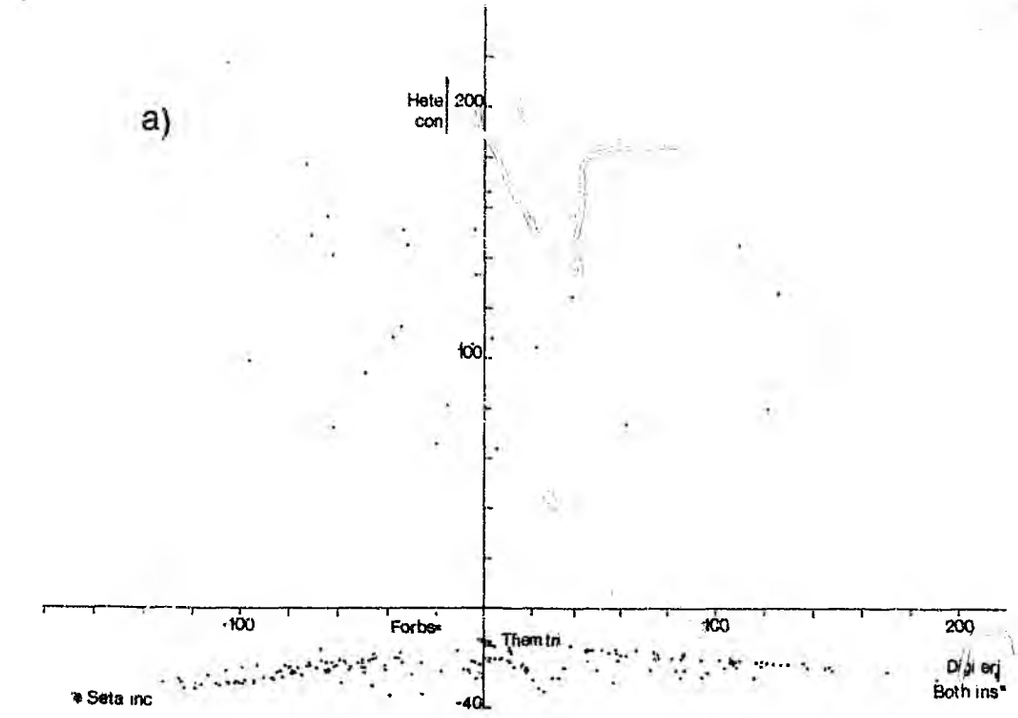
The Utha grassland was species poor, and only five species occurred frequently enough to be entered into the ordination. The first axis of reciprocal averaging (eigenvalue=0.39) described a gradient from quadrats exclusively occupied by *Setaria*, through quadrats exclusively occupied by *Themeda*, through to quadrats with increasing amounts of *Digitaria* and *Bothriochloa* together with *Themeda* (Figure 4.1a). A very small number

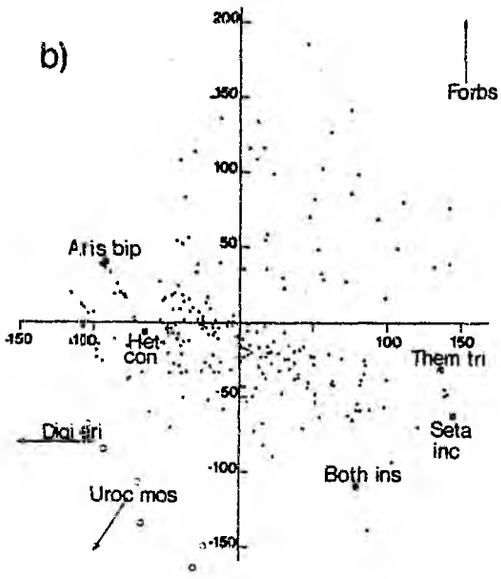
of quadrats were almost pure patches of *Digitaria* and *Bothriochloa*. The second axis (eigenvalue=0.27) separated out all those quadrats with *Heteropogon*, a few of which were patches exclusively of the species (Figure 4.1a). The third axis (eigenvalue=0.22) separated quadrats with *Bothriochloa* as a prominent species from quadrats with herbaceous dicotyledons, whilst the fourth axis (eigenvalue=0.15) separated quadrats that were predominantly either *Bothriochloa* or *Digitaria*. Hurlbert's coefficient showed that *Setaria* was negatively associated ($p<0.05$) with *Themeda*, *Bothriochloa* and *Digitaria*, while *Themeda* was positively associated with *Bothriochloa* and *Digitaria*, as was *Bothriochloa* ($p<0.05$).

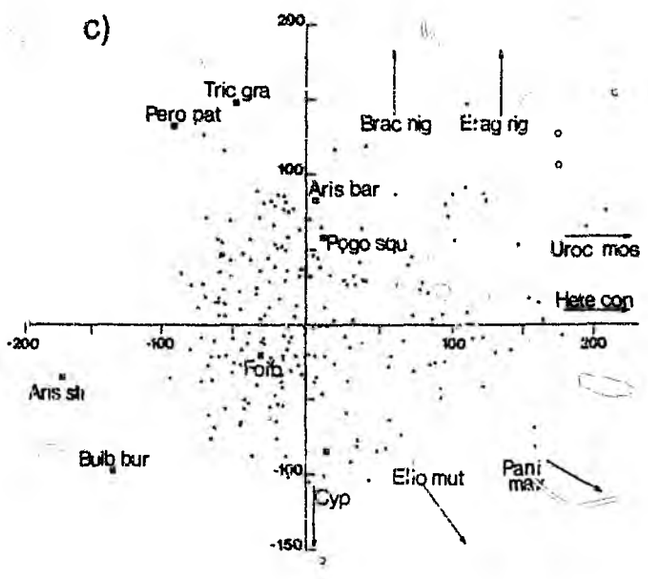
The pattern of association between species and their spatial dispersion appeared to conform to a two-phase mosaic, which was further investigated for the lightly grazed treatment (Carter & O'Connor 1991). Species local frequency was sampled along three 150 m transects up the slope, and three 70 m transects along the contour. One phase was dominated by *Setaria*, which was negatively ($p<0.05$) or not associated with any of the perennial grasses or common herbaceous dicotyledons. The other phase was dominated by *Themeda*, which was positively associated ($p<0.05$) with *Bothriochloa*, *Digitaria* and *Chaetacanthus burchellii*. Paired quadrat variance analyses revealed similar significant anisotropic scales of contagion of both *Setaria* and *Themeda*, with a mosaic scale of about 9 m up the slope and 4 m along the contour. *Setaria* was positively ($p<0.05$) and *Themeda* negatively ($P<0.05$) associated with the tree canopy. *Setaria* was also associated with deeper soils of higher organic content than *Themeda* ($P<0.05$). *Heteropogon contortus* and *Panicum maximum* formed two distinct but uncommon patch types, neither of which was associated with *Setaria* or *Themeda* or with each other ($p<0.05$).

The Thlavekisa grassland shared the same grass species as Utha, although they were more equitably represented. An initial ordination revealed that a number of quadrats dominated by *Urochloa mosambicensis* or herbaceous

Figure 4.1. An ordination of the first two axes of a correspondence analysis of the composition of the 0.5 m square quadrats of the a) Utha, b) Thlavekisa, and c) Sandveld sites for 1984/85. Key to species: a) Bi - *Bothriochloa insculpta*, De - *Digitaria eriantha*, Hc - *Heteropogon contortus*, Si - *Setaria incrassata*, Tt - *Themeda triandra*. b) Ab - *Aristida bipartita*, Bi - *Bothriochloa insculpta*, De - *Digitaria eriantha*, Fb - herbaceous dicotyledons, Hc - *Heteropogon contortus*, Si - *Setaria incrassata*, Tt - *Themeda triandra*; c) Ab - *Aristida congesta* subsp *barbicollis*, As - *Aristida stipitata*, Bb - *Bulbostylis burchellii*, Bn - *Brachiaria nigropedata*, Cy - Cyperaceae, De - *Digitaria eriantha*, Ea - *Elionurus muticus*, Er - *Eragrostis rigidior*, Fb - herbaceous dicotyledons, Hc - *Heteropogon contortus*, Pm - *Panicum maximum*, Pp - *Perotis patens*, Ps - *Pogonarthria squarrosa*, Tg - *Trichoneura grandiglumis*, Um - *Urochloa mosambicensis*. Open circles denote passive quadrats (not all shown). Some quadrats are hidden. Scale of axes = 10^{-2}.


a)
Hete con
200
100
-100
Forbs
Them tri
100
200
Digi eri
Both ins
Seta inc
-40


b)
200
150
100
50
-50
-100
-150
-150
-100
Het con
100
150
Forbs
Them tri
Aris bip
Digi siri
Seta inc
Both ins
Uroc mos


c)
200
100
-100
-150
-200
-100
100
200
Tric gra
Pero pat
Brac nig
Brag nig
Aris bar
Pogo squ
Uroc mos
Hete con
Forb
Aris sti
Bulb bur
Ellio mut
Pani max
Cyp

dicotyledons strongly influenced the ordination. These anomalous quadrats were then entered as passive quadrats, and a second ordination revealed a pronounced gradient along the first axis (eigenvalue=0.224) from quadrats dominated by *Aristida* and/or *Heteropogon* through to quadrats dominated by *Setaria* and/or *Themeda* (Figure 4.1b). *Aristida* and *Digitaria* were more clumped than the other species. The second axis (eigenvalue=0.18) separated out quadrats which were influenced by either herbaceous dicotyledons or by the uncommon grasses *Urochloa* or *Bothriochloa*. The third (eigenvalue=0.172) and fourth (eigenvalue=0.158) axes separated out quadrats dominated by either *Aristida* or *Heteropogon*. There were significant positive associations between *Themeda* and *Setaria*, *Bothriochloa* and *Setaria*, and *Heteropogon* and *Digitaria*, while negative associations were found between *Aristida* and both *Setaria* and *Themeda*, and between *Heteropogon* and *Bothriochloa*.

The predominant species of the sandveld were *Pogonarthria squarrosa*, *Digitaria eriantha* and herbaceous dicotyledons. A first ordination was strongly influenced by 23 quadrats which were dominated by uncommon species. These quadrats were made passive in a second ordination. Because of the high frequency of occurrence of *P. squarrosa* and *D. eriantha*, these two species exercised little influence on the first axis of reciprocal averaging (eigenvalue=0.239). The first axis described a gradient of usually mutually exclusive species, from *Aristida stipitata* and *Bulbostylis burchellii* through to *Panicum maximum*, *Heteropogon contortus* and *Urochloa mosambicensis*. The second axis (eigenvalue=0.2) partly separated out the quadrats dominated by *P. squarrosa* or *D. eriantha*. *Perotis patens* and *Trichoneura grandiglumis* were similarly distributed, and there was some similarity in the distribution of *P. squarrosa* and *Aristida congesta* subsp *barbicollis*, but otherwise the species were not closely associated (Figure 4.1c). *Urochloa mosambicensis* was negatively associated (Hurlbert's coefficient - $p<0.05$) with *P. squarrosa*, *Perotis patens*, *Trichoneura grandiglumis* and

Bulbostylis burchellii, while *B. burchellii* was positively associated ($p<0.05$) with *Aristida stipitata*, *Trichoneura grandiglumis* and *D. eriantha*. *Perotis patens* and *Bulbostylis burchellii* were the most clumped of the sandveld species.

A consistent pattern across all three sites therefore was that the individuals of each species were aggregated, and there was close association between pairs or groups of species. Thus intra-specific interactions were in general likely to be more important than interspecific ones, and interspecific interactions were ordered.

Relationships with neighbours

The correlations between the sum of the areas of a target individual and its nearest neighbour, or with its largest neighbour, and the distance between them, was significant for most species (Tables 4.1, 4.2). For *Themeda* at Utha, these relationships were partly dependent on the species identity of the neighbour. There was a significant relationship for all four treatments if *Themeda* was the nearest or largest neighbour, for three treatments with *Setaria* as the largest neighbour, but for only one treatment with *Setaria* as the nearest neighbour, and for one treatment with *Digitaria* as the nearest neighbour. There were only five significant ($p<0.05$) or near significant correlations between the size of a tuft and the neighbourhood index. Four of these, three for *Setaria* and one for *Digitaria* at Utha, were not in the expected direction, while one relationship for *Bothriochloa* at Thlavekisa was.

There was a general tendency for the nearest or largest neighbour of an individual to be of the same species. At Utha, this was the case for all

Table 4.1. The distance (l) between a focal tuft and its nearest or largest neighbour, and the Pearson's product moment correlation between this distance and the combined areas of the two tufts, for seven species at the Thlavekisa site, for four treatments in 1987 (HD - heavily grazed, rainfall interception, HR - heavily grazed, normal rainfall; LD - lightly grazed, rainfall interception; LR - lightly grazed, normal rainfall).

	HD			HR			LD			LR		
Species	n	r	l (cm)	n	r	l (cm)	n	r	l (cm)	n	r	l (cm)
Nearest Neighbour												
Aristida	39	0.19ns	6.6	38	0.40*	6.5	44	0.07ns	8.4	49	0.47***	7.5
Bothriochloa	26	0.48*	7.7	31	0.38*	5.5	31	0.25ns	7.6	29	0.34(*)	9.9
Digitaria	12	0.64*	7.9	19	0.43(*)	6.9	6	0.92**	7.5	10	0.15ns	7.4
Heteropogon	39	0.30(*)	7.8	41	0.46**	7.4	30	0.40*	8.9	47	0.25ns	10.1
Setaria	31	0.66***	10.0	23	0.85***	8.8	38	0.76***	9.3	25	0.35ns	9.3
Themeda	29	0.48**	8.5	44	0.52***	8.3	40	0.45**	9.0	33	0.40*	9.1
Urochloa	16	0.61*	9.1	5	0.79ns	6.4	5	0.90*	10.2	9	0.62(*)	7.2
Largest Neighbour												
Aristida		0.39*	15.6		0.50**	13.9		0.35*	13.5		0.20ns	14.7
Bothriochloa		0.56**	14.8		0.29ns	12.4		0.21ns	17.0		0.14ns	21.4
Digitaria		0.22ns	14.3		0.21ns	13.4		0.24ns	13.7		0.95***	15.6
Heteropogon		0.62***	15.2		0.45**	15.5		0.65***	14.9		0.08ns	19.7
Setaria		0.56**	17.7		0.70***	14.0		0.79***	17.8		0.70***	16.9
Themeda		0.29ns	15.3		0.48***	15.5		0.27ns	16.1		0.52**	16.6
Urochloa		0.37ns	13.9		0.83*	16.0		-0.22ns	18.2		-0.13ns	13.4

*** - $p<0.001$; ** - $p<0.01$; * - $p<0.05$: (*) - $p<0.06$; ns - not significant

Table 4.2. The distance (l) between a focal tuft and its nearest or largest neighbour, and the Pearson's product moment correlation between this distance and the combined areas of the two tufts, for four species at the Utha site, for four treatments in 1987 (HD - heavily grazed, rainfall interception; HR - heavily grazed, normal rainfall; LD - lightly grazed, rainfall interception; LR - lightly grazed, normal rainfall).

	HD			HR			LD			LR		
Species	n	r	l (cm)	n	r	l (cm)	n	r	l (cm)	n	r	l (cm)
Nearest Neighbour												
Bothriochloa	19	0.04ns	7.0	6	0.25ns	6.0	22	0.67***	6.9	11	0.27ns	8.6
Digitaria	50	0.06ns	7.2	23	0.31ns	7.1	26	0.33ns	7.2	21	0.50*	7.3
Setaria	34	0.62***	7.3	40	0.44**	6.7	69	0.39**	9.2	66	0.58***	9.6
Themeda	108	0.36***	7.0	121	0.35***	7.3	69	0.61***	8.1	79	0.43***	8.9
Largest Neighbour												
Bothriochloa		0.26ns	14.1		0.15ns	16.3		0.41(*)	14.2		0.07ns	18.9
Digitaria		0.35*	11.9		0.48*	12.2		0.42*	13.2		0.46*	14.5
Setaria		0.45**	13.4		0.18ns	12.2		0.62***	15.4		0.74***	17.8
Themeda		0.26**	13.5		0.56***	13.8		0.58***	15.8		0.33	16.8

*** - $p<0.001$; ** - $p<0.01$; * - $p<0.05$; (*) - $p<0.06$; ns - not significant

treatments for *Themeda*, *Setaria* and *Digitaria*. At Thlavekisa, *Themeda* and *Heteropogon* on three, *Bothriochloa* on two and *Aristida* on one treatment, did not have the same species as nearest neighbour in any greater proportion than they occurred in the surrounding vegetation. Nor

did *Aristida* on all and *Themeda* and *Bothriochloa* on two treatments have the same species as the largest neighbour in any greater proportion than expected.

The nearest neighbour of an individual was usually <10 cm away, while the largest neighbour was about 15 cm away (Table 4.1, 4.2). There was a tendency for the nearest or largest neighbour to be further from the focal tuft on the lightly grazed treatment.

Growth Patterns

The within and between season pattern of rainfall influenced the growth of all species in a similar manner (Figures 4.2, 4.3). In the 1985/86 season, all species consistently gained height from early November through to mid-Februaury following a succession of moderately sized rainfall events. There was a month-long dry period during February and March 1986 during which height of all species declined. Substantial rain in late March and mid-April resulted in a spate of late season growth until late May. The 1986/87 wet season differed in that total annual rainfall was lower, but there were very substantial rains during December 1986 and January 1987, which resulted in rapid growth. An intervening five-week dry spell did not prevent the sward from growing far taller than in the previous season. However, the length of the 1986/87 season was attenuated compared to the previous season; following rains in March, there was no further growth.

Under lightly grazed conditions, there were clear differences between species in the extent, but not the pattern, of growth. *Themeda* had the tallest leaf height, up to 80 cm high, while *Setaria* maintained a similar

Figure 4.2. The a) number of cattle (dotted lines represent the light grazing treatment, solid columns the heavy grazing treatment), b) rainfall, and c) the mean height of extended leaves of the common grasses at Thlavekisa during the 1985/86 and 1986/87 growing seasons. Open symbols denote the heavily grazed treatment, closed symbols the lightly grazed treatment. Key to species: *Aristida bipartita* (inverted triangle), *Bothriochloa insculpta* (circle), *Heteropogon contortus* (dash for lightly grazed, plus in open circle for heavily grazed), *Setaria incrassata* (triangle) and *Themeda triandra* (square).

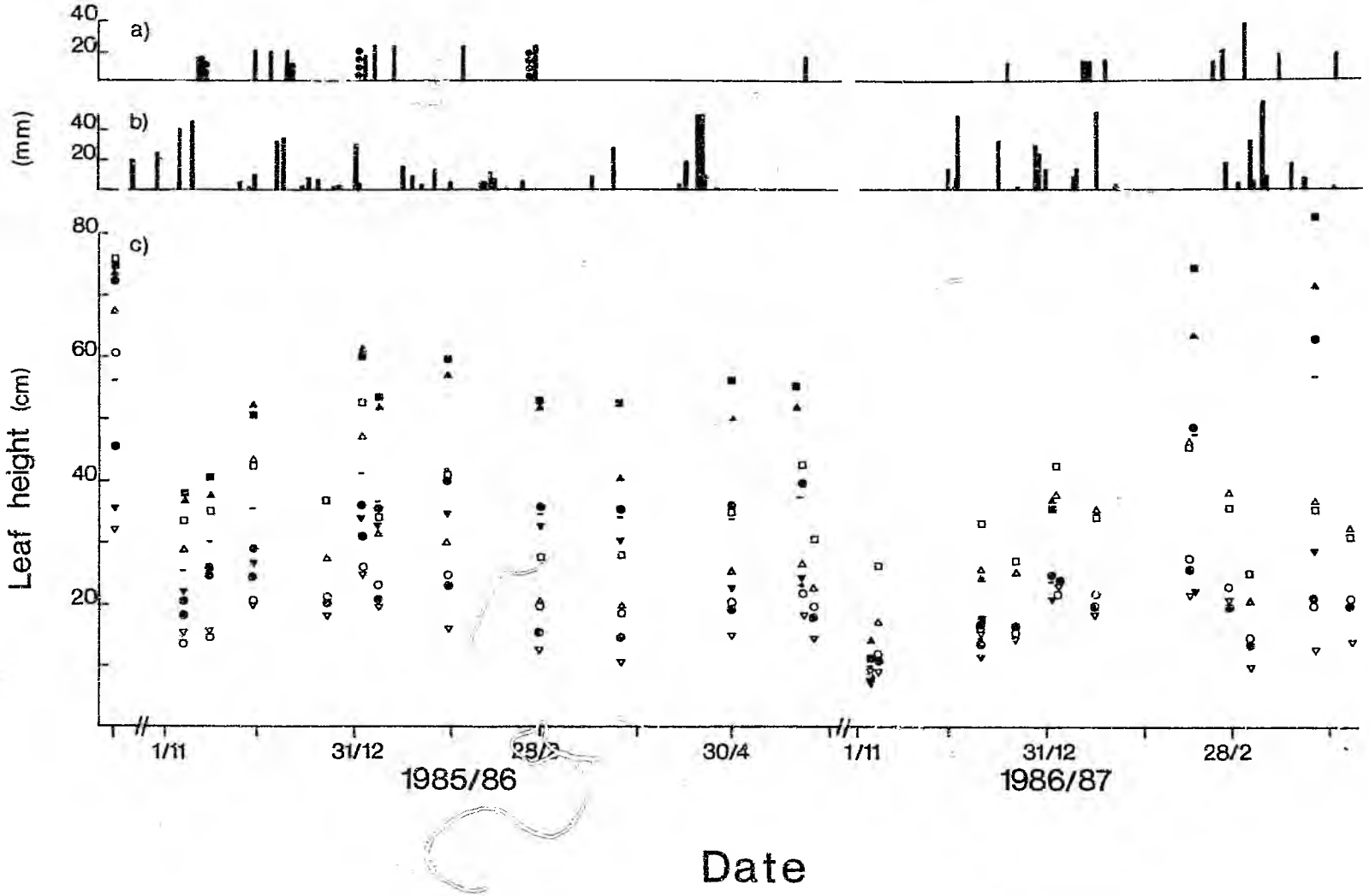
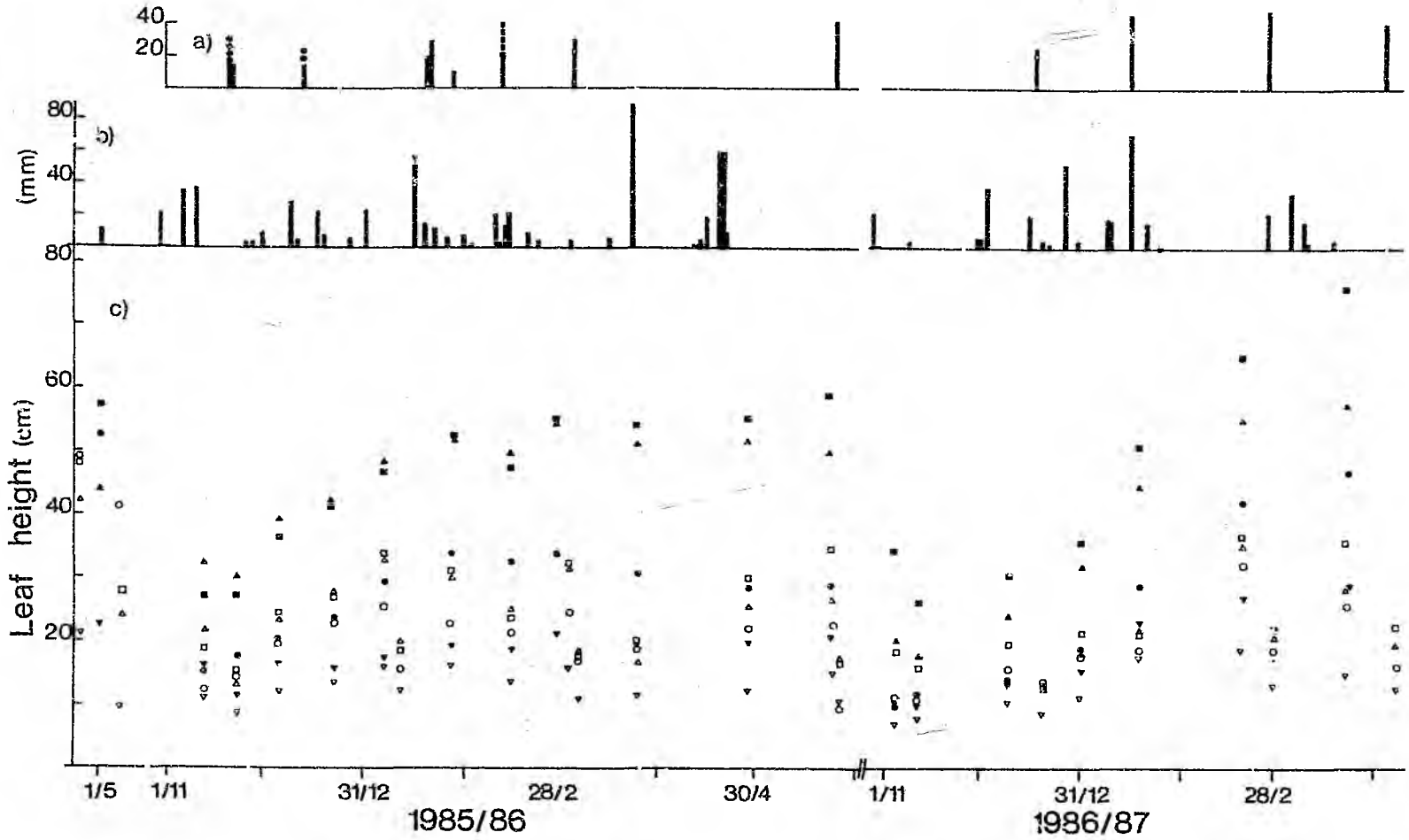

a)
b)
c)
40
20
40
20
80
60
40
20
(mm)
Leaf height (cm)
1/11
31/12
28/2
30/4
1/11
31/12
28/2
1985/86
1986/87
Date

Figure 4.3. The a) number of cattle (dotted lines represent the light grazing treatment, solid columns the heavy grazing treatment), b) rainfall, and c) the mean height of extended leaves of the common grasses at Utha during the 1985/86 and 1986/87 growing seasons. Open symbols denote the heavily grazed treatment, closed symbols the lightly grazed treatment. Key to species: *Bothriochloa insculpta* (circle), *Digitaria eriantha* (inverted triangle), *Setaria incrassata* (triangle) and *Themeda triandra* (square).


40
20
a)
80
b)
(mm)
40
80
c)
60
40
20
Leaf height (cm)
1/5
1/11
31/12
28/2
30/4
1/11
31/12
28/2
1985/86
1986/87
Date

height to *Themeda* in the first half of each grazing season, its leaf height was up to 20 cm less by the end of the season. *Digitaria* and *Aristida* were by far the shortest species at Utha and Thlavekisa respectively, while *Bothriochloa* and *Heteropogon* were of intermediate height. *Bothriochloa* had, however, attained the same height as the tallest species in the 1984/85 season.

Grazing reduced the leaf height of all species by up to 50% in the 1985/86 season, and in excess of this the following season, with a single grazing event lowering the leaf height by up to 15%. However, the pattern of difference between species was largely unaltered, except that there was little difference between *Setaria* and *Themeda* by the end of the season.

DISCUSSION

The significant correlations between the combined size of a focal tuft and its nearest or largest neighbour and the distance between them, has been shown for a wide variety of species of different growth forms in very different environments (Yeaton & Cody 1976; Mack & Harper 1977; Nobel 1981; Waller 1981; Liddle *et al.* 1982; Cody 1986; Smith & Goodman 1986; Firbank & Watkinson 1987). However, even in the more successful studies which have used a correlation approach to infer competition, only about 20% of the variance has been accounted for (Firbank & Watkinson 1987), which is a similar order of magnitude to this study.

Caution is required in the evaluation of nearest neighbour correlation analyses (Firbank & Watkinson 1987). Firstly, it is assumed that the predictor variables (measures of neighbours) are statistically independent of the response variables (focal tuft), but this requirement

is not upheld, because a focal tuft is both affected by its neighbours and affects them (Cormack 1979). Secondly, the neighbourhood approach implicitly assumes that competition can be completely described in two dimensions (Firbank & Watkinson 1987), and the approach would therefore be most appropriate for describing two-sided competition, in which there is little overlap in either shoot or root systems. Two-sided competition therefore occurs only when there is no encroachment by one plant into another plants zone of influence, which is more likely when light is not a limiting factor or when plants grow predominantly in two dimensions (Firbank & Watkinson 1987). In this study, the pronounced differences in height between species (Figures 4.2, 4.3) and their close proximity (Tables 4.1, 4.2), and the pronounced size hierarchies within species (Tables 7.1, 7.2) indicate the potential for pronounced intra- and interspecific interference in the vertical dimension, at least under lightly grazed conditions. It is probable that root systems also intermingle (pers. obs.). Hence competition is likely to tend to one rather than two-sided. This second fundamental flaw of a neighbourhood approach was only recognised retrospectively, but in part explains the poor amount of variation accounted for. In contrast, most successful studies have been of desert and dune systems (Yeaton & Cody 1976; Mack & Harper 1977; Nobel 1981; Cody 1986) where competition can be expected to tend to two-sided. Thirdly, the fragmentation of tufts over the course of the study (fully described in chapters 7 and 9) in accordance with a trend of decreasing rainfall, suggests that intra-tuft rather than between tuft interference was more important for the conditions during the study. Fourthly, there were positive correlations between species in the change in basal area between years (Chapter 6) and in population growth rates (Chapter 9), suggesting that an extrinsic force, considered to be the trend of rainfall, overrode interspecies interactions.

In conclusion, correlative methods are not considered to be an appropriate means of investigating interference in grasslands of this nature, an

experimental approach is needed from the outset. I therefore speculate below on some of the key competitive interactions shaping the dynamics of these communities, garnered from circumstantial evidence, and suggest some key experiments.

The apparent restriction of *Aristida*, *Digitaria*, *Heteropogon* and *Urochloa* to between tree canopies at Thlavekisa (Griffioen & O'Connor 1990) suggests that the local distribution of these species is partly determined by irradiance levels. *Themeda* and *Setaria* have a pronounced height advantage over these species under lightly grazed conditions (Figures 4.2, 4.3), but the potential shading effect of tall species depends on their local density. The hypothesis is that the short species are shaded out by *Themeda* and *Setaria* during sequences of good growth years, providing their local density is sufficient. Manipulation on a small patch scale (e.g. 1 m^2) of light (shadecloth) and water (irrigation) for a sequence of years over a range of local densities of both the tall and the short species (or the manipulation of local density through the supply of seeds or transplants) would test this.

A second experiment could test if soil moisture and light are the factors ultimately responsible for the pronounced mosaic of *Themeda* and *Setaria* at Utha. On a regional scale *Themeda* is found in more xeric environments than *Setaria*, and is usually found between tree canopies, while *Setaria* is usually most common in the open, low-lying wet areas. The hypothesis for the Utha mosaic is that *Themeda* has a superior competitive ability for soil moisture, but requires high irradiance levels, while *Setaria* has a superior ability under low light levels, but requires high moisture levels. An assumption is that a woody canopy cover promotes a more benign soil moisture regime (easily tested). An experiment would manipulate the light and water regimes of *Themeda* patches in the open and of *Setaria* patches with the tree canopy removed, having introduced either species as seeds and/or transplants.

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CHAPTER 5

THE INFLUENCE OF RAINFALL AND GRAZING ON THE COMPOSITIONAL CHANGE OF THE HERBACEOUS LAYER OF A SANDVELD SAVANNA

INTRODUCTION

The primary influence of grazing on herbaceous layer compositional change is a central tenet of range management, yet the evidence from the long term data sets for the savanna grasslands of southern Africa suggest that the effect of grazing is contingent upon rainfall (O'Connor 1985). However, the majority of these long term studies were either not designed appropriately or not sampled intensively enough to partition the relative effects of rainfall and grazing on compositional change. Furthermore, an explanation of compositional change has to be sought in the population mechanisms of mortality and recruitment of the component species (Jones & Mott 1980), an approach which has prevailed little in the study of southern African savannas.

The purpose of this study was to determine the influence of rainfall and grazing on the compositional change of a sandveld savanna grassland in the short term.

METHODS

Details of site and treatments

The study was initiated in 1984/85, a wet year, which was preceded by a wet year, while the 1985/86 and 1986/87 seasons were successively drier (Table 5.1). The site supported a woodland (approximately 50% canopy cover) with *Terminalia sericea*, *Sclerocarya birrea* and *Strychnos madagascariensis* as the predominant elements, while *Dichrostachys cinerea*, *Combretum collinum*, *Combretum hereroense* and *Diospyros mespiliformis* were also common. The study was restricted to the between canopy areas. Grazing occurred as discrete events, usually for one or two days, with 5-20 cattle for each event (Table 5.1). The frequency of grazing depended on vegetation regrowth, but was at approximately monthly intervals through the growing season for the heavily grazed treatment. Most of the available herbage of the light grazing treatment was grazed during the dry season of 1986 (not by design), but because the material was dormant at the time it is not believed that the grazing event had a significant effect on results. The annual rainfall of the 1985/86 season was reduced by 87 mm (14%) on the rainfall interception plots.

Data analysis

Because the grazing treatments are an example of pseudo-replication (Hurlbert 1984), inferences concerning the effects of grazing are external to the statistical analyses. Conclusions regarding grazing have

Table 5.1. The number of cattle grazing days and the number of grazing events (in parenthesis) per growing season, for the heavily and the lightly grazed treatments (each 0.64 ha), and the annual (July to June) rainfall.

	Grazing days (events)		
Season	Heavily grazed	Lightly grazed	Rainfall (mm)
1983/84	Heavy communal grazing		714
1984/85	69 (2)	28 (2)	821
1985/86	122 (6)	49 (3)	619
1986/87	52 (3)	0	425

been based on trends through time of means of density and their confidence intervals. The precision of confidence intervals was improved because sample estimates of variance could be calculated for a two stage sampling process (Cochran 1977). There were three primary units (plots) for each rainfall treatment within each grazing treatment, with 20 sampling units (quadrats) per primary unit. The number of primary units sampled was a negligible fraction of the total number of units of the site, and hence the sample estimate of the variance simply approximates to

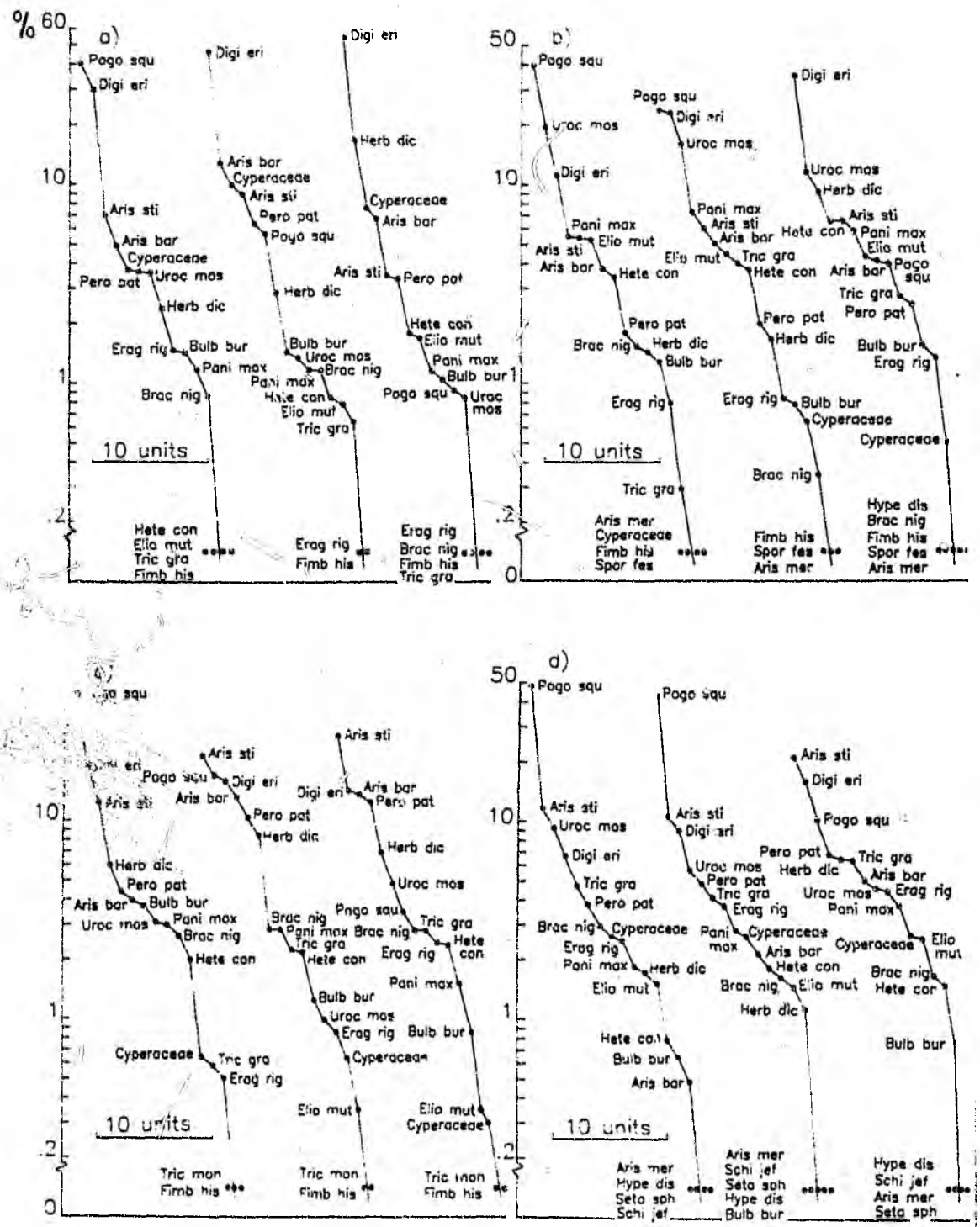
$Var(y) = (y_i - y)^2 / n(n-1)$, where y_i= unit mean (i=1-3), (Cochran 1977, p279).

Thus the estimated variance can be computed from a knowledge of the unit means only.

The differences between the rainfall treatments of each grazing treatment were amenable to ANOVA's. A univariate approach to the analysis of repeated measures of density was adopted (Gurevitch & Chester 1986), individually for each species, and for all grasses and sedges combined. The mean density of each variable for each of the three years per rainfall treatment was reduced to a single weighted sum by fitting orthogonal polynomials. Two sets of orthogonal polynomials were separately fitted, for both linear and quadratic contrasts between rainfall treatments. These contrasts were separately tested by ANOVA as a completely randomised design with two treatments. In this case the Grand Mean of the ANOVA is used to test the hypothesis that the overall linear or quadratic trend of time for both treatments is zero. The F test associated with treatment tests the hypothesis that the linear or quadratic trends for the two treatments are equal, that is, it tests whether there is an interaction between the treatment effects and the linear effects of time. Finally, the main effects of the treatments is analysed by an ANOVA of the sum of all observations on each plot.

The influence of rainfall treatment on the change in tuft size and on tuft mortality between 1985 and 1986, and between 1985 and 1987, was tested for each species for each grazing treatment. The change in tuft size was analysed by 2-way ANOVA, where observations included tufts which had died (circumference=0). Tuft mortality was analysed by G-tests (Sokal & Rohlf 1981, p731) (pooled sample for each treatment). The influence of rainfall on the leaf height and cover of each grazing treatment was also analysed by ANOVA.

Figure 5.1. The percentage contribution to biomass (logarithmic scale) of the herbaceous sward over three years (1985 on left to 1987 on right) for a) rainfall interception, heavily grazed; b) normal rainfall, heavily grazed; c) rainfall interception, lightly grazed; and d) normal rainfall, lightly grazed. Key to the species: Aris bar - *Aristida congesta* subsp. *barbicollis*, Aris mer - *Aristida meridionalis*, Aris sti - *Aristida stipitata*, Brac nig - *Brachiaria nigropedata*, Bulb bur - *Bulbostylis burchellii*, Cyperaceae - all sedges other than *Bulbostylis burchellii* and *Fimbrystylis hispidula*, Digi eri - *Digitaria eriantha* var *stolonifera* (plus very small amount of *D. eriantha* var *pentzii*), Elio mut - *Elionurus muticus*, Erag rig - *Eragrostis rigidior*, Fimb his - *Fimbrystlis hispidula*, Herb dic - herbaceous dicotyledons (forbs), Hete con - *Heteropogon contortus*, Hype dis - Hyperthelia dissoluta, Pani max - *Panicum maximum*, Pero pat - *Perotis patens*, Pogo squ - *Pogonarthria squarrosa*, Schi jef - *Schizachyrium jeffreysii*, Seta sph - *Setaria sphacelata*, Spor fes - *Sporobolus festivus*, Tric gra - *Trichoneura grandiglumis*, Tric mon - *Tricholaene monachne*, Uroc mos - *Urochloa mosambicensis*.

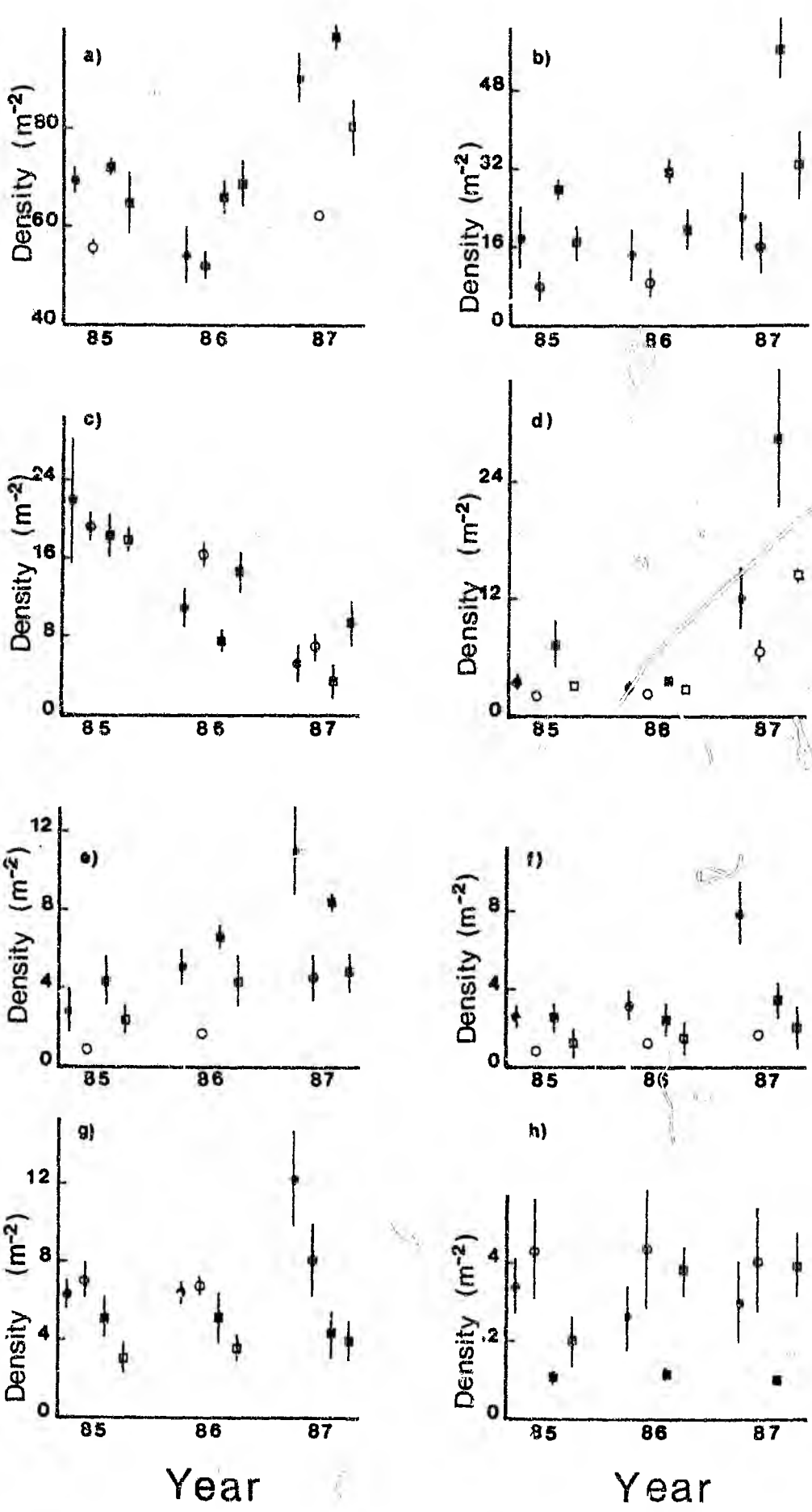

%
a)
b)
c)
d)
10 units
Species Rank
Species Rank

RESULTS

Change in relative biomass

There were two consistent changes in contribution to biomass which were independent of the imposed treatments (Figure 5.1), and which are ascribed to the prevailing rainfall pattern. Firstly, the sward was diverse, with >20 grass and sedge species, but *Pogonarthria squarrosa* was the most abundant species on all treatments in 1985 (40-50%). By 1987, however, its contribution had declined to only 1-10%. For each grazing treatment, the contribution of *P. squarrosa* declined more rapidly on the rainfall interception pl[illegible]. Secondly, forbs were a minor biomass component of all treatments in 1985, with little change between 1985 and 1986, but by 1987 the contribution of forbs had dramatically increased on all treatments except the normal rainfall, lightly grazed treatment. Although *Digitaria eriantha* var *stolonifera* was a major component of all treatments in 1985, its contribution had markedly increased on the heavily grazed treatment by 1987 (Figure 5.1). On the lightly grazed treatment, *D. eriantha* declined slightly on the rainfall interception treatment between 1985 and 1987, but increased on the normal rainfall treatment. The contribution of *Aristida stipitata* and *A. congesta* subsp. *barbicollis* increased considerably on the lightly grazed, but not on the heavily grazed, treatment.

Figure 5.2. The mean number / m^2 (± 1 S.E.) of individuals of a) total for all grasses and sedges combined, b) *Digitaria eriantha*, c) *Pogonarthria squarrosa*, d) forbs, e) *Aristida congesta* subsp. *barbicollis*, f) *Aristida stipitata*, g) *Perotis patens* and h) *Trichoneura grandiglumis* for the rainfall interception, lightly grazed ( ), normal rainfall, lightly grazed ( ), rainfall interception, heavily grazed (--) and normal rainfall, heavily grazed (--) treatments over three years. S.E.'s not shown are contained within the symbols.


a)
b)
c)
d)
e)
f)
g)
h)
Density (m-2)
85
86
87
Year

Changes in density

The density of *Pogonarthria squarrosa* declined linearly ($p<0.05$), and did not appear to be influenced by grazing (Figure 5.2c). There was a tendency for a greater rate of population decline on the rainfall interception treatments. A linear increase ($p<0.05$) in density was observed for *Aristida stipitata* (*Figure 5.2f*), *A. congesta* subsp. *barbicollis* (Figure 5.2e), forbs and all grasses (plus sedges) combined (Figure 5.2a). The significant increase in density of *Aristida congesta* subsp. *barbicollis* on both grazing treatments tended to be greater on the rainfall interception treatments ($p>0.05$). The response of *A. stipitata* was similar to that of *A. congesta* subsp. *barbicollis*. There was a linear and quadratic increase of forbs ($p<0.05$) on both grazing treatments (Figure 5.2d). The majority of the forbs censused in 1985 were perennials, with *Waltheria indica* the most common species. The "explosion" of forbs in 1987 was more pronounced on the heavily than the lightly grazed treatment, and particularly on the rainfall interception treatment. The forb community in 1987 was predominantly annual in composition, with *Tephrosia purpurea*, *Indigofera costata* and *Cassia absus* as prominent species, and differed slightly between the grazing treatments (Table 5.2).

Digitaria eriantha responded mainly to grazing (Figure 5.2b); density on the lightly grazed treatment changed little, but increased linearly ($p<0.05$) on the heavily grazed treatment. It was not influenced by the rainfall treatments. The density of the four longer-lived perennials *Brachiaria nigropedata*, *Elionurus muticus*, *Heteropogon contortus* and *Panicum maximum* changed little (Table 5.3), but some fragmentation of large tufts occurred. The density of *Perotis patens* (Figure 5.2g), *Trichoneura grandiglumis* (Figure 5.2h), *Urochloa mosambicensis*, *Eragrostis rigidior* and *Bulbostylis burchellii*, was essentially unchanged

Table 5.2. The composition (% of total number per treatment) of the forb component of the sandveld site in April 1987.

Species	Lightly grazed	Heavily grazed
Cassia absus	12.6	17.7
Cassia mimosoides	0	0.8
Cucurbitaceae species	0	0.2
Cyphocarpa angustifolia	7.4	0
Dicoma macrocephala	1.4	1.5
Hermbstaedtia odorata	4.9	0
Indigofera costata	20.4	15.1
Indigofera inhambensis	2.1	0.5
Kouhautia caespitosa	1.1	0.8
Oxygonum dregeanum	0	1.0
Phyllanthus maderaspatensis	0.4	0.8
Ptycholobium plicatum	0	0.2
Rhynchosia sp.	0.7	0
Stylosanthes fruticosa	3.2	1.0
Tephrosia purpurea	4.6	37.0
Waltheria indica	6.3	5.2
Wormskioldia lacerata	0.4	0

for the three years, except for an increase of *Perotis patens* and *Trichoneura grandiglumis* on the rainfall interception treatment of the lightly and heavily grazed treatments respectively (Figure 5.2g, h).

Table 5.3. The mean density (m^{-2}) of four longer-lived perennial grasses between 1985 and 1987, for four treatments.

	Rainfall interception			Normal rainfall		
	1985	1986	1987	1985	1986	1987
Heavily grazed						
Brachiaria nigropedata	0.33	0.07	0.07	1.47	2.73	1.33
Elionurus muticus	0.47	0.47	0.47	2.53	1.80	1.67
Heteropogon contortus	0.47	0.40	0.40	1.20	1.33	2.07
Panicum maximum	0.28	0.20	0.27	1.47	2.73	1.33
Lightly grazed						
Brachiaria nigropedata	0.60	0.47	1.47	0.40	0.40	0.93
Elionurus muticus	0.13	0.13	0.07	0.69	0.73	0.73
Heteropogon contortus	0.53	0.53	0.60	0.60	0.60	0.53
Panicum maximum	0.33	0.40	0.47	0.27	0.47	0.33

As stated, the combined density of all grasses and sedges showed a linear and quadratic ($p<0.05$) response (Figure 5.2a). The quadratic response was due to a slight decrease in density between 1985 and 1986, attributable to the decline of *Pogonarthria squarrosa*, and a pronounced increase in the following season, attributable to *Digitaria eriantha* and *Aristida congesta* subsp. *barbicollis* on the heavily grazed treatment and of *Aristida stipitata* and *A. congesta* subsp. *barbicollis* on the lightly grazed treatment.

Changes in tuft size

Tuft mortality of *Pogonarthria squarrosa* was higher ($p<0.05$) on the rainfall interception treatment of both grazing treatments for the 1985 to 1987 interval (Table 5.4). There was also substantial mortality of *Digitaria eriantha* on all treatments over three years (up to 87%), which was most pronounced on the lightly grazed treatment. There was comparatively less mortality of *Aristida stipitata* (up to 25%) or of *Perotis patens* (up to 36%) than of *Pogonarthria squarrosa* or of *Digitaria eriantha*, on the lightly grazed treatment.

There was a decline in tuft size between 1985 and 1986, which continued into 1987, on all treatments (Table 5.5). On the heavily grazed treatment, there were differences ($p<0.05$) between rainfall treatments and between species (*P. squarrosa* and *D. eriantha*) for the change between 1985 and 1986 (and a significant interaction effect) and between 1985 and 1987. The difference between rainfall treatments was due to the greater decrease in the size of *P. squarrosa* tufts on the rainfall interception plots ($p<0.05$), although *D. eriantha* tufts showed the same direction of response (Table 5.5). The lightly grazed treatment showed the same pattern, except only the species main effect was significant between 1985 and 1987. The tuft size of *Aristida stipitata*, *Panicum maximum* and *Perotis patens* tended to increase on the lightly grazed treatment. The decrease in tuft size of *P. squarrosa* reflected the mortality patterns.

Table 5.4. The percentage survival of tufts of the key species, and of the combined number for all species, for the four treatments, for different periods.

	Heavy Grazing				Light Grazing			
	Rainfall Interception		Normal Rainfall		Rainfall Interception		Normal Rainfall	
	n	%	n	%	n	%	n	%
Total								
1985-86	139	82	137	97	133	89	140	94
1985-87	140	58	137	69	129	53	136	71
1985-88	115	34	128	45	118	41	118	48
Pogonarthria squarrosa								
1985-86	45	53	38	97	46	80	46	96
1985-87	47	11	42	33	46	20	45	47
1985-88	47	9	41	15	46	13	43	35
Digitaria eriantha								
1985-86	56	98	37	100	31	87	46	80
1985-87	54	83	34	76	31	55	46	20
1985-88	36	47	33	36	27	26	46	13
Aristida stipitata								
1985-86					6	100	14	100
1985-87					5	80	13	92
1985-88					5	80	8	75
Perotis patens								
1985-86					13	84	16	81
1985-87					13	84	15	73
1985-88					11	82	14	64

Table 5.5. The decrease in tuft circumference (cm) between 1985 and 1986, and 1985 and 1987, for *Pogonarthria squarrosa*, *Digitaria eriantha* and the total on the rainfall interception and normal rainfall treatments of the heavily and lightly grazed treatments.

		1985 to 1986		1985 to 1987	
		Normal Rainfall	Rainfall Interception	Normal Rainfall	Rainfall Interception
Heavy Grazing	*Pogonarthria*	0.92	6.78	7.9	11.34
	Digitaria	0.43	1.61	2.41	4.24
	Total	0.68	3.91	5.74	7.55
Light Grazing	*Pogonarthria*	0.75	1.20	6.60	7.17
	Digitaria	1.24	1.45	6.00	4.41
	Total	0.05	0.95	3.85	4.42

Changes in sward structure

The mean (per plot, n=12) height of leaves and of culms were highly correlated in both 1986 ($r=0.94$, $p=0.0001$) and in 1987 ($r=0.87$, $p=0.0002$). Cover was significantly correlated with leaf height in 1986 ($r=0.64$, $p=0.0242$).

The height of the sward was 30-100 cm, but the height of the leaf table was not >55 cm (Table 5.6). Projected aerial cover varied from 30-75%. One year's rainfall interception influenced the structure of the sward.

Table 5.6. The structure of the sward in 1986 and 1987. The treatments are abbreviated as follows; HD - heavily grazed, rainfall interception; HR - heavily grazed, normal rainfall; LD - lightly grazed, rainfall interception; LR - lightly grazed, normal rainfall.

	1986				1987			
	HD	HR	LD	LR	HD	HR	LD	LR
Leaf height (cm)	14	22	20	28	32	41	44	51
Culm height (cm)	30	49	47	78	67	76	91	100
Cover (%)	33	46	32	44	62	63	73	59
Moribund (%)	-	-	-	-	12	15	8	13

- not recorded

Leaf height was lower on the rainfall interception treatments of either grazing treatment in 1986, and cover was lower on the heavily but not the lightly grazed treatment ($p<0.05$).

DISCUSSION

This community has undergone a major change in structure, with a complete rearrangement of the dominant species in only two years. *Pogonarthria squarrosa* was the predominant species in 1985, but declined dramatically in both a relative (Figure 5.1) and an absolute (Figure 5.2) manner, as a result of extensive tuft die-back (Tables 5.4, 5.5). The consistent

direction of change of *P. squarrosa* and of forbs over all treatments indicates an overriding influence. This is considered to be the trend of rainfall that prevailed during the study, commencing in the second of two successive wet years, and continuing into drier years (Table 5.1). Notwithstanding this trend, both rainfall manipulation and grazing had a discernible effect on the rate and degree of compositional change, as *P. squarrosa* displayed the greatest decline on the rainfall interception treatment of the heavily grazed treatment, and least on the normal rainfall treatment of the lightly grazed treatment.

The most notable effect of the single year of rainfall interception was the heightened tuft mortality of *P. squarrosa* on the heavily grazed treatment. The most distinctive difference between grazing treatments was the pronounced increase of *Digitaria eriantha* on the heavily but not the lightly grazed treatment, and the converse pattern of *Aristida stipitata* and *A. congesta* subsp. *barbicollis*. The increase in density of *Digitaria eriantha* occurred despite quite substantial mortality (Table 5.4), and although not quantified, most, if not all, of the recruitment was vegetative from stolons rooting at their nodes (pers. obs.). The positive response of *Digitaria eriantha* on the heavily grazed treatment may possibly be due to the altered structure of the sward (Table 5.6) improving the light regime. This needs to be further investigated. The increase of *Aristida congesta* subsp. *barbicollis* and *A. stipitata* was due to improved seedling recruitment.

The compositional changes of this savanna differ somewhat from the recorded changes of sandveld savannas with a similar rainfall regime. On the mesic Matopos sandveld, composition was relatively stable under 15 years of sustained grazing during which very dry and very wet years occurred (Kennan 1969). *Digitaria pentzii* and *Heteropogon contortus* persisted under 15 years of heavy grazing, while *Perotis patens* was favoured and *Trachypogon spicatus* eliminated, *Pogonarthria squarrosa* was

stable under heavy grazing, but was eliminated with protection from grazing. In a six year experiment in which the last three years were well above average rainfall, the composition of the Matopos sandveld responded to rainfall variability rather than grazing treatments (Denny & Barnes 1977). *Hyperthelia dissoluta*, *Diheteropogon amplectens*, *Rhynchelytrum repens*, *Pogonarthria squarrosa*, *Hyparrhenia filipendula* and *Loudetia simplex* increased, while *Heteropogon contortus* and *Aristida* species decreased. In a 10-year bush-clearing experiment (without grazing) on the Nyamandhlovu sandveld, the abundance of *Hyperthelia dissoluta* and *Schizachyrium jeffreysii* increased, while that of *Schmidtia pappophoroides* and *Eragrostis rigidior* decreased, during a number of years of above average rainfall (Dye & Spear 1982).

It is suggested that these different patterns across regions are at least partly a consequence of the different life history characteristics of the main species. The majority of the species recorded in this study, including the predominant species *Pogonarthria squarrosa*, *Aristida stipitata*, *A. congesta* subsp. *barbicollis*, *Trichoneura grandiglumis* and *Perotis patens*, are relatively short lived perennials, as judged from the degree of population turnover which occurred during this study (Table 5.4). In the studies mentioned above, most of the predominant species were longer-lived perennials such as *Hyperthelia dissoluta*, *Hyparrhenia filipendula*, *Diheteropogon amplectens*, *Loudetia simplex*, *Schizachyrium jeffreysii*, *Heteropogon contortus* and *Trachypogon spicatus*. The longer-lived perennial species of the present study included *Hyperthelia dissoluta*, *Brachiaria nigropedata*, *Setaria sphacelata*, *Schizachyrium jeffreysii*, *Heteropogon contortus*, *Panicum maximum*, *Aristida meridionalis* and *Elionurus muticus*, but in very small amounts. The scarcity of longer-lived perennial species may possibly be a result of the very severe history of grazing that the site is believed to have had.

Most of the species in this study would be described as increaser species in range management terms (Foran *et al*. 1978). It is therefore noteworthy that *Pogonarthria squarrosa*, considered an increaser species, was all but eliminated by heavy grazing, although the species was extremely prolific when the study was initiated, also a regime of sustained severe grazing. Instances such as these reveal the limitation of the increaser-decreaser classification, in which it is assumed that only one driving variable (grazing) is primarily responsible for the dynamics of a species. The increase of *Aristida* species on the lightly grazed treatment is a similar example.

Explosions of forbs have been widely reported in savannas, but usually on heavier textured soils and in wet years following drought years in which the vegetation had been opened up (MacDonald 1982). The available herbage of both grazing treatments had been removed in the winter of 1986, hence cover was low at the beginning of the growing season (pers. obs.). Although 1986/87 was not a wet year, some substantial individual rainfall events occurred, with 250 mm of rain in December and January. The timing of rainfall may therefore have been critical.

Different life history characteristics of these species influenced the pattern of response. The absence of the forb species in the first two years which became prolific in the final year indicates that these species must have a persistent seed bank (*sensu* Thompson & Grime 1979). Many of the forb species were hard seeded legumes. The increase of *Aristida congesta* subsp. *barbicollis* and *A. stipitata* was similarly facilitated by an adequate seed bank. The increase of *Digitaria eriantha* between 1986 and 1987 was primarily due to recruitment by stolons rooting at their nodes. The small increase of *Digitaria* between 1985 and 1986, and part of the increase between 1986 and 1987, was due to the fragmentation of larger tufts. Stoloniferous growth was also responsible for the

successful colonisation of cleared areas by *Digitaria eriantha* var *pentzii* on heavy textured soils in this region (Chapter 11).

This study provides a clear example that a decrease in annual rainfall, in conjunction with heavy grazing, can be a primary influence on compositional changes, even when annual differences in rainfall are not that large, because of the different mortality and recruitment patterns of different species, and of a species under different environmental conditions. Future research on the compositional changes of savanna grasslands could be improved if less attention was paid to single driving variables such as grazing (or fire), but the interaction of these with not only rainfall conditions of single years but also the cumulative effect of medium term directional trends of rainfall. Further insight will be provided by more explicit consideration of the life history characteristics of the predominant species.

SUMMARY

The influence of heavy and light grazing by cattle for three years, and of rainfall interception for one year, on the composition of a sandveld savanna grassland in Gazankulu, Transvaal, was investigated. The composition of the community and the relative contribution to biomass and absolute density of the predominant species changed substantially over three years. Rainfall had a greater influence on change than grazing. *Pogonarthria squarrosa*, generally considered to increase under heavy grazing, was initially the most abundant species, but declined markedly on all treatments, and most rapidly on the rainfall interception, heavy grazing treatment. Mortality of *Pogonarthria squarrosa* was greater on the rainfall interception treatment of either grazing treatment.

Digitaria eriantha increased markedly on the heavily grazed treatment, despite up to 24% tuft mortality, because of extensive vegetative recruitment from stoloniferous growth. *Aristida congesta* subsp. *barbicollis* and *Aristida stipitata* increased on the lightly grazed treatment with the demise of *Pogonarthria squarrosa*. There was an explosion of annual forbs, predominantly *Tephrosia purpurea*, *Indigofera costata* and *Cassia absus*, on all treatments in the third year. The trend of rainfall over the course of the study, initially wet and successively drier, apparently had a greater influence on compositional trends than the imposed treatments.

CHAPTER 6

THE INFLUENCE OF RAINFALL AND GRAZING ON THE COMPOSITIONAL CHANGE OF THE HERBACEOUS STRATUM OF TWO SAVANNAS ON HEAVY SOILS

INTRODUCTION

The primary objective of this study was to differentiate the relative effect of rainfall and grazing on compositional change, but because the experiment was disrupted this could only be done for one season. However, grazing treatments were maintained for five seasons, during which time there was a general decrease in rainfall This chapter therefore describes the influence of rainfall and grazing on changes in the relative contribution to biomass, absolute density, basal cover and the structure of the sward, for the Thlavekisa and Utha sites. These two heavy textured soils supported the same floristic elements but in different amounts.

The available empirical knowledge of compositional changes on similar soils under heavy grazing (O'Connor 1985; Chapter 2) provided the *a priori* expectation that *Heteropogon* and *Themeda* would be negatively affected by a sequence of dry years, and particularly so by the co-occurrence of drought and heavy grazing, and positively affected by a sequence of wet years. *Aristida* species were expected to respond in a reciprocal fashion in general. There were no specific *a priori* predictions for *Setaria*, *Bothriochloa* or *Digitaria*, other than the general wisdom that *Setaria* and

Digitaria are sensitive to grazing, while *Bothriochloa* is not known as a preferred species (e.g. Tainton *et al.* 1976).

METHODS

The influence of the single year of rainfall interception on the relative contribution to biomass and absolute density of each species was examined. The influence of rainfall interception on the changes in density between 1984/85 and 1986/87 was tested with the univariate ANOVA approach to repeated measures of density (Gurevitch & Chester 1986) (as described in Chapter 5), using the data of 20 quadrats per plot. Conclusions regarding the differences in density and basal area between grazing treatments over five years were based on the trends of the mean and their confidence intervals (using five quadrats per plot). Confidence intervals were derived from an estimate of the variance for a two-stage sampling process (Cochran 1977, p279 - described in Chapter 5). Rainfall figures are given in Table 3.1. Note that although the figures for Thlavekisa are incomplete because of the disruption, the pattern of rainfall over the final years was the same as that of Utha.

Pearson's product moment correlations were sought between species, separately for each site, in the absolute change in basal area per year. for the combined data of both grazing treatments, to identify if any species might have a negative effect on the growth of another.

RESULTS

Utha

Changes in density

Influence of rainfall manipulation. 1984/85-1986/87. There was a linear increase ($p<0.05$) of the total density of grasses on both grazing treatments, associated with an increase ($p<0.05$) of *Themeda*, *Setaria* and *Bothriochloa* on the heavily grazed treatment. The increase in total grass density on the heavily grazed treatment was greater ($p<0.05$) on the normal rainfall than on the rainfall interception treatments. The increase in total grass density on the lightly grazed treatment was associated with an increase ($p<0.05$) in the density of *Setaria*. The increase of *Setaria* was more pronounced between 1985/86 and 1986/87 (quadratic trend - $p<0.05$), particularly on the normal rainfall than on the rainfall interception treatment ($p=0.007$). There was also a quadratic trend ($p<0.05$) for the total grass density, with a slightly greater increase between 1985/86 and 1986/87. There was a linear increase ($p<0.05$) in forb density on both grazing treatments, which, on the heavily grazed treatment was more pronounced between 1984/85 and 1985/86 (quadratic - $p<0.05$ - trend).

Influence of grazing. 1984/85-1988/89. There was a consistently marked increase of the density of all grasses on the heavily grazed treatment from 1984/85 to 1987/88, while the lightly grazed treatment showed a marked increase between 1984/85 and 1985/86, a slight increase in the

following year, but was thereafter stable (Figure 6.1g). The pattern for *Themeda* was similar to that for total grasses, and from 1986/87 to 1988/89 the density on the heavily grazed treatment was twice that of the lightly grazed treatment (Figure 6.1e). *Setaria* increased on both grazing treatments between 1984/85 and 1986/87, particularly on the lighly grazed treatment, was relatively unchanged after 1986/87, with no marked difference between grazing treatments in 1988/89 (Figure 6.1d). *Digitaria* increased gradually on both grazing treatments between 1984/85 and 1988/89, whereas *Bothriochloa* was unchanged (Figures 6.1b, c). *Aristida* increased substantially on the heavily but not on the lightly grazed treatment, with a marked increase in the wet year of 1987/88 (Figure 6.1a).

Forb density showed a similar increase on both grazing treatments between 1984/85 and 1986/87, but the continued increase in the wet year of 1987/88 was more pronounced on the lightly grazed treatment (Figure 6.1e). *Chaetacanthus burchellii*, *Crabbea velutina*, *Phyllanthus maderaspatensis* and *Hibiscus pusillus* were the four most common forb species (Figure 6.2). The marked increase in forbs on the lightly grazed treatment was principally due to *Chaetacanthus burchellii*, and to a lesser extent to *Crabbea velutina*. Survivorship of the pre-existing population was high, except for *Phyllanthus maderaspatensis*. It was 100% over three years for *Crabbea velutina*, *Hibiscus pusillus* and *Chaetacanthus burchellii* (lightly grazed treatment only). Thus these three species live at least four years.

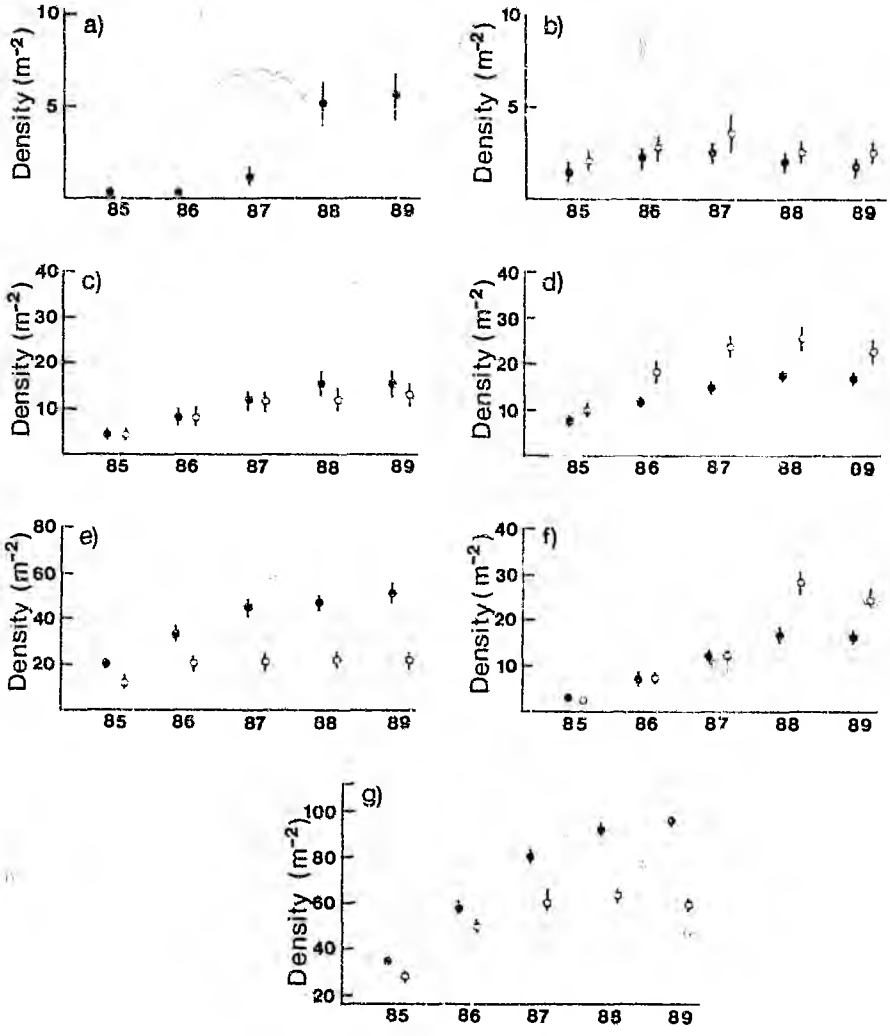


Figure 6.1. The changes in density over five years at the Utha site of a) *Aristida bipartita*, b) *Bothriochloa insculpta*, c) *Digitaria eriantha*, d) *Setaria incrassata*, e) *Themeda triandra*, f) forbs and g) all grasses combined. Closed circles represent the heavily grazed treatment, open circles the lightly grazed treatment. Vertical bars represent ± 1 S.E.. Bars not shown are contained within the symbols. Rainfall is given in Table 3.1.

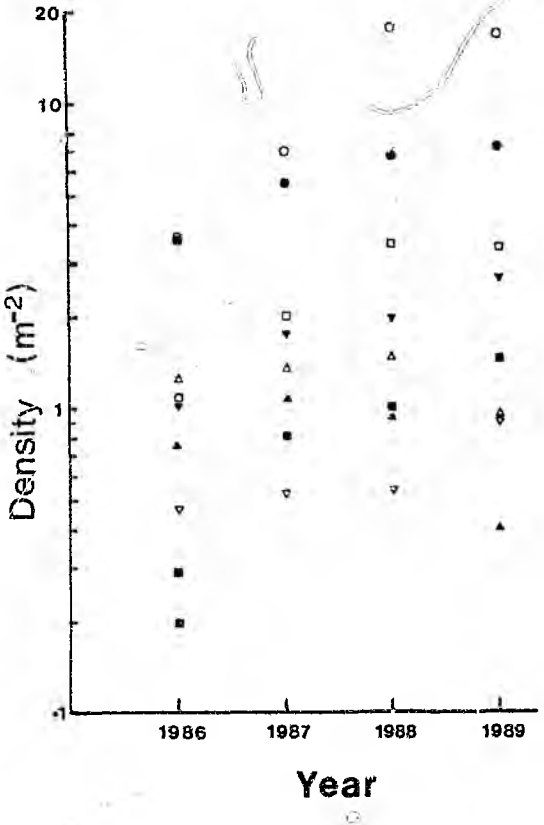


Figure 6.2. The change in density of *Chaetacanthus burchellii* (circles), *Crabbea velutina* (squares), *Hibiscus pusillus* (inverted triangle) and *Phyllanthus maderaspatensis* (triangle) at Utha over four years. Open symbols denote the light grazing treatment, closed symbols the heavy grazing treatment. Rainfall is given in Table 3.1.

Changes in basal cover

There was a pronounced decrease in the total basal cover of both grazing treatments over the four year period (Figure 6.3e), principally associated with a decrease in the basal cover of *Setaria* (Figure 6.3a). The cover of *Themeda* was unchanged on the lightly grazed treatment between

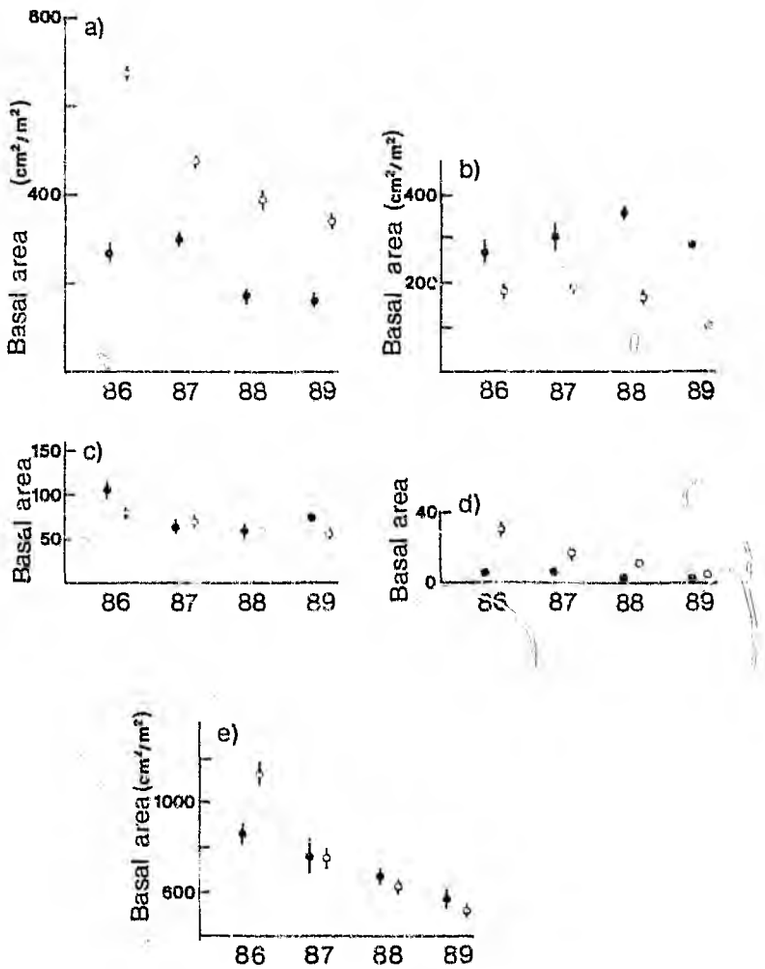


Figure 6.3. The changes in basal cover over four years at the Utha site of a) *Setaria incrassata*, b) *Themeda triandra*, c) *Digitaria eriantha*, d) *Bothriochloa insculpta* and e) all grasses combined. Closed circles represent the heavily grazed treatment, open circles the lightly grazed treatment. Vertical bars represent ± 1 S.E.. Bars not shown are contained within the symbols. Rainfall is given in Table 3.1.

1985/86 and 1987/88, but declined markedly in the following dry year (Figure 6.3b). In contrast, the cover of *Themeda* increased in the wetter year of 1987/88 on the heavily grazed treatment, but also declined in the following year. The basal cover of *Themeda* responded primarily to rainfall, not grazing. *Bothriochloa* declined gradually and *Digitaria* was relatively stable (Figures 6.3c, d). Overall the response of basal cover to grazing was not marked. The major changes appeared to be associated with the relatively wet 1987/88 and following dry 1988/89 seasons. The lightly grazed treatment had consistently higher cover of *Setaria* and of *Bothriochloa* but lower cover of *Themeda* than the heavily grazed treatment. The proportional contribution to basal area by the main grass species was relatively consistent over four years, with a slight decrease in the contribution of *Setaria* and an increase in that of *Themeda* on the heavily grazed treatment (Table 6.1).

There was a correlation ($p<0.05$) between the absolute change in basal cover between two years and the basal cover of the first year on the lightly grazed treatment. There was a tendency for all years for quadrats with a higher amount of basal cover to experience a greater decrease in basal cover. This pattern was also evident on the heavily grazed treatment between 1986/87 and 1987/88. There was only a correlation ($p<0.05$) for the annual change in basal cover between *Bothriochloa* and *Setaria*. There were negative non-significant ($p>0.18$) correlations between *Themeda* and both *Bothriochloa* and *Setaria*, indicating a possible tendency for negative interaction between these species.

Table 6.1. The percentage contribution to basal cover of the main grass species at Thlavekisa and Utha over four years (measured in April/ May).

Site, species	Heavy grazing				Light grazing			
	1986	1987	1988	1989	1986	1987	1988	1989
Thlavekisa								
Aristida	4	9	10	13	9	10	8	12
Bothriochloa	5	4	5	5	7	7	7	9
Digitaria	8	11	11	19	5	5	5	10
Eragrostis	2	4	4	1	1	3	3	5
Heteropogon	13	14	14	5	30	26	18	9
Setaria	53	45	42	48	38	38	46	42
Themeda	9	10	12	9	9	10	11	11
Urochloa	5	2	2	<1	<1	<1	<1	<1
Forbs	<1	<1	<1	<1	<1	<1	<1	<1
Utha								
Aristida	<1	<1	1	1	0	0	0	0
Bothriochloa	<1	1	<1	<1	<1	2	2	<1
Digitaria	13	8	12	13	8	8	9	11
Heteropogon	7	10	8	6	<1	<1	<1	<1
Setaria	33	40	26	28	70	63	62	66
Themeda	44	41	55	52	19	26	27	21
Forbs	<1	<1	<1	<1	<1	<1	<1	<1

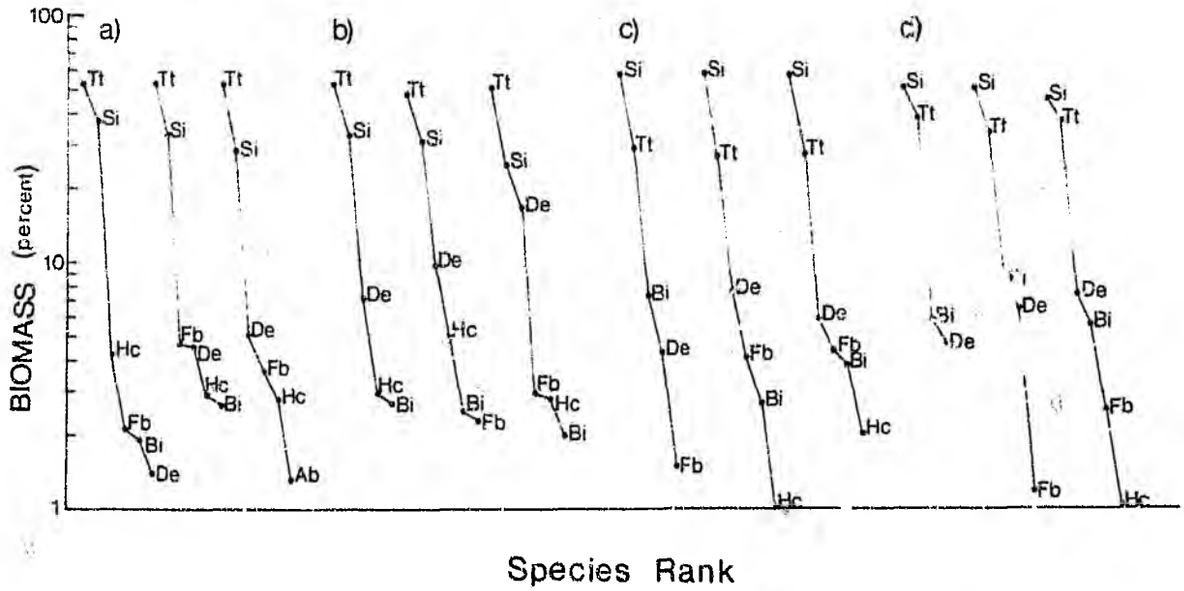


Figure 6.4. The dominance-diversity curve for the herbaceous stratum at Utha for four treatments over three years, for a) heavily grazed, normal rainfall; b) heavily grazed, rainfall interception; c) lightly grazed, normal rainfall; d) lightly grazed, rainfall interception. The set of curves for each treatment read from left to right as 1984/85, 1985/86 and 1986/87. The key to the species: Ab - *Aristida bipartita*, Bi - *Bothriochloa insculpta*, De - *Digitaria eriantha*, Fb - herbaceous dicotyledons, Hc - *Heteropogon contortus*, Si - *Setaria incrassata*, Tt - *Themeda triandra*. Rainfall is given in Table 3.1.

Changes in contribution to biomass

Setaria and *Themeda* constituted most of the biomass (Figure 6.4), and were respectively the major components on the lightly and heavily grazed treatments. There was little change in the contribution to biomass between 1984/85 and 1986/87. *Setaria* decreased on the heavily grazed treatment, *Bothriochloa* decreased slightly on all treatments, *Digitaria* and forbs consistently increased slightly on all treatments, and *Aristida* increased on the heavily grazed treatment.

Structure of the sward

The height and cover of the vegetation, and the proportion of moribund material was twice as great on the lightly than on the heavily grazed treatment. , while the amount of litter was lower (Table 6.2). The same pattern was evident in 1986. The single year of rainfall manipulation had no effect. Sustained grazing between 1986 and 1987 decreased the amount of litter from 82% to 64%, and increased the amount of bare ground from 13 to 30%. The cover of litter and of bare ground remained constant on the lightly grazed treatment over the same period.

Table 6.2. The structure and condition of the herbaceous layer of the Utha and Thlavekisa sites in April/May 1987.

	Utha		Thlavekisa	
	Lightly grazed	Heavily grazed	Lightly grazed	Heavily grazed
Leaf height (cm)	87	35	81	40
Aerial cover (%)	72		67	49
Bare ground (%)	13	30	67	44
Litter cover (%)	78	64	24	49
Moribund grass (%)	23	12	6	10

Thlavekisa

Changes in density

Influence of rainfall manipulation. 1984/85-1986/87. The total density of grasses increased linearly ($p<0.05$) on both grazing treatments. The increase on the heavily grazed treatment was the result of increases ($p<0.05$) in *Setaria* and *Aristida*, and was more pronounced between 1985/86 and 1986/87 (quadratic trend - $p<0.05$). Forb density also increased linearly ($p<0.05$) on the heavily grazed treatment. The density of *Themeda*, *Setaria* and *Heteropogon* increased linearly ($p<0.05$) on the lightly grazed treatment. For *Heteropogon*, the increase was more pronounced ($p<0.05$) on the normal rainfall than the rainfall interception

plots, and was more pronounced between 1985/86 and 1986/87 (quadratic trend - $p<0.05$). Forbs increased linearly ($p<0.05$) on both grazing treatments, particularly between 1985/86 and 1986/87 on the lightly grazed treatment (quadratic trend - $p<0.05$).

Influence of grazing. 1984/85-1988/89. Irrespective of treatment, there was a pronounced increase in total density and the density of *Setaria*, *Heteropogon*, *Themeda*, *Digitaria*, *Bothriochloa*, *Urochloa* and forbs, with an especially marked increase between 1986/87 and 1987/88 for *Aristida* (Figure 6.5).

Changes in basal cover

There was a consistent increase of the total basal cover of the lightly grazed plot between 1985/86 and 1987/88, with no apparent effect of a fire in the dry season of 1986, but a marked decrease in the dry 1988/89 season (Figure 6.6e). The total basal cover of the heavily grazed plot also declined in 1988/89, although cover had been more stable in the preceding years. The changes of total basal cover were mainly a consequence of the changes of *Setaria* and *Heteropogon*, the initial primary constituents of the sward (Table 6.2). The cover of *Setaria* decreased markedly on the heavily grazed treatment between 1985/86 and 1986/87, and 1987/88 and 1988/89 (Figure 6.6d). *Setaria* increased on the lightly grazed treatment between 1985/86 and 1987/88, but declined to initial levels in the drier 1988/89 season, when the treatment was heavily grazed. *Setaria* appears therefore to be sensitive to grazing. The basal cover of *Heteropogon* on both grazing treatments, and *Themeda* and *Bothriochloa* on the heavily grazed treatment, was unchanged between 1985/86 and 1987/88, but decreased sharply in the following drier 1988/89 season (Figures 6.6b,

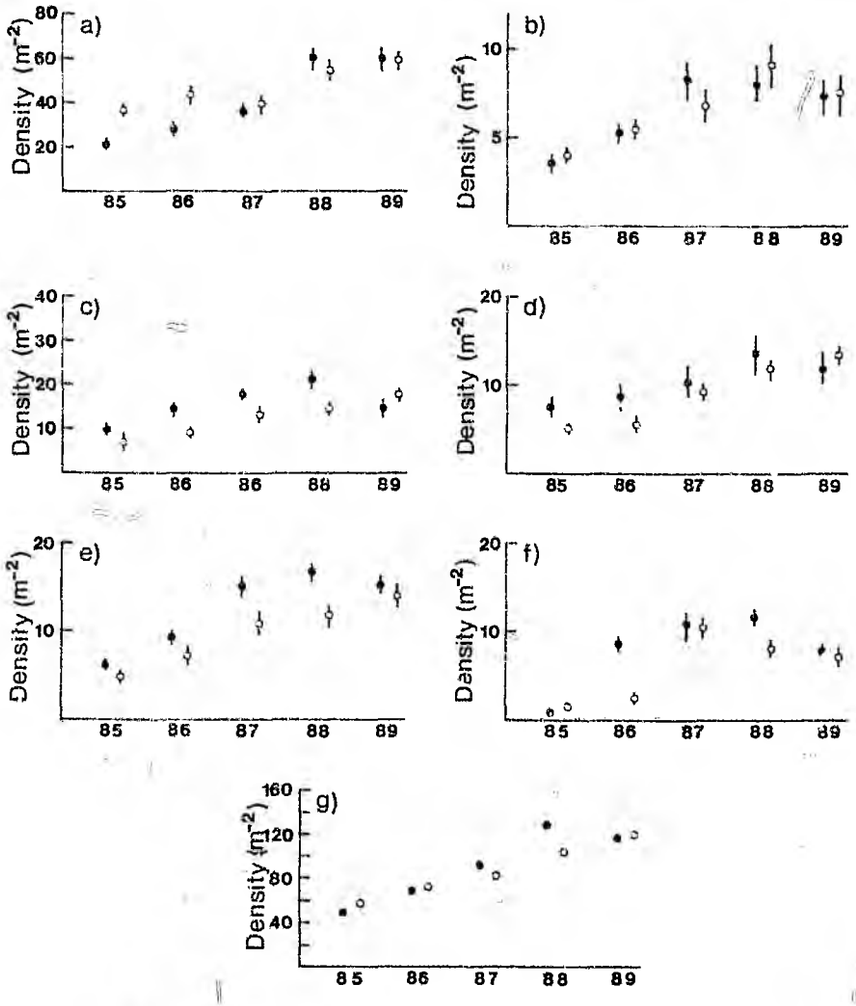


Figure 6.5. The changes in density over five years at the Thlavekisa site of a) *Aristida bipartita*, b) *Rothriochloa insculpta*, c) *Heteropogon contortus*, d) *Themeda triandra*, e) *Setaria incrassata*, f) herbaceous dicotyledons, and g) all grasses combined. Closed circles represent the heavily grazed treatment, open circles the lightly grazed treatment. Vertical bars represent ± 1 S.E.. Bars not shown are contained within the symbols. Rainfall is given in Table 3.1.

c, e). The cover of *Themeda* decreased on the lightly grazed treatment in the 1988/89 season, but had increased between 1985/86 and 1987/88. The cover of *Bothriochloa* changed little on the lightly grazed treatment. There was a substantial increase in the cover of *Aristida* over three years under heavy grazing (1985/86 to 1987/88), but the drier 1988/89 season resulted in a decrease (Figure 6.6a). *Aristida* showed a slight increase on the lightly grazed treatment between 1985/86 and 1987/88, but did not decrease in the following year. Cover of *Digitaria* was unchanged on the heavily grazed (68 to 90 cm^2m^{-2}) but doubled on the lightly grazed treatment (32 to 68 cm^2m^{-2}) over four years.

Setaria contributed the most to basal cover over the four years (Table 6.2). *Heteropogon* declined from being the second most predominant species to one of the less conspicuous constituents, while *Digitaria* showed the converse pattern. The contribution of *Aristida* increased on the heavily but not on the lightly grazed treatment. *Urochloa* and *Eragrostis superba* decreased on the heavily grazed plot, while the latter species increased on the lightly grazed plot. *Bothriochloa* and *Themeda* contributed a consistent amount to cover.

There were correlations ($p<0.05$) between the absolute change in the basal cover of a quadrat and its cover in the preceding year for all treatments and years except for the heavily grazed treatment between 1986/87 and 1987/88. There was a tendency for a greater dieback on quadrats with higher amounts of basal cover with a change from a wetter to a drier year (eg 1985/86 to 1986/87 and 1987/88 to 1988/89). Conversely, there was a tendency on the lightly, but not on the heavily grazed treatment, for the quadrats with the lowest basal cover to have the highest absolute gain in basal cover with a change from a drier to a wetter year (1986/87 to 1987/88). There were correlations ($p<0.05$) for the annual change in basal area between *Themeda* and all species except *Digitaria*, and also between *Bothriochloa* and *Setaria* and *Digitaria*, and between *Aristida* and

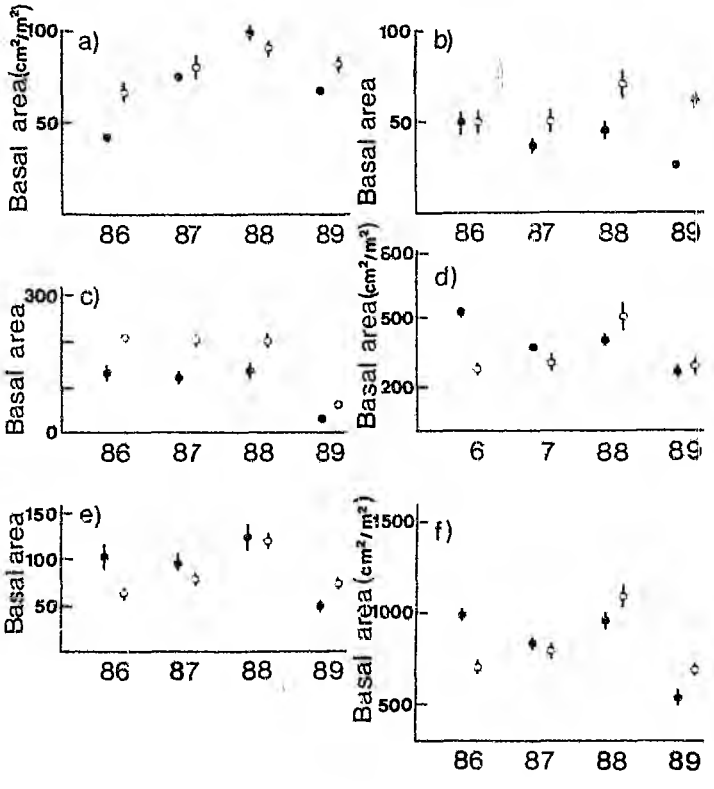


Figure 6.6. The changes in basal cover over four years at the Thlavekisa site of a) *Aristida bipartita*, b) *Bothriochloa insculpta*, c) *Heteropogon contortus*, d) *Setaria incrassata*, e) *Themeda triandra* and f) all grasses combined. Closed circles represent the heavily grazed treatment, open circles the lightly grazed treatment. Vertical bars represent ± 1 S.E.. Bars not shown are contained within the symbols. Rainfall is given in Table 3.1.

Heteropogon. All correlations, whether significant or not, were positive, indicating no species had an adverse effect on the change in basal area of another.

Changes in biomass

There were consistent changes in the species contribution to biomass across all treatments (Figure 6.7). *Setaria* increased on all treatments to become the major component of 3 of 4 treatments by 1986/87. *Heteropogon* was initially the major component on 3 of 4 treatments, but decreased, particularly on the heavily grazed treatment. The contribution of *Aristida* decreased on the lightly grazed but increased on the heavily grazed treatments. The contribution of *Digitaria* and of forbs increased slightly on all treatments.

Structure of the sward

The differences in structure between treatments at Thlavekisa were similar to those at Utha, except that the fire in 1986 on the lightly grazed plot reduced litter cover from 74 to 24%, and increased the area of bare ground from 14 to 67% (Table 6.3). Consequently there was a lower proportion of moribund material on the lightly than on the heavily grazed treatment. There was a also a decrease in litter cover on the heavily grazed plot between 1985/86 and 1986/87, from 69 to 49%, and a doubling of the cover of bare ground. The single year of rainfall manipulation had no effect.

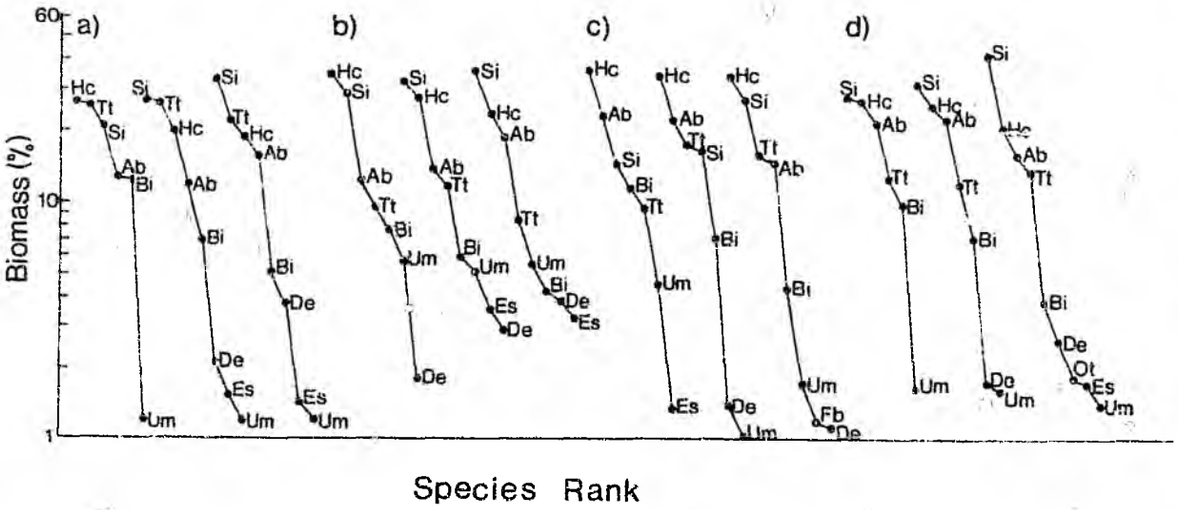


Figure 6.7. The dominance-diversity curve for the herbaceous stratum at Thlavekisa for four treatments over three years, for a) heavily grazed, normal rainfall; b) heavily grazed, rainfall interception; c) lightly grazed, normal rainfall; d) lightly grazed, rainfall interception. The set of curves for each treatment read from left to right as 1984/85, 1985/86 and 1986/87. The key to the species: Ab - *Aristida bipartita*, Bi - *Bothriochloa insculpta*, De - *Digitaria eriantha*, Es - *Eragrostis superba*, Fb - herbaceous dicotyledons, Hc - *Heteropogon contortus*, Ot - other grasses, Si - *Setaria incrassata*, Tt - *Themeda triandra*, Um - *Urochloa mosambicensis*. Rainfall is given in Table 3.1.

DISCUSSION

The herbaceous community at Utha was dominated by two species, in common with some North American prairies (Bazzaz & Parrish 1982), whereas there was a more equitable pattern of dominance amongst the main species at Thlavekisa.

A striking result was the continued increase in density, at least until 1987/88, irrespective of grazing treatment or site, and despite a general decrease in the basal area of a species. Some of the density increases could be attributed to increased recruitment. For example, there was substantial seedling recruitment of *Themeda* at Utha in 1985/86, and of *Aristida* at Thlavekisa in 1987/88 (Table 7.4). However, much of the increase was due to the fragmentation of large tufts into a number of smaller tufts (Chapter 7). The significant correlations between the amount of change in basal cover with the initial amount of basal cover further suggest that these changes are in part influenced by density-dependent processes corresponding to the self-thinning rule (Westoby 1984; Weller 1987), driven by available moisture. However, there was a far lower density and basal cover of *Themeda*, *Heteropogon* and *Bothriochloa* on sites with a history of sustained heavy grazing compared to sites with a history of light grazing in the region (Pickett 1987).

The year of rainfall interception had a limited effect on compositional change, only *Heteropogon* (Thlavekisa - lightly grazed) and *Setaria* (Utha - lightly grazed) showed significant differences between rainfall treatments. Rainfall interception was expected to result in greater compositional change on the heavy textured rather than on the sandy soils (O'Connor 1985), but the converse occurred (see Chapter 5). A potential explanation is the different life-history patterns of the main species of each soil type. All the species on the clay soils, to a lesser extent

for *Aristida*, are long-lived species with slow population turnover (Chapter 7), whereas most species on the sandy soils were shorter lived (Chapter 5). The limited effect of the rainfall interception is interpreted as inherent population inertia of a long-lived species.

Most of the changes in basal cover, except those on the lightly grazed treatment at Utha, can be related to the pattern of increasing aridity which prevailed during the study, temporarily ameliorated in 1937/88. The tendency for both *Themeda* and *Heteropogon* to increase in wetter periods and decrease in drier ones, whether grazed or ungrazed, has been widely reported in southern Africa (Louw 1973; Denny *et al*. 1977; Dye & Spear 1982; MacDonald 1982; Donaldson *et al*. 1983). *Digitaria eriantha* has also been recorded to decrease during consecutive dry years (Matopos - Denny *et al*. 1977; Towoomba - Donaldson *et al*. 1983), but increased slightly in this study. Similarly, the changes in the botanical composition of *Astrebla* grassland in Queensland over eight years appeared to be influenced more by trends in rainfall than grazing (Orr 1980b, 1981), although basal cover decreased more under heavy than light grazing.

The positive correlations between species for the annual change in basal cover suggests that rainfall has an overriding effect. The tendency for a negative correlation between *Themeda* and both *Setaria* and *Bothriochloa* at Utha suggests that interference may be operating (given the small sample size). Also, the dynamics of *Bothriochloa* may be dependent on those of *Themeda*, given the spatial association of the two species and the scarcity of the former. *Setaria* and *Themeda* seem to respond quite differently to prevailing environmental conditions. An increased sample size would resolve these suppositions.

There were overall few marked differences between grazing treatments. *Aristida* increased under heavy but not under light grazing at Utha, as in Uganda (Edroma 1985), and increased on both grazing treatments at

Thlavekisa, but particularly on the heavily grazed treatment. The lack of establishment of *Aristida* on the lightly grazed treatment at Utha may have been a consequence of the inhibitory effect of a relatively tall, closed sward (Table 6.2) on the growth of this short species (Figure 4.3), which is accustomed to a high irradiance environment (Griffioen & O'Connor 1990). In corroboration, *Aristida* was one of the most successful colonisers of cleared 1 m diameter patches on the lightly grazed treatment at Utha (Chapter 11). Although *Aristida* species have been recorded to increase in drought years (Donaldson *et al*. 1983), the absolute basal area of *Aristida* decreased in the dry 1988/89 season at Thlavekisa, but the proportional contribution to basal area increased (Table 6.2). The response of *Setaria* and *Bothriochloa* at Thlavekisa suggests that these two species are sensitive to grazing. The difference between sites in the response of *Setaria* may have been in part due to the different structure of the grasslands (Chapter 4). The pronounced mosaic and extensive clonal growth of *Setaria* at Utha meant that most ramets were interacting with ramets of the same species, whereas at Thlavekisa a far higher proportion were interacting with different species. The fire at Thlavekisa was a confounding factor, but can be viewed as an integral part of any light grazing regime. The heavily grazed treatment did not burn because there was an insufficient fuel load (pers. obs.).

It was predicted that the co-occurrence of heavy grazing and drought would eliminate *Heteropogon* and *Themeda*, but this did not occur. However, their pronounced decrease at Thlavekisa suggests that it could (considered in the general discussion - Chapter 12).

Although this study failed in its primary objective of differentiating the relative influence of extreme levels of rainfall and grazing on compositional change, it has provided a detailed data set which is further evidence that a directional trend of rainfall can initiate small but cumulative changes in composition (O'Connor 1985).

SUMMARY

The influence of heavy and light grazing by cattle for five years, and of rainfall interception for one year, on the composition of two savanna grasslands on clay soils, which supported the same species but in different amounts, was studied. The year of rainfall interception had little effect on changes in density. There was an increase of all grass species and of forbs, with little difference between grazing treatments. The basal cover of all grass species decreased at Utha, except that of *Themeda* which increased on the heavily grazed treatment during the wet 1987/88 season. The basal cover of most species was initially constant at Thlavekisa, rose in the wet 1987/88 season, declined quite markedly in the dry 1988/89 season, with *Heteropogon* almost eliminated. The basal cover of *Aristida* consistently increased at both sites (although it was absent from the lightly grazed treatment at Utha) but declined in the final year at Thlavekisa. The proportional contribution to basal cover at Utha was relatively stable, except for a consistent increase of *Digitaria*. The Thlavekisa community changed markedly. The relative importance of *Heteropogon* declined considerably, that of *Aristida* and *Digitaria* increased, while the other species were relatively stable. At Utha, grazing decreased vegetation height and cover, and moribund material, and increased the amount of bare ground, but the fire at Thlavekisa removed most litter cover and increased the amount of bare ground.

The compositional changes were mainly the result of cumulative changes related to the prevailing rainfall trend, rather than the result of the imposed treatments.

CHAPTER 7

THE INFLUENCE OF RAINFALL AND GRAZING ON THE DEMOGRAPHY OF THE COMMON PERENNIAL GRASSES OF TWO CLAY SOIL SAVANNAS

INTRODUCTION

Our knowledge of the demography of African savanna grasses is scant. Basic natural history questions such as the longevity of tufts or the persistence of seeds remain unanswered. In similar environments elsewhere, the lifespan of tufts can exceed twenty years, but the majority of tufts do not survive for half this length of time (Canfield 1957; Williams 1970; Williams & Roe 1975; West *et al.* 1979; Mott *et al.* 1985). Recruitment is often episodic in semi-arid or mesic environments, in relation to rainfall events (Williams 1970; Williams & Roe 1975; Crisp 1978; Griffin & Freidel 1985), and can be influenced by grazing (Crisp & Lange 1976; Wright & van Dyne 1976; Salihi & Norton 1987). Artificial defoliation can have a profound impact on the growth and survival of tufts (e.g. Tainton & Booysen 1965; Ndawula-Senyimba 1972; Edroma 1985; Hodgkinson *et al.* 1989), but the realism of artificial defoliation for the field situation is somewhat unclear. Drought periods can also have a marked effect on survival (Fourie & Roberts 1977; Scholes 1985). Studies of the influence of grazing on population change in the field, as indexed by compositional change, are ambiguous because of the contingency of driving variables upon one another (McNaughton 1983; O'Connor 1985). Competition between individuals, as stated by the self-thinning rule (White 1979; Westoby 1984; Weller 1987), has provided

us with one of the few "laws" of population dynamics. Yet the importance of resource competition in a heavily grazed system, where survival may be a function of the rate of leaf area replacement (e.g. Hodgkinson *et al*. 1989) even with adequate resources available, has been little examined. Hence the appropriate focus may be on the frequency of leaf removal when growing conditions are favourable.

A population response is the summed response of a collection of individuals, and the variability of this response needs to be sought in the attributes of the individuals. It would appear that size rather than age is an appropriate descriptor of an individuals performance, including reproductive output, growth and survival (Rabotnov 1969; Harper & White 1974; Harper 1977; Caswell 1989). Yet the simple fact that plants senesce indicates that age is an important attribute. Individuals would be expected to vary in the manner in which they were affected by grazing. Certainly, discrimination between plant species by grazing ungulates is the norm (Westoby 1974), but little investigation has been made from the "plant-eye view" of the consequences of grazing selectivity.

This chapter investigates the demography of the main perennial grasses, specifically the influence of rainfall and grazing on their population turnover, population structure, reproductive output, recruitment, growth and survival, and evaluates the importance of size (and age) for these processes. Evidence was sought for the effect of competition on some of these population processes. In chapter 8 the patterns of grazing selectivity are defined to aid in the interpretation of population responses. The significance of seed production and the seed bank for population dynamics is considered in Chapter 9. The annual rainfall data are given in Table 3.1.

METHODS

The demographic analysis was based on permanently tagged tufts, including both those on transect lines and within permanently located quadrats. There were approximately 6000 tufts from both sites combined, but the numbers obviously varied between years.

Population turnover

The proportion of the basal area, and of the number of individuals, constituted by the starting population (censused May 1985) and by the recruits of each year, were calculated for four years.

Population structure

The population structure of each species was described by measures of central tendency and dispersion. In addition, a measure was sought to describe the inequality in size between individuals of a population. Weiner & Solbrig (1984) proposed the Gini coefficient (G), a popular measure of economic inequality in human populations, in preference to the coefficient of variation (CV) or the third central moment (g_1 - skewness). Both the CV and G are sensitive to changes in location (i.e. mean), whereas g_1 is invariant to changes in both location and scale - it is primarily a shape statistic, and all three statistics are usually closely correlated (Bendel *et al.* 1989). I therefore used CV and g_1 as two

measures of population structure, calculated with PROC UNIVARIATE of SAS (1985).

Reproductive output

Multiple regression analyses were used to investigate the variation between tufts in the number of culms produced over a season by a tuft in terms of the size of the tuft (circumference in cm), the extent to which it had been grazed that season, the amount of moribund material, and the effects of neighbouring tufts. Analyses were conducted separately for each species, for each year, for each grazing treatment. The number of culms was the sum of the number of culms recorded at each census (not transformed), which accommodates the continual production and removal of culms. The values for grazing and mor material were the mean (per individual tuft) of the rankings for gr ; or moribund material for all censuses of that season. An index of the combined effect of all neighbours was derived as described in chapter 4. In addition, the approximate number of seeds produced per individual of the main species under light grazing in 1987 was summarised.

Recruitment and early growth

Recruitment.

Data on recruitment for each of four years were obtained from permanently located quadrats. An established individual is defined as one still alive

at the end of the growing season in which it had emerged. G-tests of 2 by 4 contingency tables (Sokal & Rohlf 1981) examined whether the influence of grazing on the number of recruits of a species was independent of the year of recruitment, and repeated contrasts of grazing treatments were made for each year.

Mortality in the first season following establishment.

The dependence of seedling survival following establishment (ie from the end of the growing season in which the seedling established until the end of the following growing season) on grazing treatment and the year of establishment was examined separately for each species with log-linear analyses (Fienberg 1979) using SAS (1985).

Seedling growth following establishment.

The difference between the grazing treatments of each site in the size (circumference) attained by the surviving seedlings of the 1985/86 and 1986/87 cohorts of each species, by the end of the 1987/88 season, was compared with t-tests (sample size permitting).

Seedling survival following emergence.

The survival of one cohort of seedlings, defined as all seedlings present at the time of census (December 1986) on the permanently located quadrats, until the end of the growing season was determined. Newly emerged grass or forb seedlings could not be reliably identified to species level without destruction, and each was therefore lumped into one category, with the exception of *Cassia mimosoides* (it has distinctive cotyledons) which was recorded separately.

In addition, at Thlavekisa four seedling cohorts were simultaneously monitored on 24 1 m^2 circles per grazing treatment, which had been cleared of all vegetation. Only 0.6 m diameter of the circles was monitored to avoid edge effects of the vegetation. (The same exercise was undertaken at Utha but constitutes Chapter 11.) Tests of independence (G-test - Sokal & Rohlf 1981) of seedling survival on locality (grazing treatment) were done separately for each plant group at each site, and separately for permanent quadrats and cleared circles.

Demographic fate of an individual

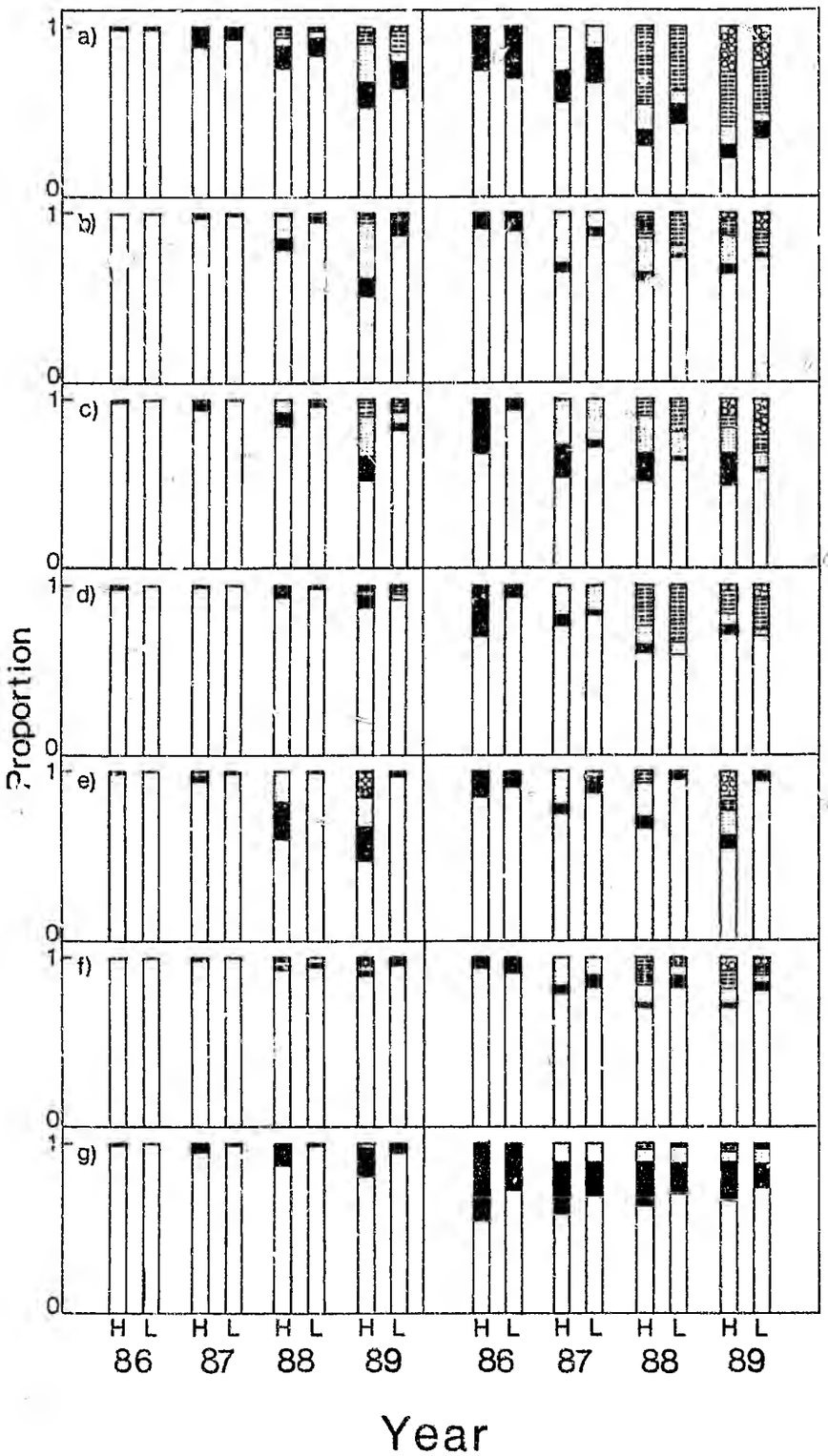
Data on the mortality and changes in the size of tufts were obtained from the permanently located quadrats and other tagged tufts. The influence of location (grazing treatment), conditional on size, on the demographic fate of individuals was examined with log-linear analyses (Fienberg 1979). (The derivation of size classes is outlined in Chapter 9, and listed in Table 9.1.) Three categories of demographic fate were defined for a transition period; an individual could (1) decline in size (or die), (2) remain the same size, or (3) increase in size. Reduction to three categories ensured adequate sample size. For individuals starting in the smallest class a decline in size means mortality. For individuals starting in the largest class only categories (1) and (2) were used. Separate log-linear analyses were undertaken for the influence of grazing treatment and year on mortality. The fate of an individual over a transition period was defined as either dying or living.

It was sought to explain the change in the size of a tuft in terms of the initial size, the mean grazing rank and mean amount of moribund material for the transition period, and the influence of neighbours (as defined

for effects on reproductive output). Two models were examined using multiple regression analyses. The two different dependent variables were the change in radius of the tuft and the change in radius as a proportion of the initial radius. If a tuft had fragmented over the transition period, a radius equivalent to the combined area was used. Separate one-way ANOVA for each species for each grazing treatment tested whether the single year of rainfall interception had an effect on changes in tuft size.

It was of interest to gain some insight into the relationship between the size and age of a tuft on its demographic fate. The most suitable contrast available was for the proportion of the smallest size class, defined by two ages, which died over the 1988 to 1989 transition period. The first age group were those in existence at the start of the study, the second those which had established in either the 1985/86 or 1986/87 growing seasons (i.e. old versus young tufts). By the 1988 to 1989 transition period sufficient fragmentation of old tufts had taken place to ensure an adequate sample size of old, small tufts. The dependence of tuft survival on location (grazing treatment) and age was tested for selected species at each site by log-linear analyses (Fienberg 1979) using SAS (1985).

Figure 7.1. The proportion of basal area (on the left), and of density (on the right), comprised by the starting population (open bar) or by individuals recruited in 1985/86 (solid bar), 1986/87 (stippled bar), 1987/88 (dashed bar) and 1988/89 (bar with circles), for a) *Aristida bipartita*, b) *Bothriochloa insculpta* (Thlavekisa), c) *Heteropogon contortus*, d) *Themeda triandra* (Thlavekisa), e) *Bothriochloa insculpta* (Utha), f) *Digitaria eriantha* (Utha), and g) *Themeda triandra* (Utha). Notation for grazing treatments: H - heavy grazing; L - light grazing.


a)
b)
c)
d)
e)
f)
g)
1
0
Proportion
H L H L H L H L H L H L H L H L
86 87 88 89 86 87 88 89
Year

RESULTS

Population Turnover

The rate of population turnover of all species was greater on the heavily grazed treatment, with the exception of turnover in numbers for *Themeda* at Thlavekisa (Figure 7.1). The proportion of the basal area in the final year comprised by the population present at the start of the experiment was >47% in all cases, despite an approximate 70% turnover in number of *Aristida*. The populations of *Themeda*, *Digitaria* and *Bothriochloa* (the latter if lightly grazed) were relatively unchanging, while there was substantial turnover of *Aristida*, *Heteropogon* and *Bothriochloa* (the latter if heavily grazed). The time invariant status of the starting populations of *Setaria* (both sites) and *Digitaria* (Thlavekisa) were even more pronounced. Although a small number of new genets of *Setaria* established at both sites, their contribution to basal area or number was <2% in all years. There were no new recruits of *Digitaria* at Thlavekisa in four years. The contribution to density of the starting populations of *Themeda* at Utha (Figure 7.1) and *Bothriochloa* at Thlavekisa increased in the final years because of tuft fragmentation and the mortality of cohorts which established during the study.

Population structure

Thlavekisa. The tuft size of *Heteropogon* and *Themeda* consistently decreased over four years, the tuft size of *Bothriochloa* tended to

decrease on the heavily grazed treatment, and the tuft size of *Setaria* decreased between 1986 and 1987 on the heavily grazed treatment (Table 7.1). In contrast, the tuft size of *Aristida* increased between 1986 and 1987, but decreased between 1987 and 1988. The size structure of all populations was right skewed, and the coefficient of skewness tended to increase over the four years, with the exception of *Aristida* on the lightly grazed treatment and *Bothriochloa* on the heavily grazed treatment. The species other than *Aristida* showed significant ($p<0.05$) or near significant ($p<0.07$) negative correlations between tuft size and g_1. The change in population inequality varied widely (Table 7.1). Tuft size and population inequality were correlated ($p<0.05$) only for *Themeda*. There were significant correlations between CV and g_1 for *Aristida*, *Bothriochloa* and *Themeda*.

Utha. Tuft size generally decreased over four years, with the exception of the heavily grazed *Setaria* population (Table 7.2). Tuft size of *Themeda* increased between 1987 and 1988, but decreased the following year. There was an associated decrease in CV, but the changing shape of population structure was highly variable. There was a positive correlation ($p<0.05$) between tuft size and CV for *Themeda*, and a negative correlation ($p<0.05$) between tuft size and g_1 for *Setaria*. Skewness and CV were correlated ($p<0.05$) for *Bothriochloa* and *Themeda*.

Table 7.1. Descriptive statistics of the change in the population size structure (by tuft circumference in cm) of six species at Thlavekisa between 1985/86 and 1988/89. H - heavy grazing; L - light grazing.

Site and species	Treatment	Year	n	$\bar{x}$	S.E.	median	CV	skewness (g_1)
Aristida	H	1986	221	3.3	0.18	3	79	1.475
		1987	267	4.1	0.19	3	77	1.392
		1988	438	3.4	0.15	2	94	1.794
		1989	454	3.0	0.11	2	77	1.524
	L	1986	343	3.2	0.16	2	92	2.213
		1987	304	3.8	0.19	3	87	1.953
		1988	399	3.4	0.16	2	92	1.691
		1989	445	3.3	0.12	3	75	1.327
Bothriochloa	H	1986	40	8.5	1.13	6.5	85	0.919
		1987	57	5.3	0.77	3	109	1.942
		1988	60	6.9	0.62	6	69	1.386
		1989	49	6.3	0.50	6	55	0.832
	L	1986	40	8.8	1.02	7	74	0.944
		1987	44	8.6	0.93	8	72	0.586
		1988	56	8.8	0.87	7	73	0.962
		1989	58	7.6	0.89	5	89	1.627
Digitaria	H	1986	18	17.7	2.60	18.5	63	0.738
		1987	29	14.7	1.60	12	58	0.400
		1988	36	14.6	1.47	12.5	60	1.039
		1989	40	13.0	1.30	10.5	63	1.258
	L	1986	5	23.0	4.4	23	43	———
		1987	9	14.7	4.7	6	96	1.285
		1988	9	20.4	4.60	18	68	1.243
		1989	12	17.4	4.58	11	91	1.784

Table 7.1 continued.

Site and species	Treatment	Year	n	$\bar{x}$	S.E.	median	CV	skewness (g_1)
Heteropogon	H	1986	112	7.5	0.71	4	101	1.077
		1987	142	6.2	0.54	4	103	1.655
		1988	155	7.1	0.47	5	82	2.108
		1989	106	3.9	0.84	3	82	1.757
	L	1986	67	14.7	1.11	13	62	0.597
		1987	97	9.9	1.02	7	101	1.122
		1988	104	9.8	0.90	6.5	94	1.464
		1989	134	5.0	0.36	4	82	1.646
Setaria	H	1986	81	18.6	1.88	11	91	0.784
		1987	153	10.4	0.91	6	109	2.436
		1988	157	11.6	0.83	10	90	2.091
		1989	129	10.2	0.81	8	90	2.865
	L	1986	60	13.4	2.04	5	117	1.583
		1987	109	10.5	1.19	7	119	4.050
		1988	113	14.0	1.41	10	107	3.061
		1989	120	11.5	0.90	8	86	1.907
Themeda	H	1986	60	9.0	1.03	8	89	1.492
		1987	75	8.0	0.80	4	87	0.927
		1988	97	7.9	0.72	5	90	1.197
		1989	80	5.5	0.57	4	94	2.227
	L	1986	42	10.2	0.92	10	58	0.301
		1987	53	9.4	1.00	9	76	0.345
		1988	82	8.5	0.91	4	97	0.908
		1989	97	6.2	0.59	4	94	1.543

Table 7.2. Descriptive statistics of the change in the population size structure (by tuft circumference in cm) of four species at Ukha between 1985/86 and 1988/89. Notation for treatment: H - heavy grazing; L - light grazing.

Site and species	Treatment	Year	n	$\bar{x}$	S.E.	median	CV	skewness (g_1)
Bothriochloa	H	1986	19	4.5	0.66	4	64	0.534
		1987	20	4.6	0.71	4	69	1.659
		1988	15	2.9	0.68	2	90	1.250
		1989	13	3.9	0.53	4	48	0.217
	L	1986	20	7.7	1.76	4	101	1.502
		1987	26	6.2	1.00	4.5	83	1.653
		1988	18	6.1	1.13	5.5	79	0.919
		1989	17	4.5	0.64	3	58	0.844
Digitaria	H	1986	61	9.6	1.09	7	89	1.822
		1987	89	6.3	0.54	5	80	1.612
		1988	113	6.5	0.47	5	76	1.209
		1989	116	6.3	0.41	5	69	1.633
	L	1986	62	8.4	0.92	5	86	1.406
		1987	90	6.2	0.56	5	85	1.454
		1988	95	6.0	0.48	5	78	1.851
		1989	98	6.0	0.45	5	75	2.255
Setaria	H	1986	142	7.0	0.96	3.5	164	4.863
		1987	213	5.6	0.70	3	183	7.215
		1988	186	6.0	0.52	4.5	73	6.469
		1989	166	5.9	0.57	4	123	7.137
	L	1986	198	10.4	1.04	4	140	2.927
		1987	342	6.5	0.51	3	147	4.371
		1988	322	6.7	0.46	4	124	3.936
		1989	254	7.6	0.52	5	109	3.612
Themeda	H	1986	285	6.2	0.52	2	141	2.895
		1987	345	6.5	0.34	4	97	2.505
		1988	354	8.0	0.31	7	73	1.404
		1989	377	7.0	0.25	6	70	1.298
	L	1986	146	6.7	0.71	3	127	2.309
		1987	165	6.9	0.63	4	117	2.272
		1988	161	6.6	0.59	4	114	2.806
		1989	160	6.1	0.40	4	85	1.522

Table 7.3. A summary of the multiple regression analyses of the effect of tuft size, grazing, moribund material and plant neighbours on individual reproductive output of five species at Thlavekisa for three growing seasons.

Site and				Parameter							
				Tuft size		Grazing		Moribund		Neighbours	
species	Year	n	R	Slope	F	Slope	F	Slope	F	Slope	F
Thlavekisa											
Heavy grazing											
Aristida bipartita	1985	55	0.60	3.56	75.09***	0.00	0.00	-0.49	0.02		
	1986	56	0.46	4.82	37.00***	-0.49	0.01	4.36	0.90		
	1987	58	0.29	2.40	21.09***	-6.96	3.92(*)	-3.27	1.35	-8.28	0.83
Bothriochloa insculpta	1985	27	0.60	0.47	25.11***	-3.80	4.18(*)	-0.16	0.04		
	1986	27	0.54	0.80	23.31***	-1.68	1.06	-1.63	2.02		
	1987	26	0.47	0.24	12.36**	0.13	0.04	-0.79	1.71	-2.84	2.92
Heteropogon contortus	1985	69	0.42	0.56	45.95***	-0.46	0.10	1.95	2.59		
	1986	69	0.31	0.48	21.38***	-0.80	0.60	-1.90	2.61		
	1987	67	0.04	0.13	0.78	-0.72	0.32	0.24	0.03	3.78	1.08
Setaria incrassata	1986	38	0.34	0.28	16.24***	-1.03	0.26	-3.94	2.60		
	1987	29	0.50	0.35	17.16***	-5.16	1.61	2.79	0.91	-7.40	0.97
Themeda triandra	1985	62	0.25	0.21	8.91**	-4.56	6.75*	1.71	1.49		
	1986	59	0.28	0.62	13.63***	-5.43	9.78**	1.12	0.13		
	1987	63	0.49	1.53	32.74***	-15.54	30.40***	-0.32	0.01	-0.53	0.00
Light grazing											
Aristida	1985	83	0.65	5.14	135.72***	0.00	0.00	-4.77	0.50		
	1986	91	0.65	10.54	154.10***	-13.69	1.89	-3.99	0.69		
Bothriochloa insculpta	1985	30	0.27	0.53	5.13*	-0.81	0.01	3.07	0.84		
	1986	30	0.10	0.23	2.47	0.52	0.11	-0.12	0.01		
	1987	31	0.32	0.11	3.03			0.98	0.23	-3.28	3.87(*)
Heteropogon contortus	1985	63	0.17	1.56	11.15**	-2.29	0.05	-0.54	0.00		
	1986	65	0.27	0.77	14.23***	-4.48	6.13*	-3.27	2.56		
	1987	63	0.40	1.00	12.91***			24.56	7.33	-6.91	0.56
Setaria incrassata	1985	39	0.11	0.12	3.76(*)	0.08	0.00	-0.32	0.02		
	1986	39	0.29	0.48	12.61**	-7.57	4.01(*)	-1.97	0.17		
	1987	29	0.64	0.62	42.45***			-6.21	0.08	12.00	0.19
Themeda triandra	1985	52	0.39	1.21	28.08***	-2.83	0.45	-1.39	0.23		
	1986	51	0.26	1.71	15.63***	-2.18	0.49	1.47	0.05		
	1987	52	0.37	0.77	21.93***			2.73	0.22	-2.93	0.57

*** - p<0.001; ** - p<0.01; * - p<0.05; (*) - p<0.06

Table 7.3 ctd. A summary of the multiple regression analyses of the effect of tuft size, grazing, moribund material and plant neighbours on individual reproductive output of four species at Utha for three growing seasons.

Site and species	Year	n	R	Parameter: Tuft size Slope	Tuft size F	Grazing Slope	Grazing F	Moribund Slope	Moribund F	Neighbours Slope	Neighbours F
Utha											
Heavy grazing											
Bothriochloa insculpta	1987	15	0.78	0.91	27.31***	-0.64	0.43	-0.37	0.04	8.14	2.69
Setaria incrassata	1986	31	0.77	0.11	9.40**	0.06	0.01	-0.63	0.51	0.83	47.60***
Setaria	1987	59	0.35	0.05	17.88***	0.04	0.04	-0.35	0.72	-0.28	0.17
Themeda triandra	1985	128	0.32	0.10	31.92***	-0.87	11.20***	0.17	0.21	-1.13	2.74
	1986	128	0.14	0.22	14.40***	-1.36	6.67*	-1.30	1.47	1.24	0.47
	1987	191	0.21	0.29	38.45***	-1.68	16.28***	-1.11	1.87	-0.52	0.11
Light grazing											
Bothriochloa insculpta	1985	23	0.50	0.12	8.87**	-0.72	0.64	-0.17	0.14	1.67	4.18*
	1986	21	0.41	0.25	5.66*	0.09	0.02	-0.59	1.02	0.32	0.08
	1987	20	0.32	0.22	3.60	0.31	0.40	-0.37	0.50	-0.17	0.03
Setaria incrassata	1986	32	0.18	0.06	5.64*	0.08	0.07	-0.11	0.08	-0.07	0.45
	1987	96	0.32	0.12	33.53***	0.16	0.23	-0.27	0.36	1.01	0.66
Themeda triandra	1985	95	0.34	0.21	11.79***	-2.04	6.43*	0.85	0.38	-0.13	0.12
	1986	95	0.35	1.03	41.83***	-3.44	4.48*	-3.00	1.69	-0.75	0.29
	1987	110	0.47	0.85	72.11***	-2.41	11.87***	-0.28	0.04	-7.83	2.82

*** - p<0.001; ** - p<0.01; * - p<0.05; (*) - p<0.06

Reproductive Output

At Thlavekisa, the mean number of seeds produced per individual in 1987 was highest for *Setaria* (1164), *Urochloa* (882) and *Aristida* (699), lowest for the obligate seed reproducers *Themeda* (106) and *Heteropogon* (92), and intermediate for *Bothriochloa* (212). At Utha, the ranking of species was *Setaria* (122), *Bothriochloa* (100), *Digitaria* (78) and *Themeda* (40). These comparisons are biased by the different tuft sizes of individuals, and a more appropriate approach to the comparison of species is given in Chapter 10.

The principal determinant of individual reproductive output, with only two exceptions, was tuft size (Table 7.3). In nine of eleven cases (including light grazing) grazing depressed the reproductive output of *Themeda* (Table 7.3). In only one instance each was the reproductive output of *Aristida*, *Bothriochloa*, *Heteropogon* or *Setaria* significantly affected by grazing. The neighbourhood environment enhanced the reproductive output of both *Setaria* (heavily grazed) and *Bothriochloa* (lightly grazed) on one occasion each, possibly only chance results. Moribund material had no effect on reproductive output. *Digitaria* at Utha could not be analysed because too few tufts produced culms.

Recruitment and early growth

Recruitment.

The number of new recruits establishing under each grazing regime was not independent of the year of establishment for *Heteropogon* (G=46.14, df=3,

$p<0.005$), *Aristida* ($G=28.71$, $df=3$, $p<0.005$) or *Bothriochloa* (Utha) ($G=12.18$, $df=3$ $p<0.05$), but was for *Themeda* (both sites) and *Digitaria* (Utha). (The other species were not tested because of small sample sizes.) For *Heteropogon*, there was initially greater recruitment on the heavily grazed treatment, but this pattern was reversed with time as the number of new recruits declined on the heavily and increased on the lightly grazed treatment (Table 7.4). There was initially greater recruitment of *Aristida* on the lightly grazed treatment, and a conspicuous increase in recruitment in the wetter 1987/88 season (also shown by *Themeda* at Thlavekisa - Table 7.4). At Utha, there was extensive recruitment of *Themeda* in the 1986/87 season, but the number of recruits on both treatments declined dramatically with time. There was an increased number of recruits of *Themeda* on the rainfall interception, lightly grazed treatment relative to the normal treatment ($G=9.4$, $df=1$, $p<0.005$) in the year following rainfall interception, but *Aristida* (Thlavekisa) showed the opposite trend ($G=4.15$, $df=1$, $p<0.05$). There were few new genets of the species capable of vegetative propagation; only 0.13 seedlings m^{-2} $year^{-1}$ of *Digitaria* and 0.31 seedlings m^{-2} $year^{-1}$ of *Setaria* at Utha, and 0.03 seedlings m^{-2} $year^{-1}$ of *Setaria* at Thlavekisa, were recruited.

Mortality in the first season following establishment.

At Thlavekisa, there was a significant year by location interaction for both *Aristida* ($G^2=17.31$, 2 df, $p=.0002$) and *Heteropogon* ($G^2=6.9$, 2 df, $p=.032$), and therefore separate G-tests were undertaken for each year. There was higher mortality ($p<0.05$) of *Aristida* seedlings on the lightly grazed treatment for the 1985/86 to 1986/87 and 1986/87 to 1987/88 transitions (Table 7.5). The response over the first transition could be attributed to the effect of fire. There was higher mortality ($p<0.05$) of lightly grazed *Heteropogon* seedlings for the 1986/87 to 1987/88 transition period (Table 7.5). Neither location nor year had any effect

Table 7.4. Summary statistics of the number of recruits m^{-2} of five species at two sites between 1985/86 and 1988/89. The year denotes April/May (end of growing season).

Site, species and year		Heavy grazing $\bar{x}$	S.E.	median	Q1-Q3	Light grazing $\bar{x}$	S.E.	median	Q1-Q3
Thlavekisa									
Aristida	1986	7.4	1.45	4	0-12	14.3	3.01	8	0-24
	1987	8.8	1.48	8	0-16	5.3	1.09	4	0-8
	1988	25.8	5.08	16	8-36	20.1	3.69	12	8-32
	1989	15.4	2.47	12	4-24	13.6	2.14	10	4-24
Bothriochloa	1986	0.5	0.31	0	0-0	0.4	0.22	0	0-0
	1987	2.2	0.64	0	0-4	0.5	0.42	0	0-0
	1988	1.2	0.42	0	0-0	1.5	0.73	0	0-0
	1989	0.1	0.13	0	0-0	0.8	0.68	0	0-0
Heteropogon	1986	5.3	1.58	4	0-8	0.7	0.34	0	0-0
	1987	3.7	0.93	4	0-4	2.4	0.59	0	0-4
	1988	1.9	0.64	0	0-4	3.7	1.13	2	0-4
	1989	1.3	0.43	0	0-4	3.6	1.07	0	0-4
Themeda	1986	1.3	0.50	0	0-0	0.5	0.32	0	0-0
	1987	1.8	0.61	0	0-4	0.9	0.42	0	0-0
	1988	3.0	1.02	0	0-4	3.7	0.86	2	0-8
	1989	0.4	0.28	0	0-0	0.7	0.39	0	0-0
Utha									
Bothriochloa	1986	0.3	0.20	0	0-0	0.3	0.21	0	0-0
	1987	0.4	0.30	0	0-0	0.1	0.14	0	0-0
	1988	0.1	0.14	0	0-0	0.0	0.00	0	0-0
	1989	0.4	0.23	0	0-0	0.0	0.00	0	0-0
Digitaria	1986	0.6	0.34	0	0-0	0.9	0.34	0	0-0
	1987	2.1	0.94	0	0-0	1.9	0.99	0	0-0
	1988	2.5	0.83	0	0-4	1.2	0.69	0	0-0
	1989	1.1	0.39	0	0-0	0.7	0.49	0	0-0
Themeda	1986	19.1	2.75	20	4-32	6.6	2.55	4	0-4
	1987	4.7	0.87	4	0-8	2.6	1.07	0	0-4
	1988	1.9	0.51	0	0-4	0.6	0.33	0	0-0
	1989	0.6	0.33	0	0-0	0.1	0.14	0	0

on the proportional survival of *Themeda* at either site. Other species were not tested because of poor sample size.

Seedling growth following establishment.

Table 7.5. The percentage survival of seedlings over the year following establishment, at two sites. Notation for site:U=Utah; T=Thlavekisa.

		Transition period					
		1985/6-1986/7		1986/7-1987/8		1987/8-1988/9	
Species	Site	Heavy grazing	Light grazing	Heavy grazing	Light grazing	Heavy grazing	Light grazing
Aristida	T	86	57	94	77	74	78
Heteropogon	T	71	75	90	67	53	79
Themeda	T	50	33	85	75	44	68
Themeda	U	71	74	63	80	85	67

The mean tuft circumference in 1988, of the heavily and lightly grazed treatments respectively, of the 1985/86 cohort was 6.1 cm and 2.6 cm, and of the 1986/87 cohort 3.3 cm and 1.4 cm (1985/86 cohort: t=7.12, df=68.3, p=0.0001; 1986/87 cohort: t=4.08, df=29.9 p=0.0003; both are t-tests for unequal variances). The mean tuft circumference of the 1985/86 cohort of *Aristida* seedlings was 5.0 cm on the heavily grazed and 3.7 cm on the lightly grazed treatment (t=2.70, df=88, p=0.0082), but there was no difference between grazing treatments for the 1986/87 cohort. There were no differences between grazing treatments in the seedling growth of the 1986/87 cohorts of *Themeda* or *Heteropogon* seedlings (all other sample sizes were too small for testing).

Seedling survival following emergence.

The percentage of individuals surviving from emergence until the end of the 1986/87 season for the heavily and lightly grazed treatments respectively were as follows: Utha - 30% and 38% for grasses ($p>0.05$), 46% and 69% for forbs ($G=7.66$, 1 df, $p<0.05$), 33% and 44% for *Cassia mimosoides* ($p>0.05$); the permanent quadrats at Thlavekisa - 31% for grasses on both grazing treatments, 66% and 44% for forbs ($p>0.05$), 19% and 66% for *C. mimosoides* ($G=22.6$, 1 df, $p<0.001$); the cleared circles at Thlavekisa - 26% and 19% for grasses ($G=7.66$, 1 df, $p<0.05$), 25% and 42% for forbs ($G=7.2$, 1 df, $p<0.05$), and 46% and 47% for *C. mimosoides* ($p>0.05$).

Demographic fate of individuals

The single year of rainfall manipulation had no influence on the size transitions of the established populations of *Aristida* or *Themeda* (Utha), nor were there any differences for the 1986 to 1987 transition ($p>0.5$ in all cases). The only significant differences between transition matrices due to grazing were for *Setaria* at Thlavekisa (1986-1987 transition - $p=0.023$), possibly a result of the fire, and *Themeda* at Utha for both the 1986-1987 ($p=0.0113$) and 1987-1988 ($p=0.0017$) transitions. The effect of grazing on *Heteropogon* was dependent on size class, only the two smallest size classes were affected ($p<0.02$).

Log-linear analyses revealed that there were differences ($p<0.05$) between years for all species for the proportion of individuals dying. In all species there was a trend of increasing mortality with time (Figure 7.2), with almost no mortality in the first season, but increasing to between 25-30% in the final transition for *Aristida*, *Bothriochloa*, *Setaria* and *Themeda*, and 46% for *Heteropogon* on the heavily grazed treatment. There

were also differences ($p<0.05$) between grazing treatments for *Aristida*, *Digitaria*, *Heteropogon* and *Setaria* (Utha). There was higher mortality on the heavily grazed treatment for *Digitaria* and *Heteropogon*, but the grazing effect for *Aristida* and *Setaria* (Utha) was dependent on year (Figure 7.2). Up to 96% (*Themeda*) and not less than 70% (*Bothriochloa*) of mortality was restricted to the smallest size class, and almost all of the remainder occurred in the next smallest size class. Large individuals did not die but fragmented (over a one year period) into a number of smaller individuals. Tuft fragmentation was observed on both sites across all species. The species with the highest proportion of tufts which fragmented were *Digitaria* at Utha and *Setaria* at Thlavekisa (each about 40%), while approximately 30% of *Themeda* and *Setaria* tufts at Utha and *Heteropogon* tufts at Thlavekisa, 20% of *Bothriochloa* and *Themeda* at Thlavekisa, 10% of *Bothriochloa* tufts at Utha and 5% of *Aristida* tufts fragmented. The majority of the tufts which fragmented were the larger rather than the smaller tufts (see the transition matrices - Table 9.2). The general pattern of dieback of tufts was to start in the centre and spread centrifugally (see Gatsuk *et al.* 1980).

Age had an effect on the survival of the smallest size class for the 1988 to 1989 transition period independently of grazing for *Aristida* ($G^2=27.6$, $p=0.0001$) and *Heteropogon* ($G^2=13.8$, $p=0.0002$), with greater mortality of the older tufts (Table 7.6). There was no influence of age on the survival of *Themeda* at either site, or on *Digitaria* at Utha.

The initial size of the tuft , the amount of moribund material, the amount grazed, and neighbourhood effects had a similar influence on changes in tuft size (Tables 7.7, 7.8) and in the proportional change in tuft size (Tables 7.9, 7.10). In all cases there was a correlation ($p<0.05$) between change in tuft size and proportional change in tuft size. Across all analyses, the size of a tuft had the most important influence. In general, the larger a tuft, and also the greater the amount of moribund

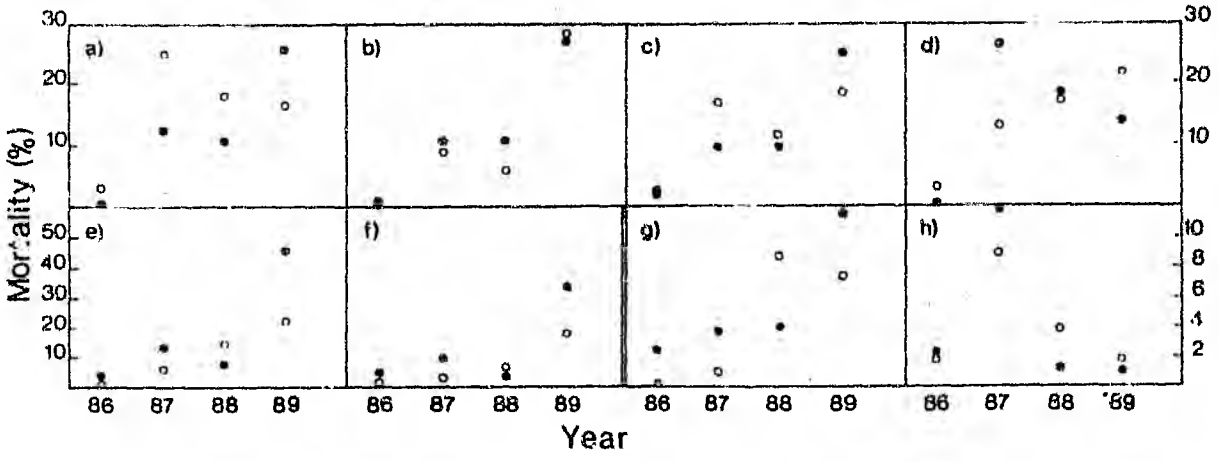


Figure 7.2. The percentage mortality over four years for the common perennial grasses: a) *Aristida bipartita*, b) *Bothriochloa* (Thlavekisa), c) *Setaria incrassata* (Thlavekisa), d) *Setaria incrassata* (Utha), e) *Heteropogon contortus*, f) *Themeda triandra* (Thlavekisa), g) *Digitaria eriantha* (Utha) and h) *Themeda triandra* (Utha). Open circles denote light grazing, closed circles denote heavy grazing.

Table 7.6. The percentage survival of old and young tufts of the smallest size class (defined in the text) for the 1987/88 to 1988/89 transition period. Notation for sites: T=Thlavekisa; U=Utha.

		Heavy grazing		Light grazing	
Species	Site	Old tufts	Young tufts	Old tufts	Young tufts
Aristida bipartita	T	55	89	85	93
Heteropogon contortus	T	33	66	60	93
Themeda triandra	T	82	57	80	82
Digitaria eriantha	U	100	92	92	90
Themeda triandra	U	74	91	87	84

material, the greater its absolute and proportional decrease in size. Grazing had an effect on the size changes of *Bothriochloa*, *Heteropogon* and *Themeda* (*Setaria* was near significant) on the heavily grazed treatment at Thlavekisa, but not in the expected direction. Heavily grazed tufts grew more, and in some instances the proportional increase in size was greater. *Digitaria* was negatively affected by the limited amount of grazing on the lightly grazed treatment at Utha, and was also the only species to be negatively affected by its neighbourhood competitive environment.

Table 7.7. Summary of the multiple regression analyses of changes in plant size for two separate seasons for five grass species at Thlavekisa.

Treatment, species year	Independent variable	Associated Slope	Associated prob=0	Associated r^2	Overall F-value	Overall r^2
Heavy grazing						
Aristida 1985-1986	Tuft size	0.187	0.045	0.450	5.96**	0.256
	Moribund	1.219	0.037	0.033		
	Grazing	0.055	0.920	0.019		
Aristida 1986-1987	Tuft size	0.089	0.0001	0.289	6.88***	0.379
	Moribund	-0.212	0.080	0.016		
	Grazing	-0.222	0.103	0.000		
	Neighbours	-0.348	0.326	0.018		
Bothriochloa 1985-1986	Tuft size	0.476	0.022	0.492	10.18***	0.581
	Moribund	2.848	0.073	0.461		
	Grazing	0.407	0.822	0.155		
Bothriochloa 1986-1987	Tuft size	0.057	0.040	0.109	3.14*	0.386
	Moribund	-0.242	0.321	0.002		
	Grazing	-0.659	0.009	0.235		
	Neighbours	0.149	0.825	0.001		
Heteropogon 1985-1986	Tuft size	0.262	0.0003	0.158	17.18***	0.439
	Moribund	2.520	0.005	0.308		
	Grazing	-1.216	0.091	0.176		
Heteropogon 1986-1987	Tuft size	0.077	0.0001	0.236	9.95***	0.395
	Moribund	-0.339	0.024	0.006		
	Grazing	-0.386	0.004	0.025		
	Neighbours	0.292	0.491	0.002		
Setaria 1985-1986	Tuft size	0.007	0.956	0.000	0.05ns	0.004
	Moribund	-0.852	0.820	0.003		
	Grazing	0.453	0.886	0.002		
Setaria 1986-1987	Tuft size	0.014	0.430	0.001	1.54ns	0.205
	Moribund	0.556	0.340	0.056		
	Grazing	-1.435	0.061	0.141		
	Neighbours	0.180	0 903	0.010		
Themeda 1985-1986	Tuft size	0.093	0.031	0.058	6.48***	0.261
	Moribund	0.551	0.494	0.067		
	Grazing	-1.512	0.001	0.165		
Themeda	Tuft size	0.033	0.0001	0.293	5.84***	0.314
	Moribund	-0.004	0.978	0 002		
	Grazing	-0.102	0.258	0.007		
	Neighbours	0.007	0.981	0.003		

Table 7.7 continued.

Treatment, species, year	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Light grazing						
Aristida	Tuft size	0.288	0.0001	0.229	14.22***	0.329
1985-1986	Moribund	0.473	0.213	0.060		
	Grazing	0.619	0.439	0.044		
Aristida	Tuft size	0.062	0.0003	0.169	14.06***	0.360
1986-1987	Moribund	0.432	0.0001	0.234		
	Neighbours	0.149	0.610	0.031		
Bothriochloa	Tuft size	0.099	0.362	0.147	2.25ns	0.206
1985-1986	Moribund	1.495	0.193	0.173		
	Grazing	-0.419	0.704	0.008		
Bothriochloa	Tuft size	0.069	0.010	0.215	3.84*	0.334
1986-1987	Moribund	-0.461	0.613	0.005		
	Neighbours	1.228	0.113	0.102		
[illegible]	Tuft size	0.383	0.0001	0.228	13.96***	0.411
	Moribund	3.051	0.0006	0.135		
	Grazing	-0.244	0.757	0.006		
	Tuft size	0.040	0.008	0.036	5.34**	0.216
	Moribund	-1.479	0.001	0.105		
	Neighbours	0.559	0.227	0.010		
Setaria	Tuft size	-0.242	0.081	0.038	1.99ns	0.145
1985-1986	Moribund	6.817	0.045	0.061		
	Grazing	2.884	0.284	0.000		
Setaria	Tuft size	-0.050	0.017	0.227	3.71*	0.326
1986-1987	Moribund	-1.600	0.611	0.095		
	Neighbours	5.246	0.194	0.096		
Themeda	Tuft size	0 106	0.244	0.072	3.75*	0.193
1985-1986	Moribund	2.416	0.011	0.145		
	Grazing	0.013	0.983	0.000		
Themeda	Tuft size	0.014	0.438	0.007	0.24ns	0.015
	Moribund	-0.328	0.545	0.002		
	Neighbours	-0.015	0.966	0.000		

*** - p<0.001; ** - p<0.01; * - p<0.05; (*) - p<0.06;
ns - not significant.

Table 7.8. Summary of the multiple regression analyses of the change in plant size between 1986 and 1987 for four grass species at Utha.

Treatment, species year	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Heavy grazing						
Bothriochloa	Tuft size	0.076	0.796	0.062	1.325ns	0.469
1986-1987	Moribund	2.067	0.350	0.226		
	Grazing	-1.096	0.307	0.180		
	Neighbours	4.037	0.381	0.131		
Digitaria	Tuft size	-0.022	0.519	0.017	0.69ns	0.010
1985-1986	Moribund	0.081	0.874	0.000		
	Grazing	0.036	0.892	0.005		
	Neighbours	-0.974	0.167	0.080		
Digitaria	Tuft size	0.521	0.0001	0.424	10.99***	0.587
1986-1987	Moribund	-8.305	0.005	0.023		
	Grazing	0.531	0.728	0.057		
	Neighbours	9.307	0.077	0.017		
Setaria	Tuft size	-0.007	0.793	0.003	0.41ns	0.059
1985-1986	Moribund	-0.097	0.883	0.001		
	Grazing	0.489	0.247	0.053		
	Neighbours	0.025	0.780	0.004		
Setaria	Tuft size	0.624	0.0001	0.212	8.36***	0.391
1986-1987	Moribund	-15.373	0.0003	0.001		
	Grazing	-0.474	0.825	0.017		
	Neighbours	-0.347	0.961	0.003		
Themeda	Tuft size	0.000	0.997	0.007	2.15ns	0.065
1985-1986	Moribund	0.423	0.043	0.053		
	Grazing	-0.143	0.162	0.021		
	Neighbours	-0.077	0.827	0.000		
Themeda	Tuft size	0.377	0.0001	0.248	17.86***	0.304
1986-1987	Moribund	-2.615	0.003	0.007		
	Grazing	-1.096	0.019	0.005		
	Neighbours	0.731	0.704	0.009		

Table 7.8 continued.

Treatment, species year	Independent variable	Associated Slope	prob=0	r^2	Overall F-value	r^2
Light grazing						
Bothriochloa	Tuft size	-0.020	0.687	0.025	2.55ns	0.375
1985-1986	Moribund	0.744	0.013	0.307		
	Grazing	0.365	0.249	0.013		
	Neighbours	0.441	0.415	0.023		
Bothriochloa	Tuft size	-0.250	0.051	0.100	6.81**	0.645
1986-1987	Moribund	2.248	0.001	0.408		
	Grazing	0.911	0.088	0.022		
	Neighbours	1.382	0.204	0.051		
Digitaria	Tuft size	-0.024	0.488	0.064	0.44ns	
1985-1986	Moribund	-0.025	0.953	0.041		
	Grazing	0.039	0.813	0.001		
	Neighbours	-0.375	0.551	0.026		
Digitaria	Tuft size	-0.274	0.060	0.227	6.20**	0.593
1986-1987	Moribund	6.303	0.002	0.128		
	Grazing	1.699	0.048	0.019		
	Neighbours	16.750	0.007	0.196		
Setaria	Tuft size	-0.054	0.020	0.192	1.89ns	0.219
1985-1986	Moribund	0.303	0.369	0.002		
	Grazing	0.156	0.547	0.006		
	Neighbours	-0.005	0.957	0.032		
Setaria	Tuft size	-0.132	0.031	0.125	1.83ns	0.076
1986-1987	Moribund	1.741	0.187	0.005		
	Grazing	0.387	0.676	0.000		
	Neighbours	5.783	0.105	0.024		
Themeda	Tuft size	0.007	0.429	0.044	1.52ns	0.062
1985-1986	Moribund	0.213	0.096	0.040		
	Grazing	0.010	0.919	0.000		
	Neighbours	-0.075	0.331	0.008		
Themeda	Tuft size	-0.076	0.218	0.261	3.68**	0.125
1986-1987	Moribund	2.497	0.006	0.102		
	Grazing	-0.230	0.592	0.041		
	Neighbours	1.765	0.534	0.028		

*** - p<0.001; ** - p<0.01; * - p<0.05; (*) - p<0.06;
ns - not significant.

Table 7.9. Summary of the multiple regression analyses of the proportional change in plant size for five grass species at Thlavekisa.

Treatment, species	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Heavy grazing						
Aristida	Tuft size	0.208	0.019	0.203	7.62***	0.305
1985-1986	Moribund	1.248	0.025	0.214		
	Grazing	-0.082	0.875	0.004		
Aristida	Tuft size	0.081	0.0002	0.222	4.34***	0.278
1986-1987	Moribund	-0.041	0.751	0.001		
	Grazing	-0.272	0.069	0.006		
	Neighbours	0.069	0.859	0.000		
Bothriochloa	Tuft size	0.092	0.224	0.412	17.59***	0.706
1985-1986	Moribund	2.132	0.001	0.685		
	Grazing	-0.116	0.866	0.296		
Bothriochloa	Tuft size	0.032	0.101	0.123	3.68*	0.424
1986-1987	Moribund	0.044	0.797	0.067		
	Grazing	-0.514	0.005	0.279		
	Neighbours	0.267	0.579	0.001		
Heteropogon	Tuft size	0.007	0.719	0.008	23.36***	0.515
1985-1986	Moribund	1.167	0.0001	0.492		
	Grazing	-0.353	0.080	0.324		
Heteropogon	Tuft size	0.034	0.0001	0.278	5.93***	0.280
1986-1987	Moribund	-0.005	0.955	0.029		
	Grazing	-0.029	0.703	0.015		
	Neighbours	0.039	0.875	0.004		
Setaria	Tuft size	0.024	0.509	0.011	0.21ns	0.019
1985-1986	Moribund	-0.490	0.630	0.004		
	Grazing	-0.059	0.946	0.004		
Setaria	Tuft size	0.025	0.018	0.245	2.46ns	0.291
1986-1987	Moribund	0.266	0.431	0.028		
	Grazing	-0.199	0.644	0.009		
	Neighbours	-0.479	0.579	0.031		
Themeda	Tuft size	0.066	0.073	0.064	6.07**	0.249
1985-1986	Moribund	1.293	0.066	0.138		
	Grazing	-0.940	0.014	0.109		
Themeda	Tuft size	0.020	0.002	0.151	3.33*	0.207
	Moribund	0.103	0.366	0.022		
	Grazing	-0.053	0.502	0.014		
	Neighbours	0.300	0.261	0.009		

Table 7.9 continued.

Treatment, species	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Light grazing						
Aristida	Tuft size	0.056	0.179	0.052	4.66**	0.127
1985-1986	Moribund	0.671	0.019	0.060		
	Grazing	1.043	0.081	0.025		
Aristida	Tuft size	0.041	0.004	0.107	9.18***	0.269
1986-1987	Moribund	0.314	0.0001	0.183		
	Neighbours	0.247	0.315	0.008		
Bothriochloa	Tuft size	-0.012	0.810	0.029	1.41ns	0.140
1985-1986	Moribund	0.818	0.134	0.104		
	Grazing	-0.523	0.320	0.036		
Bothriochloa	Tuft size	0.092	0.082	0.117	1.92ns	0.201
1986-1987	Moribund	-0.074	0.969	0.000		
	Neighbours	2.218	0.164	0.078		
Heteropogon	Tuft size	0.163	0.004	0.125	3.66*	0.155
1985-1986	Moribund	0.748	0.225	0.016		
	Grazing	-0.037	0.948	0.000		
Heteropogon	Tuft size	0.056	0.0001	0.231	12.07***	0.384
1986-1987	Moribund	-1.084	0.0004	0.049		
	Neighbours	0.260	0.408	0.000		
Setaria	Tuft size	-0.002	0.957	0.001	0.89ns	0.071
1985-1986	Moribund	1.294	0.157	0.070		
	Grazing	-0.063	0.931	0.012		
Setaria	Tuft size	0.015	0.190	0.049	2.40ns	0.238
1986-1987	Moribund	-1.090	0.542	0.059		
	Neighbours	3.936	0.090	0.174		
Themeda	Tuft size	0.020	0.605	0.041	4.86**	0.237
1985-1986	Moribund	1.300	0.001	0.199		
	Grazing	-0.151	0.544	0.005		
Themeda	Tuft size	0.035	0.065	0.121	2.60ns	0.145
1986-1987	Moribund	0.640	0.268	0.078		
	Neighbours	-0.065	0.861	0.001		

*** - $p<0.001$; ** - $p<0.01$; * - $p<0.05$; (*) - $p<0.06$;
ns - not significant.

Table 7.10. Summary of the multiple regression analyses of the proportional change in plant size for four grass species at Utha.

Treatment, species, year	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Heavy grazing						
Bothriochloa	Tuft size	0.526	0.307	0.234	0.760ns	0.336
	Moribund	0.574	0.872	0.147		
	Grazing	-0.453	0.793	0.007		
	Neighbours	5.648	0.461	0.050		
Digitaria	Tuft size	-0.027	0.176	0.007	2.61(*)	0.295
1985-1986	Moribund	0.556	0.064	0.140		
	Grazing	0.157	0.304	0.042		
	Neighbours	-0.677	0.093	0.133		
Digitaria	Tuft size	0.132	0.003	0.138	3.21*	0.293
1986-1987	Moribund	-2.314	0.079	0.013		
	Grazing	-0.938	0.193	0.010		
	Neighbours	2.696	0.264	0.042		
Setaria	Tuft size	-0.008	0.254	0.031	0.40ns	0.058
1985-1986	Moribund	0.133	0.434	0.006		
	Grazing	0.046	0.669	0.000		
	Neighbours	0.003	0.896	0.002		
Setaria	Tuft size	0.094	0.0001	0.048	5.14**	0.283
1986-1987	Moribund	-2.957	0.0007	0.027		
	Grazing	-0.994	0.029	0.028		
	Neighbours	1.091	0.461	0.001		
Themeda	Tuft size	0.001	0.733	0.022	3.90**	0.113
1985-1986	Moribund	0.219	0.004	0.100		
	Grazing	-0.047	0.205	0.016		
	Neighbours	0.005	0.970	0.003		
Themeda	Tuft size	0.141	0.0001	0.226	14.13***	0.256
1986-1987	Moribund	-0.435	0.268	0.033		
	Grazing	-0.478	0.023	0.010		
	Neighbours	0.366	0.671	0.008		

Table 7.10 continued.

Treatment, species, year	Independent variable	Associated			Overall	
		Slope	prob=0	r^2	F-value	r^2
Light grazing						
Bothriochloa 1985-1986	Tuft size	-0.035	0.158	0.052	2.46ns	0.367
	Moribund	0.314	0.030	0.236		
	Grazing	0.098	0.525	0.136		
	Neighbours	0.223	0.407	0.071		
Bothriochloa 1986-1987	Tuft size	-0.183	0.114	0.070	3.16*	0.457
	Moribund	1.373	0.015	0.307		
	Grazing	0.479	0.317	0.028		
	Neighbours	0.425	0.665	0.012		
Digitaria 1985-1986	Tuft size	-0.018	0.274	0.015	0.34ns	0.066
	Moribund	0.180	0.364	0.001		
	Grazing	0.055	0.478	0.002		
	Neighbours	0.029	0.921	0.001		
Digitaria 1986-1987	Tuft size	-0.084	0.257	0.137	2.39ns	0.360
	Moribund	1.624	0.091	0.054		
	Grazing	0.092	0.830	0.012		
	Neighbours	6.516	0.036	0.219		
Setaria 1985-1986	Tuft size	-0.023	0.002	0.276	3.10*	0.314
	Moribund	0.068	0.513	0.002		
	Grazing	-0.033	0.683	0.005		
	Neighbours	0.018	0.528	0.018		
Setaria 1986-1987	Tuft size	-0.031	0.165	0.056	0.74ns	0.032
	Moribund	0.117	0.812	0.001		
	Grazing	0.070	0.840	0.000		
	Neighbours	1.454	0.273	0.009		
Themeda 1985-1986	Tuft size	0.002	0.512	0.041	5.60***	0.197
	Moribund	0.177	0.001	0.174		
	Grazing	-0.052	0.143	0.045		
	Neighbours	-0.008	0.804	0.005		
Themeda	Tuft size	-0.015	0.587	0.162	6.45***	0.200
	Moribund	1.876	0.0001	0.196		
	Grazing	0.101	0.609	0.023		
	Neighbours	-0.036	0.978	0.014		

*** - $p<0.001$; ** - $p<0.01$; * - $p<0.05$; (*) - $p<0.06$;
ns - not significant.

DISCUSSION

Reproductive output

The controls of the reproductive output of these species were size and grazing. Over the range of tuft sizes within each species in this study, a larger tuft simply has a larger number of tiller primordia from which inflorescences will be produced (Jewiss 1972). Once a reproductive apex begins to extend, it may be removed by grazing. The direct consumption of developing reproductive culms by grazing animals commonly depresses reproductive output (Jameson 1963; Tainton & Booysen 1963; Ambasht & Maurya 1970; Rethman *et al.* 1971). The reproductive output of *Themeda* was strongly affected by grazing because it was a preferred species (Chapter 9), the production of reproductive culms was more widespread through the growing season than for *Bothriochloa*, *Heteropogon* or *Setaria* (Chapter 10), and the reproductive culms differ from those of the last mentioned species in that they bear leaf material almost to the height of the seed heads (the others are bare). *Aristida* shares these characteristics of *Themeda*, except that it is relatively unpalatable, but it was casually observed that *Aristida* inflorescences were readily consumed if in their first flush before culms had hardened. Although the amount of grazing had no significant effect on the individual reproductive output of other species, grazing overall markedly depressed the seed production of these species (Chapter 10). This suggests that the culms of the other species are more prone to being removed irrespective of how much the grazing animal removes of a tuft.

There are a number of competing explanations for the between year and between species variation in recruitment; namely the availability of seed (Fowler 1986; Peart 1989a), the availability of safe sites (eg Andersen 1989) and especially the availability of gaps in the vegetation (eg Gross 1984; Peart 1989b), and the occurrence of appropriate environmental conditions for germination and establishment (eg Griffin & Friedel 1985). The different patterns of recruitment between species would have to further consider the life history attributes of the species.

The marked differences between species in the number of seedling recruits (Table 7.4) reflects in part their differences in seed production, and consequent representation in the seed bank, and their modes of growth. For the obligate seed reproducers at Thlavekisa, the prolific seed production of *Aristida*, compared to *Heteropogon* or *Themeda* (Chapter 10), would explain the substantially higher recruitment of *Aristida*. The low seedling recruitment of *Digitaria* at Utha can be attributed to the negligible output of viable seed (Chapter 10). However, *Setaria* was the main (Utha) and second main (Thlavekisa) component of the seed bank of both sites (Chapter 10), yet only a handful of seedlings were recruited (Table 7.4). The infrequency of recruitment from seed by *Digitaria* and *Setaria* is common among similar species capable of vegetative reproduction (Harberd 1961; Putwain *et al*. 1968; Tamm 1972; Sarukhan & Harper 1973; Thomas & Dale 1974; Abrahamson 1979).

There was recruitment of most species in all four years, and recruitment is thus not episodic as is characteristic of more semi-arid areas (e.g.'s Williams 1970; Williams & Roe 1975; Crisp & Lange 1976; Griffin & Freidel 1985). However, the non-independence between time and grazing treatment, and differences between years and between sites, suggests that the

variation in recruitment numbers is primarily accounted for by the influence of rainfall and grazing on the availability of seed and on vegetation structure. There was generally higher recruitment of obligate seed reproducers in the first year on the heavily grazed treatment, but with time this declined to become less than or equivalent to recruitment on the lightly grazed treatment. The initial high levels of recruitment are possibly a consequence of a high availability of viable seed following two consecutive high rainfall seasons and the opening up of the vegetation by grazing. Seedlings in mesic grasslands usually need gaps in the vegetation to become established (Caruso 1970; Miles 1972; Fenner 1976; Gross & Werner 1982; Goldberg & Werner 1983; Gross 1984; Winn 1985; Peart 1989b, Peart 1989c). The colonisation of cleared patches (Chapter 11) was also more successful on the heavily grazed patches. A fire followed by rain increased the recruitment of *Themeda* twenty fold when compared to unburnt standing vegetation (Ndawula-Senyimba 1972), but the fire at Thlavekisa had no effect on the recruitment of any of the species. The dimunition of seedling recruitment under heavy grazing over years, especially of *Themeda* at Utha, is explained by the marked reduction of seed production and the seed bank by heavy grazing (Chapter 10), and hence limited seed availability for recruitment. *Aristida* produced copious amounts of seed (Chapter 10) and was not heavily grazed (Chapter 9), and was hence not affected. The high levels of seed predation found (Capon & O'Connor 1980) would compound the effect of decreased availability of seed. Under lightly grazed conditions the number of safe sites rather than seed availability probably limited recruitment (Andersen 1989). The availability of seed similarly influenced recruitment in a Californian perennial grassland (Peart 1989a), and the recruitment of *Bouteloua rigidiseta* in Texas (Fowler 1986).

The seedling densities recorded in the present study are broadly comparable to the low number of *Themeda* seedlings (2-8 m^{-2}) in the Monsoon Tallgrass savannas of Australia under optimal conditions (Mott *et al.*

1985), the 100 seedlings m^{-2} of *Heteropogon* in Australian savannas (Shaw 1957), and to the range of seedling recruitment from 30 m^{-2} for *Anthoxanthum odoratum* to 5 m^{-2} for other perennials in a Californian perennial grassland (Peart 1989a).

Population turnover

The percentage mortality (Figure 7.2) does not necessarily give a realistic picture of population turnover (Figure 7.1), because there can be a substantial decrease in basal area (Chapter 6) with tuft die-back without mortality of individuals. The rates of population turnover (Figure 7.1) suggest that the starting population will have been replaced in about ten years, and *Aristida* in less. The population turnover period for *Themeda* and *Heteropogon* is in general agreement with the mean longevity of these species in Australia (Mott *et al.* 1985), although the size of some tufts suggest that a proportion of individuals live substantially longer, as with most perennial grasses (Canfield 1957; Williams 1970; Williams & Roe 1975; West *et al.* 1979).

The influence of grazing

Grazing did not have a profound impact on population dynamics, but a number of smaller effects, and this needs to be reconciled with the current paradigm of grazing as a major secondary determinant of savanna composition and structure (McNaughton 1983; Frost *et al.* 1986). The log-linear analyses revealed only two clear differences between grazing

treatments for any year, in which the *Themeda* population at Utha had better growth on the heavily grazed treatment, partly due to the rapid increase in size of smaller individuals. Grazing did have an influence on mortality, but not as marked an influence as differences between years, considered to be the trend in rainfall. Seedlings had the opportunity to establish because they were consistently the most lightly consumed size class (Chapter 8). Similarly, the proportional survival of *Agropyron spicatum* seedlings rose with a decreased frequency of grazing and an increased age at initial grazing (Pyke 1987).

Mott *et al.* (1991) found that *Heteropogon* became somewhat prostrate under heavy grazing, which was also observed but not quantified in this study. Tillers were erect on lightly grazed plots, but most were closer to the horizontal on the heavily grazed plots.

Most artificial defoliation experiments on *Themeda* have consistently found that this species is sensitive to heavy defoliation (Tainton & Booysen 1965; Ndawula-Senyimba 1972; Coughenour *et al.* 1985a; Edroma 1985), due to the inability of the species to maintain sufficient leaf area to develop resources to expand photosynthetic surface (Hodgkinson *et al.* 1989). In the latter study frequent defoliation (once a week for five weeks to 5 cm) did not lead to plant death, but it was suggested that death would ensue. Edroma (1985) could also not induce mortality with high levels of clipping. It is questionable whether such extreme levels of defoliation occur in a field situation - a negligible number of tufts in this study were ever reduced to this height. Clipping experiments have been recognised for some time to remove more tissue than a herbivore would, and this exaggerates the severity of the effects (Jameson 1963). Experimental water stress had a more marked and adverse effect on the growth of *Chloris gayana* and *Panicum coloratum* than clipping (Pande & Singh 1985). This effect was not found for *Themeda* (Coughenour *et al.* 1985a) in one experiment, but the mortality of *Themeda* during the growing

season under grazing was dependent on the preceding dry season rainfall (Mott *et al.* 1991), although *Heteropogon* did not show this effect. Irrigation rather than clipping frequency had an overriding effect on the yield and root mass of *Themeda* in the eastern Cape (Danckwerts & Nel 1989).

However, grazing had a negative impact on the reproductive output of individuals of *Themeda* (Tables 7.7, 7.8) and of the seed production and seed bank density of most species (Chapter 10). Considering the slow rate of turnover of all species, except perhaps *Aristida* (Figure 7.1), the effect of grazing on the recruitment phase is only likely to impact population dynamics once the established population starts dying out. The five year window of this study was therefore too short to assess the eventual importance of grazing. It is unfortunate that the study did not continue, because a major dieback occurred in the final year at Thlavekisa, and the prediction would be that heavy grazing would cause the elimination of *Themeda* and *Heteropogon* from this time on. Dankwerts & Stuart-Hill (1988) report that the grazing history following rather than during a drought period, which had associated high levels of mortality, had the greatest negative impact on the abundance of *Themeda* in the eastern Cape.

Role of competition

The absence of any marked relationship between the neighbourhood environment and plant size (Chapter 4) and changes thereof, and the high incidence of tuft fragmentation, and the influence of initial tuft size on the proportional change in tuft size, suggests that density dependent processes of intraclonal interference may have had a greater effect than

inter-tuft interference, as recorded for *Schizachyrium scoparium* (Butler & Briske 1988; Briske & Butler 1989). *Schizachyrium scoparium* is a bunchgrass similar to *Themeda*, whose ramet populations were under density dependent regulation due to both interclonal and intraclonal interference. The reduction of interclonal and intraclonal interference increased ramet recruitment by 57% and 71% respectively. Similarly, the tillers of *Lolium perenne* self-thinned under density stress according to the 3/2 thinning rule (Kays & Harper 1974). Tuft fragmentation may be considered as the normal ontogenetic development of a plant, corresponding to the sub-senile or senile stage of a tuft (Gatsuk *et al.* 1980), except the effect was so widespread across species and tuft size. This pattern of tuft fragmentation is a further shortcoming of a neighbourhood approach to competition, at least for bunchgrasses. *Bouteloua rigidiseta* showed only weak density dependent effects in a semi-arid environment, which was similarly attributed to the prevailing drought conditions (Fowler 1986a). However, preferential defoliation of either the focal tuft or neighbours can alter the competitive interaction between the two (Norman 1960; Jones 1967; Jones & Cross 1971), but this level of interaction was not examined.

Although neighbourhood effects appear to influence the size of tufts, they had little effect on the reproductive output or the change in size of a tuft. However, both reproductive output and the change in size of a tuft were strongly influenced by size, which may partly explain the limited effect of the neighbourhood environment. As discussed in chapter 4, neighbourhood models implicitly assume that competition occurs in only two dimensions, but the pronounced size hierarchies within a species in terms of height (and size), and the differences in height between species (Figures 4.2, 4.3), indicates the potential for intra- and inter-species interference in the vertical dimension, at least under lightly grazed conditions. The greater rate of growth of *Themeda* recruits under heavily rather than lightly grazed conditions (Chapter 7) is potential evidence

for this, but the role of the light regime in individual interaction in this environment awaits a rigorous approach. Similarly, *Themeda* growing as an understory species in a tall grassland in the Serengeti-Mara system showed increased growth when released from competition by the opening up of the canopy by buffalo (McNaughton 1977). Newly recruited individuals of *Bouteloua rigidiseta* grew better when adults were removed (Fowler 1986a).

The study of the genesis of size distributions in plant populations has largely concentrated on mono-specific crop plants (Benjamin & Hardwick 1986; Weiner & Thomas 1986), with some study of natural mono-specific populations (e.g. Thomas & Weiner 1989). The development of size distributions in the multi-species perennial communities of this study illustrate that recruitment and tuft fragmentation are key processes, rather than only the distribution of growth rates and the distribution of mortality amongst individuals (Thomas & Weiner 1989). The change in population structure was attributed to rainfall trends rather than grazing, while the tuft size and population skewness of *Astrebla* populations in Queensland declined as a result of heavy grazing (Orr 1980). The species of this study showed a decrease in mean tuft size over a gradient from a history of light to heavy grazing (Pickett 1987).

In conclusion, the trend of increasing aridity appeared to have a greater influence on demographic processes than the imposed treatments. The influence of grazing is only likely to become strongly apparent over a longer time period once the depletion of the seed bank limits recruitment and when the established population begins to die out.

SUMMARY

The influence of rainfall and grazing on the population turnover, population structure, reproductive output, recruitment, growth and survival of the main perennial grass species of the clay soil sites, and the patterns of selection by cattle, were investigated. *Setaria* and *Themeda* were the most, and *Bothriochloa* the least, heavily grazed species at either site, while *Heteropogon*, *Digitaria* and *Aristida* were intermediate. Tufts with greater amounts of moribund material, or smaller in size, were less grazed.

There was approximately 50% turnover in basal area and up to 70% turnover in number of all species except *Setaria* (<2%) over five years, with slightly greater turnover on the heavily grazed treatment. Tuft sizes of all species decreased over five years. The size structure of all populations was right skewed. Tuft size was the major determinant of individual reproductive output of all species. The amount of grazing consistently depressed the reproductive output of individual *Themeda* plants. Recruitment varied between years in accordance with rainfall, with up to 26 seedlings m^{-2} of *Aristida* in the wet 1988 season. There was initially greater recruitment of *Bothriochloa*, *Heteropogon* and *Themeda* on the heavily grazed treatments, but this was reversed by the end of the study.

Themeda (Utha) and *Aristida* seedlings grew twice as large on the heavily than on the lightly grazed treatment in their first two years. The only effect of grazing on the size class changes was for *Themeda* at Utha. There was increasing mortality with time of all species, with up to 56% in the final season, almost exclusively of the smaller individuals, many of which had originated from the 5-40% fragmentation of large tufts of all species. Grazing increased the mortality of *Aristida*, *Digitaria*,

Heteropogon and *Setaria* (Utha). Older tufts of the smallest size class of *Aristida* or *Heteropogon* were more likely to die than younger tufts. In general, the larger a tuft, and the greater its amount of moribund material, the greater its absolute and proportional decrease in size. Heavy grazing increased the growth of tufts of *Bothriochloa*, *Heteropogon* and *Themeda* (Thlavekisa), but decreased the growth of *Digitaria*.

The majority of the changes were better explained by the trend of decreasing rainfall than grazing which had a number of small effects rather than an overriding effect.

CHAPTER 8

PATTERNS OF PLANT SELECTION BY GRAZING CATTLE IN TWO SAVANNA GRASSLANDS

INTRODUCTION

A grassland community offers a grazing ungulate a range of species which might differ in their dietary qualities, morphology and other aspects which influence their acceptability. Species discrimination is the norm of ungulate response (eg Heady 1964; Westoby 1974; O'Reagain & Mentis 1989), and there has been a wealth of study (not reviewed here) which has attempted to understand and predict dietary selection from the perspective of the animal.

The influence of species discrimination by grazing ungulates on the dynamics of grassland communities has long been recognized (Weaver & Clements 1938), and is implicit in the increaser-decreaser classification of rangeland species (Ellison 1960; Fo n *et al*. 1978). But the consequences of grazing selection, both within and between species, on the population processes responsible for compositional change, have received less attention. Selective defoliation of one species may disadvantage its competitive relationship with co-occurring species (Norman 1960; Jones 1967). Sustained defoliation of individual tufts may lead to their mortality (Edroma 1985; Hodgkinson *et al*. 1990; Mott *et al*. 1991), thereby creating gaps for establishment. The number and composition of the seed rain of obligate seed reproducers can also be

influenced by grazing (Chapters 2, 10). Developing theories of vegetation dynamics implicitly recognize the importance of a spatial context for theory (eg Pickett & White 1987), and grazing is a recognized determinant of patch formation within grasslands (Mott *et al*. 1991). Plant population responses to their environment are often highly variable and the causes of this variability need to be sought in the determinants of population change.

This chapter specifically addresses the patterns of grazing selectivity over two years with respect to species identity, vegetation structure, tuft size, and spatial location, so as to explain the population changes described in chapter 7.

METHODS

The data base is the tufts which were sampled at regular intervals over the 1985/86 and 1986/87 growing seasons, usually preceding and following individual grazing events. The data collected on each tuft were the proportion of biomass constituted by moribund material (prior to grazing), the proportion of biomass removed by grazing, both estimated on an eight point scale (Walker 1976: 0=0%; 1=1-10%; 2=11-25%; 3=26-50%; 4=51-75%; 5=76-90%; 6=91-99%; 7=100%), tuft height (cm), the number of reproductive culms, and, at least once a growing season, tuft circumference (cm). This chapter is concerned only with the patterns recorded on the heavy grazing treatments for the six main grass species.

Multiple linear regression was used as an exploratory rather than as a predictive technique (Sokal & Rohlf 1981) to identify which factors influenced the amount a tuft was grazed (examples of this approach can

be found in ter Braak 1987). Separate regression analyses were done for each grazing event at each site on a pooled sample of all tufts. The ranking of the proportion of biomass of a tuft removed by grazing (dependent variable) approximates a logarithmic transformation (Jager & Looman 1987). The independent variables initially included were tuft circumference and height (both $\log_e$ transformed), the number of reproductive culms (square root transformed), the amount of moribund material, the amount of the tuft grazed in the previous grazing session (except if it was the first grazing session of that growing season), location on the slope, and species. Both location and species were entered as nominal variables (Jager & Looman 1987), where a value of 1 is given if the attribute is present and 0 if it is absent. The most frequent species (*Aristida* at Thlavekisa and *Themeda* at Utha) and one of the location classes was deleted to reduce collinearity. Collinearity amongst the other variables was identified with collinearity diagnostics (SAS 1989). Tuft height and the number of culms were therefore deleted from final analyses. All models assumed an origin intercept.

The influence of each of the independent variables on the amount a tuft was grazed was further examined with ANOVA, separately for each census. The influence of species and of moribund material was examined with two-way ANOVA. The influence of tuft size on the proportion of a tuft eaten was analysed separately for each species, by one-way ANOVA. Tuft size was defined by size classes, which are derived in chapter 9 for transition matrix models. The differences between the positions on the slope was examined with one-way ANOVA, separately for each species and for the 1985/86 and 1986/87 seasons, with the response variable as the mean grazing rank of all censuses of that season. Tukey's studentized range test was used for multiple comparisons of means for all ANOVA. The sample size for *Bothriochloa* at Utha was sufficient only for the ANOVA of species and moribund material.

To identify if a tuft was more likely to be heavily grazed over a growing season if it had been heavily grazed the previous season, Pearsons product-moment correlations were sought between the means of the grazing ranks of an individual tuft for each of two succesive growing seasons. To identify if a tuft was more likely to be heavily grazed in the course of a season if it had already been heavily grazed, correlations were sought between the grazing ranks of all grazing censuses for that season, separately for each species and for each season.

RESULTS

The multiple linear regressions (Table 8.1) identified that the amount a tuft was grazed was influenced, to a greater or lesser degree, by tuft size, moribund material, the amount of previous grazing, species identity and location. Tuft size and the amount a tuft had been previously grazed had the most consistent influence, spatial location had a more consistent influence at Utha than at Thlavekisa, and moribund material had a relatively slight influence (Table 8.1). *Digitaria* (at Utha) was the only individual species which had a consistent influence, but there was usually an influence of at least one or another of the species.

The ANOVA showed that there was selection of species by grazing cattle for most census periods, and relatively consistent patterns of selection over time (Table 8.2). At Utha, *Themeda* and *Setaria* were consistently the most, and *Digitaria* and *Bothriochloa* the least, heavily grazed species. An exception to this pattern was seen in the two censuses at the end of the 1984/85 season, in which *Digitaria* was the most heavily grazed species (Table 8.2). Similarly at Thlavekisa, *Setaria* and *Themeda*

Table 8.1. Summary of the multiple regression analyses of the influence of various variables on the amount of a tuft grazed. The t-values given are for the hypothesis that the variable=0. An entry of ___ denotes the variable was not entered into the model. See text for further details.

	Date 5/85	11/85	3/86	2/86	3/86	5/86	12/86	1/87	2/87	3/87	4/87
Thlavekisa											
Tuft size	0.57	6.63***	6.89***	6.24***	7.22***	5.83***	8.86***	8.37***	2.50*	10.14***	5.62***
Grazing	1.60	___	4.92***	7.86***	9.46***	6.72***	___	4.59***	6.38***	3.24**	5.42***
Moribund	-1.90	-4.62***	-2.97**	-1.51	-0.17	-1.81	-4.74***	-0.50	-2.20*	-0.81	-0.04
Bothriochloa	3.04**	0.03	-0.07	-3.44***	-3.09**	-0.15	-1.02	-1.22	1.22	-2.18*	-1.08
Heteropogon	5.46***	2.38*	0.96	-2.32*	-1.83	-0.02	1.36	-1.78	3.20**	-4.05***	-1.13
Setaria	7.37***	4.63***	0.56	-2.11*	-2.29*	-1.51	4.89***	-1.24	2.94**	-3.87***	0.44
Themeda	6.79***	4.22***	1.45	-1.50	-1.48	2.08*	4.82***	-0.89	3.93***	-3.32***	0.21
lower slope	2.75**	-2.62**	2.77**	4.22***	2.58*	-0.09	0.60	-0.13	1.22	3.71***	-0.52
Middle slope	0.94	-2.61**	-0.55	-0.58	3.35***	-2.49*	-0.32	0.69	-1.53	0.84	-2.98
F value	58.77***	44.90***	75.81***	90.85***	164.71***	97.62***	73.88***	84.88***	71.54***	121.30***	89.23***
Adj R-square	0.67	0.58	0.72	0.76	0.85	0.77	0.71	0.76	0.71	0.81	0.75
Sample size	256	256	257	259	258	257	240	239	259	257	258
Utha											
Tuft size	8.80***	7.75***	5.76***	12.11***	9.48***	7.70***	7.63***	5.44***	9.68***		6.30***
Grazing	5.42***	9.60***	5.00***	6.16***	7.87***	___	5.67***	6.03***	8.81***		7.01***
Moribund	-3.00**	-1.43	-0.99	-3.05**	-1.56	0.58	-1.16	-0.55	-4.03***		-1.51
Bothriochloa	-2.78**	1.92	-1.90	0.77	0.78	-4.47***	-0.53	-0.25	-0.22		-0.43
Digitaria	2.80**	-3.20**	-2.19*	-3.37***	-2.65**	-4.23***	-1.04	-3.80***	1.36		-4.21***
Setaria	-0.26	-3.48***	0.88	-2.00*	-2.70**	-4.67***	0.42	0.75	0.45		0.23
Lower slope	5.56***	4.52***	0.18	3.49***	4.36***	1.05	4.44***	2.56*	4.48***		6.04***
Middle slope	2.17*	4.20***	-1.37	0.81	4.48***	0.11	2.20*	2.83**	2.26*		2.30*
F value	136.65***	193.64***	68.44***	147.52***	256.44***	55.31***	127.92***	116.16***	209.99***		161.50***
Adj R-square	0.79	0.85	0.65	0.80	0.88	0.53	0.75	0.73	0.83		0.78
Sample size	292	281	285	286	285	334	331	336	350		356

*** - P<0.001
** - P<0.01
* - P<0.05

Table 8.2. The amount of individual tufts grazed of six grass species at two sites for 12 censuses over three growing seasons (April 1985 to May 1987). Values indicate the mean rank of the proportion of a tuft removed by grazing (Walker 1976). Species with the same letter (within a column - separately for each site) were not significantly different ($p<0.05$) by Tukey's test.

Site and species	Census Date (month and year) 4/85	5/85	11/85	1/86	2/86	3/86	5/86	11/86	12/86	1/87	2/87	3/87	4/87
Thlavekisa													
Aristida bipartita	0.0a	+a	0.3a	1.2a	1.7bc	3.0b	1.7a		0.6a	1.5ab	0.6a	2.4b	1.1ab
Bothriochloa insculpta	0.1ab	0.3ab	0.2a	0.8a	0.5a	1.1a	1.0a		0.3a	1.0a	0.8ab	1.6a	0.9a
Heteropogon contortus	0.3b	0.7bc	0.8b	1.4a	1.4b	2.5b	1.6a		0.8a	1.3a	1.2b	2.0ab	1.0ab
Setaria incrassata	0.7c	1.2d	1.7c	2.2b	2.2cd	3.0b	1.7ab		2.0b	2.1b	1.8c	2.4b	1.7c
Themeda triandra	0.1a	0.9c	1.3c	2.3b	2.3d	3.1b	2.4b		1.9b	2.0b	1.7c	2.3b	1.4bc
Utha													
Bothriochloa insculpta	0.4a	0.7a	0.9a	3.4ab	0.6a	1.8ab	2.7ab	0.1a	1.7a	1.7ab	1.8a		1.8ab
Digitaria eriantha	1.2b	2.5c	2.2ab	2.5a	0.9a	1.4a	2.4a	0.6a	2.0a	1.2a	2.0a		1.4a
Setaria incrassata	1.2b	1.9b	3.2c	2.9ab	2.0b	2.2b	2.7b	0.6a	2.0a	2.0b	2.3a		2.1b
Themeda triandra	0.7a	1.7b	2.5b	3.2b	1.8b	2.6b	3.4c	1.4b	2.3a	2.0b	2.2a		2.0b

Table 8.3. The amount of individual tufts grazed of tufts classified by the amount of moribund material (following Walker 1976), at two sites for 12 censuses over three growing seasons (April 1985 to May 1987). Values indicate the mean rank of the proportion of a tuft removed by grazing. Moribund classes with the same letter (within a column - separately for each site) were not significantly different ($p<0.05$) by Tukey's test. The probability value for each column refers to the F-value for the main effect of moribund material of the Anova.

Site and moribund class	Census Date (month and year)												
	4/85	5/85	11/85	1/86	2/86	3/86	5/86	11/86	12/86	1/87	2/87	3/87	4/87
Thlaveklsa													
0%	0.1	0.7	0.8ab	2.1a	2.2a	1.3b	1.2ab		1.2ab	0.9b	1.0	2.0	0.7
1 to 10%	0.3	0.6	1.2a	2.0a	2.0a	2.7ab	2.0a		1.5a	1.9a	1.3	2.3	1.2
11 to 25%	0.3	0.6	1.1a	1.2b	1.6ab	3.2a	1.9a		1.3ab	1.6ab	1.3	2.2	1.3
26 to 50%	0.0	0.2	1.0ab	1.4ab	1.1bc	2.7ab	1.4ab		0.8b	1.4ab	0.8	1.8	1.1
51 to 75%	0.0	0.0	0.4bc	0.2b	0.5c	2.1b	0.0b		0.2b	1.3ab	0.3	1.0	0.7
76 to 90%	---	0.0	0.5abc	0.0b	0.0c	1.9b	0.0ab		0.0b	0.0b	---	---	---
91 to 99%	---	---	0.0c	0.0b	0.5c	1.0b	0.0ab		0.0b	0.0b	0.0	0.0	---
Probability	0.27	0.59	0.09	.0001	0.04	.002	.005		0.02	.007	0.69	0.10	0.44
Utha													
0%	0.8	1.8	2.2ab	3.3	1.8	0.6b	2.7	---	0.9b	1.7	2.3		1.3ab
1 to 10%	0.9	1.8	3.0a	2.8	1.6	2.3ab	3.4	1.2ab	2.3a	1.9	2.1		2.0a
11 to 25%	1.1	1.7	2.2b	2.7	1.6	2.6a	3.0	0.9ab	2.3ab	1.9	2.0		1.6b
26 to 50%	0.3	1.3	2.0ab	1.3	0.3	2.3ab	2.8	1.3a	1.6ab	1.7	1.8		1.3ab
51 to 75%	1.0	1.0	0.0ab	0.0	0.0	0.5b	2.5	0.7b	1.5ab	2.0	1.0		---
76 to 90%	---	---	---	---	---	0.0b	---	0.3b	---	---	---		---
91 to 99%	---	---	0.0ab	---	---	---	---	0.0b	---	---	---		---
Probability	0.78	0.47	0.19	0.25	0.33	.0003	0.14	0.28	0.03	0.88	0.17		0.09

were the most heavily grazed, *Bothriochloa* the least, while *Aristida* and *Heteropogon*, which differed little, were intermediate (Table 8.2).

The effect of moribund material on the proportion of a tuft eaten was less consistent (Table 8.3), but where the effect was present, tufts with less moribund material were usually more heavily grazed. In a few cases the least grazed tufts had a negligible amount of moribund material (Table 8.3). Invariably the smallest size class of a species was the least heavily grazed, while the most heavily grazed tufts were most often the largest tufts, but on some occassions intermediate size tufts were more heavily grazed than larger tufts, particularly for *Setaria* (Table 8.4).

For each of the species, the amount of a tuft grazed differed widely across individuals for any one grazing event (Figure 8.1). The majority of tufts of palatable species were moderately grazed on each occassion, but a fair proportion of tufts were either ungrazed or very heavily grazed. Even although the majority of the tufts of the unpalatable species were ungrazed or lightly grazed, some individuals were heavily grazed. Therefore across all types of species the grazing pressure was not uniformly borne by the individuals of that species. There was a pronounced tendency across all species for a tuft which had been more heavily grazed in the 1985/86 season to be more heavily grazed in the 1986/87 season (Table 8.5). A similar pattern was evident for the degree a tuft was grazed within a season (Figure 8.2), particularly for the palatable species.

There were differences ($p<0.001$) in the amount a tuft was grazed for locations up the slope only for *Themeda* at Utha in the 1986/87 season, and *Heteropogon* in the 1985/86 and 1986/87 seasons. For *Themeda* the lowest slope was most heavily grazed, while for *Heteropogon* the mid-slope was the least grazed.

Table 8.4. The frequency distribution of the least and most heavily grazed size classes of six species at two sites. Each value is the number of times that size class was the most or least heavily grazed size class of twelve censuses following grazing between April 1985 and May 1987. Only data from ANOVA with $p<0.05$ have been included.

	Most heavily grazed					Least heavily grazed				
Site,	Size classes					Size classes				
species	1	2	3	4	5	1	2	3	4	5
Thlavekisa										
Aristida bipartita	0	7	3			10	0	0		
Bothriochloa insculpta	0	1	5	4		5	1	2	2	
Heteropogon contortus	0	2	1	9		12	0	0	0	
Setaria incrassata	1	2	4	5		7	3	2	0	
Themeda triandra	1	0	3	4	4	9	3	0	0	0
Utha										
Bothriochloa insculpta	1	4	3			6	1	1		
Digitaria eriantha	1	2	9			10	1	1		
Setaria incrassata	0	0	7	3	2	11	1	0	0	0
Themeda triandra	0	1	2	7	2	12	0	0	0	0

Figure 8.1. Box-whisker plots of the amount individual tufts were grazed for selected grazing events over two growing seasons. The top row is Thlavekisa, the bottom row is Utha. Notation for species: Ab - *Aristida bipartita*, Bi - *Bothriochloa insculpta*, De - *Digitaria eriantha*, Hc - *Heteropogon contortus*, Si - *Setaria incrassata*, and Tt - *Themeda triandra*.

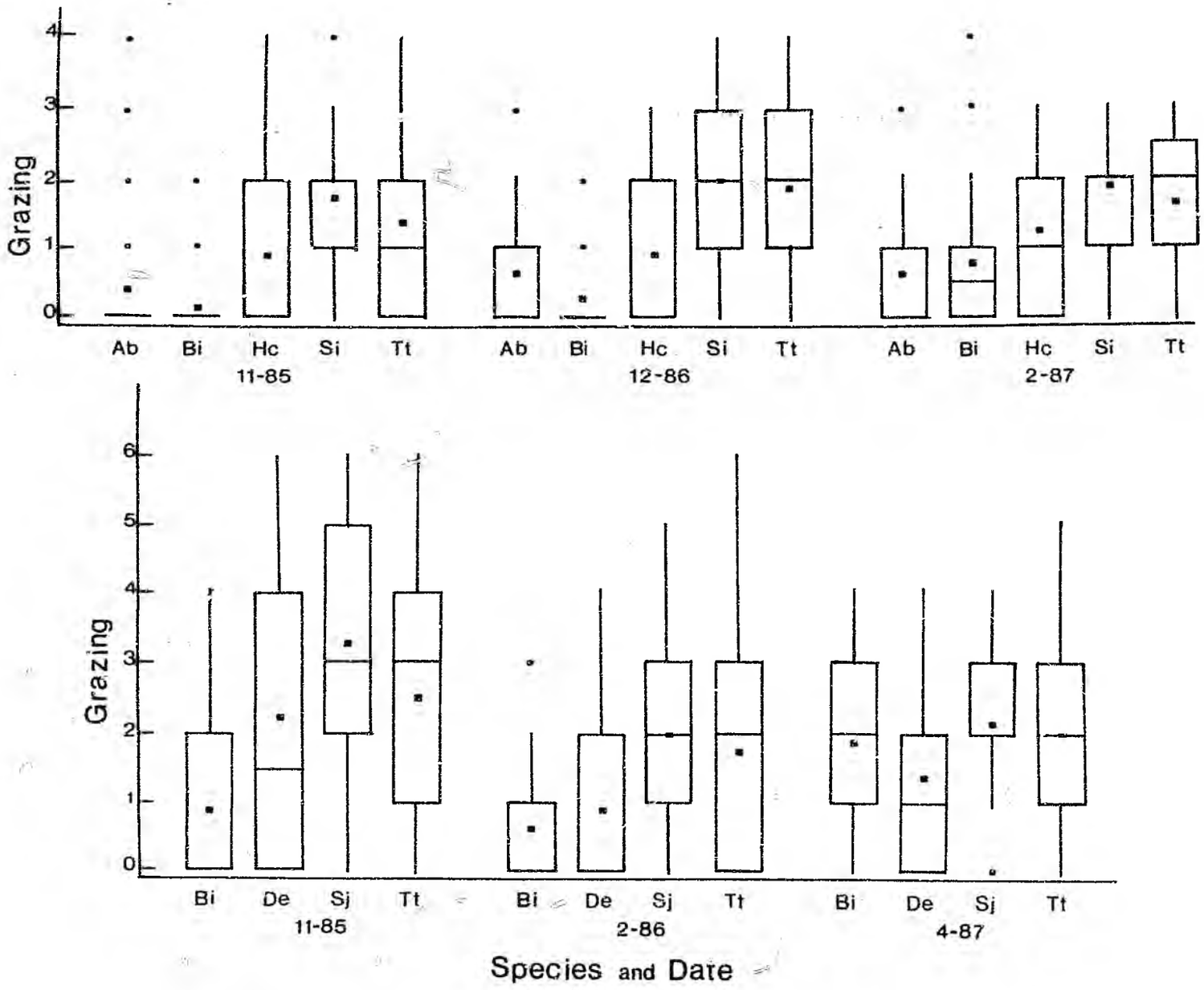

Grazing
0
1
2
3
4
Ab
Bi
Hc
Si
Tt
11-85
12-86
2-87
Grazing
0
1
2
3
4
5
6
Bi
De
Sj
Tt
11-85
2-86
4-87
Species and Date

Figure 8.2. The relationship of Pearsons product-moment correlation coefficient to the interval between censuses of grazing. The significance of the relationship is denoted by an asterisk for $p=<0.05$ and a dot for $p>0.05$. Graphs a to e are for Thlavekisa in 1987, and f to h for Utha 1987. Key to graphs: a - *Aristida bipartita*, b - *Bothriochloa insculpta*, c - *Heteropogon contortus*, d - *Setaria incrassata*, e - *Themeda triandra*, f - *Digitaria eriantha*, g - *Setaria incrassata*, h - *Themeda triandra*.

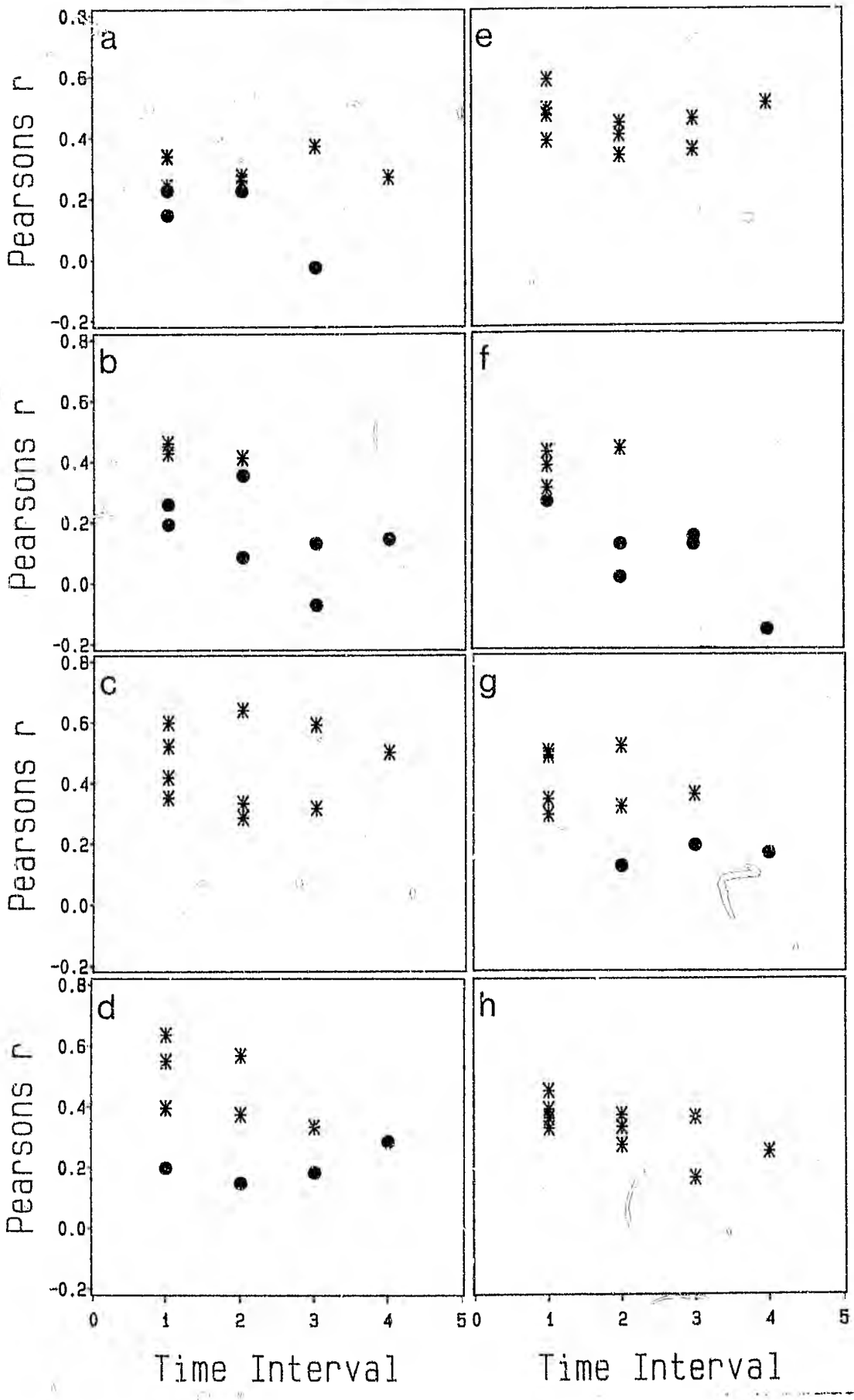

a
b
c
d
e
f
g
h
Pearsons r
Pearsons r
Pearsons r
Pearsons r
0.8
0.6
0.4
0.2
0.0
-0.2
0 1 2 3 4 5
Time Interval
Time Interval

Table 8.5. The Pearsons product moment correlation coefficient, and associated probability, between the mean grazing ranks of individual tufts in the 1985/86 and 1986/87 seasons. An entry of ___ denotes not calculated.

	Thlavekisa			Utha		
Species	n	r	p	n	r	p
Aristida bipartita	52	0.404	0.0030	___	_____	_____
Bothriochloa insculpta	24	0.776	0.0001	___	_____	_____
Digitaria eriantha	___	_____	_____	35	0.515	0.0015
Heteropogon contortus	63	0.827	0.0001	___	_____	_____
Setaria incrassata	32	0.514	0.0026	61	0.392	0.0018
Themeda triandra	58	0.679	0.0001	148	0.476	0.0001

DISCUSSION

Factors influencing the grazing of a tuft

As expected, species identity was a major factor which rendered a tuft susceptible to grazing. The pattern of species selection corresponded with the conventional wisdom on the palatability of *Themeda* (depending on growth stage) and *Setaria*, and the poor palatability of *Aristida* and

Bothriochloa (e.g. Lightfoot 1975; Tainton *et al.* 1976). However, *Heteropogon* and *Digitaria* are considered palatable species (Tainton *et al.* 1976) but were generally not heavily grazed, while *Aristida* was on occassion as heavily grazed as *Heteropogon* (Table 8.2). It is speculated that *Digitaria* was usually passed over because of its short leaf table height relative to *Themeda* and *Setaria*. Similarly, the growth form of a proportion of the *Heteropogon* tufts (not quantified) was quite prostrate, a trait also recorded in Australia (Mott *et al.* 1991). Although moribund material can deter selection by cattle (Willms *et al.* 1980), its limited influence (Tables 8.1, 8.3) was attributed to the low amount of moribund material on most tufts (<10% by mass). The limited consumption on some occassions of individuals with negligible amounts of moribund material is possibly explained by the majority of these being small individuals, which were not heavily consumed.

Selected species were not uniformly grazed, as small individuals were spared the attention intermediate or larger sized tufts received. This pattern may have been particularly evident because of the population structure of selected species. Mean tuft size of most species declined subsequent to this study (Chapter 7). For example, at Thlavekisa the mean tuft circumference of *Heteropogon* declined from 7.5 to 3.9 cm, and that of *Themeda* from 9 to 5.5 cm, between 1986 and 1989 (Chapter 7). Thus there was a far higher proportion of larger tufts for cattle to select at the time of this study, whereas in 1989 the majority of tufts were small.

Tuft size was correlated with tuft height and the number of reproductive culms, and therefore reflected tuft structure. Plant structure influenced the acceptability of nine species to cattle in Natal (O'Reagain & Mentis 1989), where acceptability was positively related to the amount of leaf and leaf table height, but negatively related to stemminess. A similar relationship for stemminess would only have been expected for *Themeda* in this study (and *Aristida* if it had been selected for), as

Digitaria, *Heteropogon*, *Bothriochloa* and *Setaria* all had a low density of reproductive culms per unit area of tuft (Chapter 10 - Table 10.1). However, grazing decreased the density of reproductive culms per m^2 of tuft basal area of *Themeda* at Utha and Thlavekisa by 70% and 77% respectively. Stemminess was therefore not considered to be an important influence in this study, but would have to be considered in lightly grazed *Themeda* grasslands.

Patterns of selection would therefore vary over years with changes in the degree of moribundness of tufts, population size structure, stemminess resulting from grazing variability, spatial location, and compositional change. These patterns are therefore pronouncedly location and time specific, and because the effect of plant structure on grazing acceptability has received little attention (O'Reagain & Mentis 1989), strong caution is needed against deriving premature generalizations.

Implications for population dynamics

The pattern of grazing selection, both within and between species, affected population and community dynamics. Patterns of species selection affected seed production and the consequent representation in the seed bank of the main species, and was especially significant for the obligate seed reproducers *Aristida*, *Heteropogon* and *Themeda*. The imposed grazing regimes reduced the number of reproductive culms of *Heteropogon*, *Bothriochloa*, *Aristida* and *Setaria* by 65%, 52%, 15% and 45% respectively (Chapter 10). As a consequence *Aristida* dominated the Thlavekisa seed bank with 1465 seeds m^{-2}, while *Themeda* and *Heteropogon* were poorly represented (50 and 118 seeds m^{-2} respectively) (Chapter 10), and *Aristida* was therefore able to colonise available gaps (Chapter 7). The selection

of larger tufts probably caused a greater depletion of seed production than if grazing had been uniformly spread over all size classes, because tuft size was strongly positively correlated with individual reproductive output (Chapter 7). The light grazing experienced by small tufts (Table 8.4) provided new recruits, whether seedlings or rooted nodes of stolons of *Digitaria* or *Bothriochloa*, an opportunity to establish under heavy grazing (Chapter 7).

The implication of species selection for community change was evident in the number of seedling recruits in the wet season following the two years of monitoring. At Thlavekisa, *Aristida* had 25.8 recruits m^{-2} against only 1.9 and 3.0 recruits m^{-2} for *Heteropogon* and *Themeda* respectively. At Utha, the number of *Themeda* recruits declined from 19.1 m^{-2} in 1985/86 to 1.9 m^{-2} in 1987/88, the latter a wet season considered favourable for recruitment. Therefore the pattern of species selection in conjunction with the seed production potential of the obligately seed reproducing species was instrumental in initiating significant compositional change.

The finding that a tuft was more likely to be heavily grazed if it had previously been heavily grazed would influence the variability of individual growth rates and possibly mortality. Sustained severe defoliation of *Themeda* can induce mortality (Ndawula-Senyimba 1972; Coughenour *et al*. 1985; Edroma 1985; Hodgkinson *et al*. 1989), but these artificial defoliation experiments involve intensive levels of clipping (eg defoliation once a week for five weeks to 5 cm - Edroma 1985). However, there was a pronounced inequality in the degree of grazing experienced by tufts at each grazing event (Figure 8.1), and only a small proportion of tufts experienced levels of defoliation comparable to those in the above studies. However, the increased degree of population decline of *Setaria* and the increased importance of *Digitaria* under heavy grazing (Chapter 6), were in accordance with the patterns of species selection,

and could be attributed to the effects of grazing on tuft growth and mortality.

In conclusion, the effects of grazing were not uniformly imposed on this grassland community or its constituent species. The inequality between species, and the effect of this on population processes, accounts for some of the observed variability of species response. The inequality of grazing between individuals of a selected species had a direct influence on seed production, establishment and growth.

SUMMARY

The amount of grazing experienced by individual tufts of the main perennial grasses of two Transvaal savannas was monitored at regular intervals over two growing seasons. *Setaria incrassata* and *Themeda triandra* were consistently the most heavily grazed, *Bothriochloa insculpta* and *Aristida bipartita* were lightly grazed, and *Heteropogon contortus* and *Digitaria eriantha* were moderately grazed. Tufts with a greater amount of moribund material were less heavily grazed. The smallest tufts of all species were the most lightly grazed, although the most heavily grazed tufts were on occassion intermediate in size rather than the largest. A tuft had an increased likelihood of being heavily grazed if it had already been heavily grazed, both within a growing season and over two successive growing seasons. A spatial pattern of grazing was evident, as individual species were less heavily grazed at different positions up the slope. The pattern of selection, both within and between species, accounted for some of the observed variability of population change.

CHAPTER 9

TRANSITION MATRIX MODELS OF POPULATION CHANGE

INTRODUCTION

The population growth rate of a species is the integrated result of seed production, germination, establishment, in some instances vegetative propagation, growth and mortality of individuals, but it is not possibile to predict the overall population response given only information on a subset of these processes. Matrix population models provide the means of both calculating the population growth rate and assessing the influence of each of the population processes on this growth rate (Caswell 1989). The coming of age of these powerful techniques has been relatively recent (see Keyfitz 1968; Charlesworth 1980; Caswell 1989 for reviews). The original modelling attempts were concerned with age-structured animal populations (Leslie 1942; Lewis 1945), but size rather than age is an appropriate descriptor of plant performance (Harper 1977; Caswell 1989). Therefore stage-structured (Lefkovitch) models are better predictors of future population states in plants or other organisms with indeterminate growth or complex life histories (Lefkovitch 1965), and several recent plant studies (mostly trees and herbs) have used Lefkovitch models (Usher 1966, 1969, 1976; Sarukhan & Gadgil 1974; Hartshorn 1975; Werner & Caswell 1977; Caswell & Werner 1978; Enright & Ogden 1979; Bierzychudek 1982; Meagher 1982; Pinero *et al*. 1984; Huenneke & Marks 1987).

In particular, a Lefkovitch model allows for transitions between a greater range of size classes, including changes from larger to smaller classes, which is appropriate for perennial caespitose grasses. Few matrix transition models of perennial grasses have appeared to date. Moloney (1988) described the fine-scaled temporal and spatial variation of *Danthonia sericea* of American prairies, while the dynamics of *Andropogon semiberbis* of the Venezuelan Llanos under fire and fire-exclusion regimes has been contrasted (Silva *et al*. 1991). However, I know of no transition matrix models of grasses as influenced by rainfall and grazing.

The objective of this section of the study was to use matrix population models to consider the influence of rainfall and grazing on the population dynamics of the main perennial grasses of the two clay soil sites, to identify the critical population processes, and to assess population stability. The population growth rates are further used to define the interspecies interactions.

METHODS

Size classes

Matrix population models were developed for all the species at Thlavekisa and Utha for which a sufficient number of tufts had been monitored. The preliminary development of matrices requires the (*a posteriori*) definition of the size classes to be used, as the apparent behaviour of a population depends on the way in which it is defined (Caswell 1989). Plant size is defined as the tuft circumference (cm). I used Moloney's (1986) algorithm for determining category size which takes into account

differences between sub-populations of treatments and between years (Table 9.1). The algorithm is an extension of Vandermeer's (1978) algorithm for choosing the category sizes of an homogeneous population sampled over only one time interval.

It is assumed with a transition matrix model that all individuals falling within the same category have the same transition probability. The distribution error increases if the category is made too large, since larger individuals will most likely have transition probabilities that differ from those of smaller individuals. However, if a size category is made too small it will lead to sampling error because it contains too few individuals. The algorithm of Moloney (1986) is designed to define size classes which minimise both the distribution and the sampling error. The only *a priori* constraint was that the smallest size class be large enough to contain all the new recruits.

Transition matrices

The time interval used in these models was one year, from the end of one growing season to the end of the next. Transition matrices for each species at each site were determined for five years (four transitions), and recognised separate sub-populations for grazing and rainfall treatments for the 1985 to 1986 and 1986 to 1987 transitions for *Aristida* at Thlavekisa and for *Themeda* at Utha, but recognised only grazing treatments for the 1987 to 1988 and 1988 to 1989 transitions. Only grazing treatments were defined for the other species for the first two transition periods because of sample size. Inadequate sample size precluded the estimation of five matrices of *Bothriochloa* at Utha. For *Bothriochloa* at Thlavekisa, the two largest size classes were combined

Table 9.1. The size classes of six species of perennial grass at two sites derived using Moloney's (1986) algorithm. The data are tuft circumference (in cm.). Notation for site: Thlavekisa=T; Utha=U.

		Size Class				
Species	Site	1	2	3	4	5
Aristida bipartita	T	1-6	7-12	>12		
Bothriochloa insculpta	T	1-6	7-13	14-17	>17	
	U	1-6	7-14	>14		
Digitaria eriantha	U	1-6	7-18	>18		
Heteropogon contortus	T	1-8	9-14	15-21	>21	
Setaria incrassata	T	1-10	11-20	21-34	>34	
	U	1-6	7-12	13-20	21-36	>36
Themeda triandra	T	1-6	7-12	13-18	19-24	>24
	U	1-4	5-10	11-16	17-24	>24

to ensure adequate sample size for the 1988 to 1989 transition on the heavily grazed treatment.

The coefficients of the matrix were obtained from the combined data set of permanent quadrats and individually tagged tufts within each plot. Each transition probability is the number of individuals moving from one size class to another over an iteration period divided by the total number of individuals in the donor size class at the beginning of that period. These are the maximum-likelihood estimates of the transition probabilities.

The fecundity values for each size class of a matrix were obtain. following Moloney (1988) for the 1987 to 1988 and 1988 to 1989 transitions. For each treatment, let c_{it} represent the number of culms produced by individuals in size class i at census t, and let $g(t+1)$ represent the number of seeds germinating and surviving to $t+1$. An estimate of the number of surviving germinants at $t+1$ attributable to each individual within size class i at t is given by

$$r_{it} = [g_{(t+1)} \cdot c_{it}] / [n_{it} \cdot \Sigma c_{it}] \qquad (1),$$

where n_{it} is the number of individuals in size class i at time t. For the 1985 to 1986 and 1986 to 1987 transitions, the reproductive terms were calculated from the mean number of culms per individual of a size class and the number of individuals per size class in the quadrats. Both estimates assume that the number of seeds produced is directly related to the number of culms produced.

These estimates of reproductive success assume a closed population, with all germinating seed being produced locally, and with no development of a seed bank of dormant seed >1 year old. The assumption for seed migration is not essential because it can be assumed that the movement of seed into an area was balanced by the movement out. The assumption of limited dormancy appears reasonable for these species (Chapter 10).

The reproductive term for *Digitaria* is primarily the number of vegetative recruits from rooted nodes of stolons. It was assumed that the number of rooted nodes per individual of a size class was directly proportional to the number of stolons per individual, which was calculated from a combined sample for all years because of sample size. *Setaria* could develop extensions of clones for which the "donor" individual could not be readily identified. The proportion of these attributed to an individual of a size class was calculated in accordance with the proportion of the basal area of the size classes.

Because all individuals which had established in the season of a particular transition matrix are always found within the smallest size class, the probabilities (a_{ij}) of the first row of the matrix are given by

$$a_{ij} = p_{ij} + r_i \quad (2),$$

and the probabilities for all other rows are given by

$$a_{ij} = p_{ij} \quad (3),$$

where p_{ij} is the probability of a tuft passing from one size class to the next.

Changes in the population over each time interval can be calculated from the matrix equation

$$n(t+1) = An(t) \quad (4),$$

where the state vector $n(t)$ gives the abundance of each size class and A is the population projection matrix. The solution to (4) can be written as

$$n(t) = A^t n(0) \quad (5),$$

where $n(0)$ is an arbitrary initial population vector.

Caswell (1989) presents the relevant mathematical considerations of population projection matrices concerning their primitivity and irreducibility, and their property of having distinct eigenvalues. Therefore the solution to (5) can be written in terms of the eigenvalues λ_i and the right (w_i) and left (v_i) eigenvectors of the projection matrix:

$$n(t) = \Sigma c_i w_i \lambda_i^t \quad (6),$$

where $c_i = v'_i n(0)$. We can expect the existence of a single real dominant eigenvalue λ_1 by the Perron-Frobenius theorem (derived in detail in Caswell 1989) as t gets large and the transient effects of the other eigenvalues decay. Equation (6) then reduces to

$$n(t) \rightarrow c_1 w_1 \lambda_1^t \quad (7).$$

The dominant eigenvalue (λ_1) is the asymptotic growth rate of the population, and is related to the intrinsic rate of population increase

by $r=\ln(\lambda_1)$. Therefore if $\lambda_1>1$ the population is expanding, if $\lambda_1= 1$ the population is stable, and if $\lambda_1<1$ the population is decreasing. The population therefore increases or decreases at an exponential rate given by λ_1. The relative magnitudes of the right hand eigenvector **w** describe the relative abundance of individuals in the corresponding size classes of each population after reaching a stable stage distribution.

The left hand eigenvector **v** is the dominant eigenvector of the transpose of the matrix (which will have the same dominant eigenvalue). The left hand eigenvector corresponding to λ_1 gives the reproductive value of each stage of the population. Reproductive value is concerned to the extent to which each stage (or age in an age structured model) will, on the average, contribute to the ancestry of future generations. The reproductive value of a stage is therefore influenced by the amount of future reproduction, the probability of surviving to realise it, and the time required for the offspring to be produced (Caswell 1989).

Elasticity analysis

Elasticity analyses (de Kroon *et al.* 1986) were used to evaluate the importance of the different transition probabilities to population growth. The elasticities are a proportional change in λ_1 due to a proportional change in the matrix coefficients, and are given by

$$e_{ij} = \frac{a_{ij}}{\lambda_1}\frac{\partial\lambda_1}{\partial a_{ij}} = \frac{a_{ij}\, v_i \cdot w_j}{\lambda_1 \quad (v,w)} \qquad (8),$$

where (v,w) is the scalar product of **v** and **w**.

Transient Dynamics

The rate of convergence to a stable stage distribution is governed by the eigenvalues of the second largest absolute magnitude, and will usually be more rapid the larger λ_1 is in relation to λ_2. This provides the definition of the damping ratio (Caswell 1989, p69)

$$\rho = \lambda_1 \; / \; |\lambda_2| \qquad (9).$$

The time taken for the contribution of λ_1 to become x times as great as that of λ_2 is estimated by (Caswell 1989, p71)

$$t_x = \ln(x) \; / \; \ln(\rho) \qquad (10).$$

The period of oscillation in the stage distribution associated with λ_2 is given by

$$P_2 = 2\,\pi \; / \; \theta_2 \qquad (11),$$

where θ_2 is the angle formed by λ_2 in the complex plane (Caswell 1989, p74).

Pearsons product-moment correlation coefficients between λ_1 and ρ, λ_1 and P_2, and λ_1 and t_5 were calculated.

Relationships between species

The correlation matrix of r ($\ln(\lambda_1)$) for the five species at Thlavekisa, and for three species at Utha (*Bothriochloa* excluded), was determined. Each value of r, the damping ratio, and t_5 was assumed to be an independent random variate, and one-way ANOVA were used to test for differences between species separately for each site (damping ratio was ln transformed).

RESULTS

Transition matrices

A consistent feature of all the transition matrices was the collapse of the larger size classes into smaller size classes due to the fragmentation of tufts (Table 9.2). The fragmentation of a single tuft could result in more than one smaller tuft. Because an individual could "multiply" in number through fragmentation, the summed transition probabilities of a column (excluding reproductive output) exceeded unity on occassion. Each element of the true first row of the transition matrices is therefore in many cases a summed datum of the number of surviving germinants and the number of tuft fragments per individual of that size class (plus the proportion surviving for the first entry). The reproductive term of the first row is usually substantially greater than the tuft fragmentation term for the larger size classes, with the converse pattern for the smaller size classes (Table 9.2). On occasion the reproductive output of the smallest size classes was zero, usually associated with heavy grazing or the dry 1988 to 1989 period. The reproductive terms for *Digitaria* at Utha are primarily the number of rooted nodes of stolons which established, as very few *Digitaria* seedlings emerged (Chapter 7). There was likewise limited establishment of *Setaria* seedlings at either site (Chapter 7).

Table 9.2. Transition matrices for size-structured populations of six species of perennial grass at two sites for four transition periods. Notation for treatment: HD - heavy grazing with rainfall interception; HR - heavy grazing with normal rainfall; LD-light grazing with rainfall interception; LR - light grazing with normal rainfall; H - heavy grazing; L - light grazing. The first row of some matrices is denoted by R, which is the reproductive output component. In this case the second row, marked 1, is the true first row of the matrix. An entry of zero is indicated by a line.

		Transition Period																			
		1985-1986					1986-1987					1987-1988					1988-1989				
Species and treatment	Size Class	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Thiavekisa Aristida HD (Treatment=H for 1987/88, 1988/89).	R	.19	.68	.88			.34	.65	1.02			.71	.81	1.72			.29	.69	1.69		
	1	1.02	.99	.88			1.01	.88	1.27			1.41	1.09	1.82			.97	1.28	2.19		
	2	.17	.69	.25			.18	.62	.75			.18	.63	.45			.03	.43	1.00		
	3	—	.08	.75			.01	.15	.25			—	.07	.45			—	—	—		
HR	R	.18	.51	1.30			.16	.53	1.13												
	1	.60	.61	1.30			.90	.72	1.13												
	2	.58	.80	.60			.10	.59	.40												
	3	—	.10	.40			.01	.13	.60												
LD (Treatment=L for 1987/88, 1988/89).	R	.20	.49	1.50			.06	.23	.34			.37	1.04	1.94			.13	.92	.86		
	1	1.00	.68	1.50			.77	.44	.50			1.03	1.20	2.19			.89	1.40	1.46		
	2	.13	.81	.36			.13	.59	.08			.14	.71	.13			.07	.51	.40		
	3	—	—	.64			—	.14	.67			—	.06	.56			—	.04	.20		
LR	R	.32	.70	1.40			.12	.33	.61												
	1	1.13	.89	1.40			.66	.72	.83												
	2	.13	.71	.50			.05	.52	.44												
	3	—	.05	.50			—	.06	.33												
Bothriochloa H	R	.01	.05	.17	.19		.05	.46	.52	1.56		.08	.57	—	.33		.01	.03	.03		
	1	.41	.15	.55	.44		.64	.92	.69	2.00		.61	.93	.26	.62		.48	.35	.78		
	2	.60	.80	.38	—		.19	.42	.50	.11		.35	.36	.40	.86		.18	.50	.25		
	3	—	.10	.25	—		.04	.17	.17	—		—	.07	—	—		—	.05	—		
	4	—	—	—	.75		—	.04	.17	.44		—	.14	.60	.29						
L	R	.06	.05	.16	.23		.03	.16	—	.18		.13	.33	—	.31		.06	.10	—	.30	
	1	.56	.38	.27	—		.63	.22	.19	.48		.67	.59	.38	.54		.63	.72	.13	.73	
	2	.50	.44	.22	.10		.24	.61	.17	.31		.25	.48	.17	.15		.07	.38	.17	.43	
	3	—	.22	.67	.10		.04	.22	.25	.31		.04	.22	.42	—		—	.19	.33	.14	
	4	—	—	—	.80		—	.06	.67	.38		—	.17	.42	.85		—	.06	.17	.43	

Table 9.2 continued.

Species and treatment	Size Class	1985-1986					1986-1987					1987-1988					1988-1989				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Heteropogon	H R	—	.40	.74	2.49		.15	.29	.44	.89		.01	.04	.24	1.84		.02	.16	.34	.07	
	1	.57	.68	.84	2.57		.76	.60	.76	1.05		.74	.35	.60	2.21		.50	.85	1.48	.93	
	2	.13	.56	.09	.21		.14	.53	.14	.17		.15	.54	.24	.06		.03	.09	—	.14	
	3	—	.16	.69	.14		.01	.14	.51	.17		.01	.23	.20	.19		—	.03	—	.14	
	4	—	—	.13	.64		—	—	.16	.67		—	—	.40	.69		—	—	—	—	
	L R	.00	.00	.00	.00		.08	.19	.30	.54		.01	.29	.49	1.18		.20	.11	.61	.24	
	1	.00	.00	.00	.00		.70	.60	.38	.69		.58	.45	.79	1.52		.84	.75	1.72	1.78	
	2	.20	.67	.17	.14		.10	.26	.25	.15		.15	.23	.10	.11		.05	.29	.28	.18	
	3	—	.20	.74	.18		.05	.38	.40	.06		—	.50	.43	.17		—	—	.17	.18	
	4	—	—	.13	.63		—	—	.30	.76		—	.16	.27	.69		—	—	—	.09	
Setaria	H 1	.76	.22	.45	.59		.74	.87	.90	1.29		.61	.38	.30	1.16		.55	.58	.20	.26	
	2	.25	.29	.24	.08		.27	.29	.52	.35		.23	.50	.31	.32		.14	.23	.47	1.20	
	3	—	.43	.24			—	.18	.24	.18		—	.18	.54	.41		—	.07	.29	—	
	4	—	—	.29	.92		—	—	.24	.59		—	.05	.08	.50		—	—	.06	.60	
	L 1	.85	.24	.39	.81		.66	.60	.77	2.00		.56	.36	.70	1.32		.66	.43	.40	1.29	
	2	.17	.40	—	.07		.10	.63	.36	.59		.18	.63	—	.07		.05	.42	.44	.33	
	3	—	.10	.64	.07		.04	.13	.57	.18		.07	.33	.40	.07		—	.12	.39	.57	
	4	—	.20	.18	.79		—	—	.14	.50		.03	.04	.50	.93		—	—	—	.33	
Themeda	H R	.02	.19	.23	.20	.46	.04	.38	.19	.94	1.35	—	.38	.48	.72	1.62	—	—	.11	.15	.25
	1	.38	.29	.29	.20	.46	.54	.52	.25	1.14	2.20	.62	.63	.69	.72	1.62	.56	.43	.68	1.65	.58
	2	.27	.68	.06	—	—	.18	.64	.03	—	.43	.30	.61	.07	.05	—	.02	.22	—	.20	—
	3	.09	.23	.67	.10	—	.03	.29	.59	.07	.14	—	.25	.34	.10	—	—	.09	.57	—	—
	4	—	—	—	.70	.25	—	—	.32	.80	—	—	—	.41	.43	.75	—	—	—	.20	—
	5	—	—	—	.20	.75	—	—	—	.07	.57	—	—	.07	.43	.75	—	—	—	—	.33
	L R	.04	.07	.12	.17	.34	.05	.11	.23	.38	.86	.04	.27	.94	1.24	4.14	—	.02	.13	.19	.48
	1	.29	.32	.12	.17	.34	.49	.25	.37	.38	.86	.54	.44	1.00	1.67	4.14	.65	.48	.90	1.63	1.81
	2	.63	.63	.09	—	—	.38	.34	.08	.33	—	.25	.43	—	.21	—	.07	.45	.15	.22	.67
	3	—	.13	.87	—	—	—	.52	.47	—	.67	.04	.43	.45	.07	—	—	.09	.54	.11	.33
	4	—	—	.04	1.00	—	—	—	.36	.17	—	—	.04	.52	.36	.14	—	—	.08	.33	.33
	5	—	—	—	—	1.00	—	—	—	.50	1.00	—	—	—	.29	.86	—	—	—	—	—

Transition Period

Table 9.2 continued.
Utha

Species and treatment	Size Class	Transition Period 1985-1986					1986-1987					1987-1988					1988-1989				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Botlriochloa	R	.01	.16	.15			.02	.03	.23			.32	.47	.25							
	L 1	.51	.37	.71			.84	.41	.43			.03	.47	.25							
	2	.25	.75	.44			.09	.56	.40			.03	---	.25							
	3	.13	---	---			---	---	.80												
Digitaria	H 1	.49	.16	.52			.57	.72	1.77			.69	.55	4.13			.71	.49	1.48		
	2	.57	.62	.27			.33	.68	.80			.28	.70	.25			.14	.63	1.50		
	3	---	.24	.73			---	.06	.45			---	.08	.75			---	.05	---		
	L 1	.76	.31	.26			.77	.64	1.71			.69	1.64	1.75			.79	.46	.72		
	2	.33	.86	.17			.27	.77	.67			.22	.75	.33			.16	.61	1.00		
	3	---	---	1.00			---	.05	.50			---	.04	.67			---	.03	.33		
Setaria	H 1	.52	.58	.77	.87	5.39	.52	.84	.86	1.92	7.45	.59	.44	.40	.36	4.24	.74	.50	.30	.09	1.18
	2	.50	.27	.20	.29	.08	.10	.41	.20	.44	.29	.17	.34	.34	.14	.30	.06	.49	.25	1.00	---
	3	---	.27	.47	.14	.08	---	.05	.40	.17	.57	.01	.16	.44	.43	.40	.01	.02	.38	---	---
	4	---	---	---	.50	.29	---	---	.08	.17	.10	---	---	.13	.43	.10	---	---	.13	---	---
	5	---	---	---	.07	.71	---	---	---	.06	.43	---	---	---	---	.50	---	---	---	---	1.00
	L 1	.92	.55	.20	.90	2.31	.72	.66	.58	1.09	3.56	.62	.45	.37	.42	2.34	.57	.42	.14	.19	.10
	2	.12	.35	.41	.21	.04	.07	.31	.33	.20	.47	.13	.30	.34	.30	.25	.09	.42	.41	.22	---
	3	---	.17	.41	.17	.15	.02	.19	.35	.23	.10	.01	.25	.32	.03	.20	.02	.11	.27	.33	---
	4	---	---	.12	.38	.12	---	.01	.04	.40	.40	.01	.03	.16	.55	.30	.00	.02	.14	.39	.33
	5	---	---	---	---	.85	---	---	---	---	.60	---	---	---	.06	.60	---	---	---	.06	.67

Table 9.2 continued.
Utha

Species and Size treatment	Class	Transition Period 1985-1986					1986-1987					1987-1988					1988-1989				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Themeab HD (Treatment=H for 1987/88, 1988/89).	R	.48	.05	.54	1.12	.92	.09	.01	.09	.20	.16	.00	.05	.16	.05	.12	.00	.00	.02	.06	.08
	1	1.18	.11	.76	1.20	1.56	.62	.12	.15	.34	.83	.37	.21	.27	.29	.34	.67	.25	.27	.56	.75
	2	.30	.53	.07	.31	.41	.19	.59	.11	.50	.87	.44	.51	.29	.24	.65	.19	.73	.34	.42	.33
	3	—	.29	.57	.23	.27	—	.23	.68	.32	.33	.01	.32	.37	.20	.22	—	.07	.52	.29	.17
	4	—	—	.21	.62	.32	—	.02	.16	.36	.33	—	.02	.35	.53	.17	—	—	.11	.33	.50
	5	—	—	—	—	.50	—	—	—	.09	.47	—	—	—	.16	.52	—	—	—	—	.33
HR	R	—	.24	2.47	1.08	2.71	—	.08	.84	.37	.92										
	1	.45	.28	2.47	1.16	2.86	.56	.30	.95	.44	1.30										
	2	.45	.65	.08	.23	.08	.23	.53	.28	.19	.73										
	3	.05	.35	.69	.31	.27	.01	.24	.65	.26	.38										
	4	—	—	.23	.38	.27	—	—	.05	.70	.15										
	5	—	—	—	—	.50	—	—	—	—	.58										
LD (Treatment=L for 1987/88, 1988/89).	R	—	.30	.28	1.04	1.60	.04	.06	.26	.64	1.52	.00	.02	.04	.07	.19	.00	.01	.01	.02	.04
	1	.43	.53	.43	1.04	1.93	.57	.24	.32	.70	1.68	.70	.14	.12	.20	.40	.71	.36	.26	.35	.24
	2	.43	.62	.14	—	.50	.26	.55	.25	—	.42	.12	.69	.13	.04	.13	.09	.65	.40	.56	.40
	3	—	.15	.71	—	.17	—	.24	.69	.06	.17	—	.18	.72	.09	.08	—	.05	.40	.22	.60
	4	—	—	—	1.00	.42	—	—	—	.56	.17	—	—	.12	.78	.25	—	—	.05	.44	.80
	5	—	—	—	—	.42	—	—	—	.38	.75	—	—	—	—	.63	—	—	—	—	.20
LR	R	.03	.09	.36	.85	.87	.01	.01	.03	.06	.11										
	1	.42	.16	.36	.85	1.03	.53	.10	.26	.18	.11										
	2	.61	.77	.38	—	.54	.27	.64	.14	—	.11										
	3	—	.15	.50	.50	.15	—	.29	.73	.11	.56										
	4	—	—	.13	.50	.15	—	—	.14	.67	.11										
	5	—	—	—	—	.62	—	—	—	.22	.78										

25×10 32×10 25×10

Asymptotic and Transient Properties

The predicted asymptotic poulation growth rates varied between species, between years, and to a lesser extent between treatments (Table 9.3). In general, the population growth rates tended to be positive in the first three years, increasing in the wet 1987-1988 transition period in all but three instances, and declining in the final dry transition period (often becoming negative) in all cases but one. There was a consistent increase in population growth rate between 1985 and 1988 for *Aristida* (heavy grazing only), *Bothriochloa*, *Heteropogon*, *Setaria* and *Themeda* at Thlavekisa, and for *Digitaria* at Utha. The most negative population growth rates witnessed in the drier 1988 to 1989 transition period were of *Heteropogon*, *Themeda* and *Setaria* at Thlavekisa, and of *Bothriochloa* at both sites. A notable exception to the general pattern for the first three years was *Setaria* at Utha. The growth rate of the *Setaria* population on the lightly grazed treatment was negative for three years, although increasing slightly in the wetter 1987 to 1988 transition period. There was a conspicuous decrease in the population growth rate of *Aristida* on the lightly grazed treatment (Thlavekisa) for the transition period of 1986 to 1987 during which a fire occurred. The population growth rates for *Themeda* at Utha, but not at Thlavekisa, and for *Aristida* at Thlavekisa were higher for the heavily grazed treatments (on the basis of annual comparisons). It was noteworthy that heavy grazing did not depress population growth rates.

Table 9.3. The dominant eigenvalue of the transition matrices of Table 9.2. Notation for treatment: H - heavy grazing; L - light grazing; HD - heavy grazing with rainfall interception; HR - heavy grazing with normal rainfall; LD - light grazing with rainfall interception; LR - light grazing with normal rainfall.

		Transition period				
Site, species	Treatment	1985-1986	1986-1987	1987-1988	1988-1989	1985-1989*
Thlavekisa						
Aristida	HD	1.326	1.346			
	HR	1.398	1.140			
	H	1.361*	1.239*	1.624	1.033	1.297
	LD	1.218	0.992			
	LR	1.336	0.823			
	L	1.276*	0.904*	1.333	1.064	1.131
Bothriochloa	H	1.051	1.117	1.189	0.761	1.015
	L	1.077	1.123	1.225	0.870	1.066
Heteropogon	H	1.049	1.069	1.127	0.532	0.914
	L	1.005	1.069	1.117	0.896	1.018
Setaria	H	1.107	1.161	1.052	0.764	1.008
	L	1.109	1.120	1.313	0.777	1.061
Themeda	H	1.102	1.161	1.260	0.625	1.002
	L	1.062	1.280	1.363	0.830	1.114

Table 9.3 continued.

Site, species	Treatment	Transition period 1985-1986	1986-1987	1987-1988	1988-1989	1985-1989*
Utha						
Bothriochloa	L	1.015	0.936	0.731	**	0.886
Digitaria	H	1.157	1.202	1.283	0.994	1.154
	L	1.133	1.242	1.351	1.004	1.176
Setaria	H	1.114	0.804	0.908	0.848	0.911
	L	1.064	0.907	0.953	0.837	0.937
Themeda	HD	1.382	1.036			
	HR	1.526	1.095			
	H	1.452*	1.065*	1.131	0.981	1.144
	LD	1.111	1.015			
	LR	1.036	1.117			
	L	1.126*	1.065*	0.975	0.896	1.011

* Denotes the geometric mean of the predicted growth rates for four years, or the two rainfall treatments of each grazing treatment.
** Denotes sample size too small.

The geometric mean of λ_1 for four years (Table 9.3) revealed that most populations were relatively stable ($\lambda_1 \approx 1$), with generally few marked differences between grazing treatments. *Aristida* (heavily grazed) had the highest population growth rate, while *Heteropogon* (heavily grazed), *Bothriochloa* (Utha) and *Setaria* (Utha, both treatments) were the only populations in overall decline. The decline of *Heteropogon* was due to

the 1988 to 1989 transition only, while *Bothriochloa* and *Setaria* experienced a more consistent decline in asymptotic growth rate.

In nearly all cases the distribution of the stable stages was a reversed J, with the highest proportion of individuals occurring in the smallest size classes (Figures 9.1, 9.2). There were eight exceptions to this pattern for the stage distributions of the 1985 to 1986 transition matrices, and only four for all other transition matrices, all of which had the highest proportion of individuals in the intermediate (usually size 2 or 3) size classes. In most cases the largest size class contained by far the smallest proportion of individuals, and in a number of cases the largest size class had been eliminated (Figure 9.1).

There are two distinct patterns for the distribution of reproductive value within size classes; the highest proportion occurs in either the largest or the smallest size class (Figures 9.3, 9.4). The latter pattern is associated with transition matrices where there is a zero value for the transition from the second largest to the largest size class.

The range in value of both ρ and t_s was small (Table 9.4). There were only two significant correlations between λ_1 and ρ for the eight site by species combinations (each n=8) examined. There was a negative correlation for *Heteropogon* at Thlavekisa ($r=-0.955$, $p=0.0002$), that is, the more rapidly growing populations converged more slowly to a stable stage distribution. The opposite trend was found for *Setaria* at Thlavekisa ($r=0.792$, $p=0.019$). In addition, the combined data of both sites for *Themeda* yielded a significant positive correlation ($r=0.496$, $n=20$, $p=0.026$). There were also conflicting patterns for the relationship between λ_1 and the time taken for the contribution of λ_1 to become five times greater than that of λ_2. There was a weak negative correlation for *Aristida* ($r=-0.55$, $p=0.07$), a stronger one for *Setaria* at Thlavekisa ($r=-0.83$, $p=0.01$) and a weak positive correlation for *Heteropogon*

Figure 9.1. The stable stage distribution of the most common perennial grasses of the Thlavekisa site. The first two letters of the code of each bar give the species, the following letter denotes the treatment, and the numerals denote the transition period. Notation for species. Ab - *Aristida bipartita*, Bi - *Bothriochloa insculpta*, Hc - *Heteropogon contortus*, Si - *Setaria incrassata*, Tt - *Themeda triandra*. Notation for treatment: h - heavy grazing; l - light grazing; hd - heavy grazing, rainfall interception; hr - heavy grazing, normal rainfall; ld - light grazing, rainfall interception; lr - light grazing, normal rainfall. Notation for transition period: the first numeral is the starting year (in May), the second numeral is the finishing year (in May), e.g. 56 is May 1985 to May 1986.

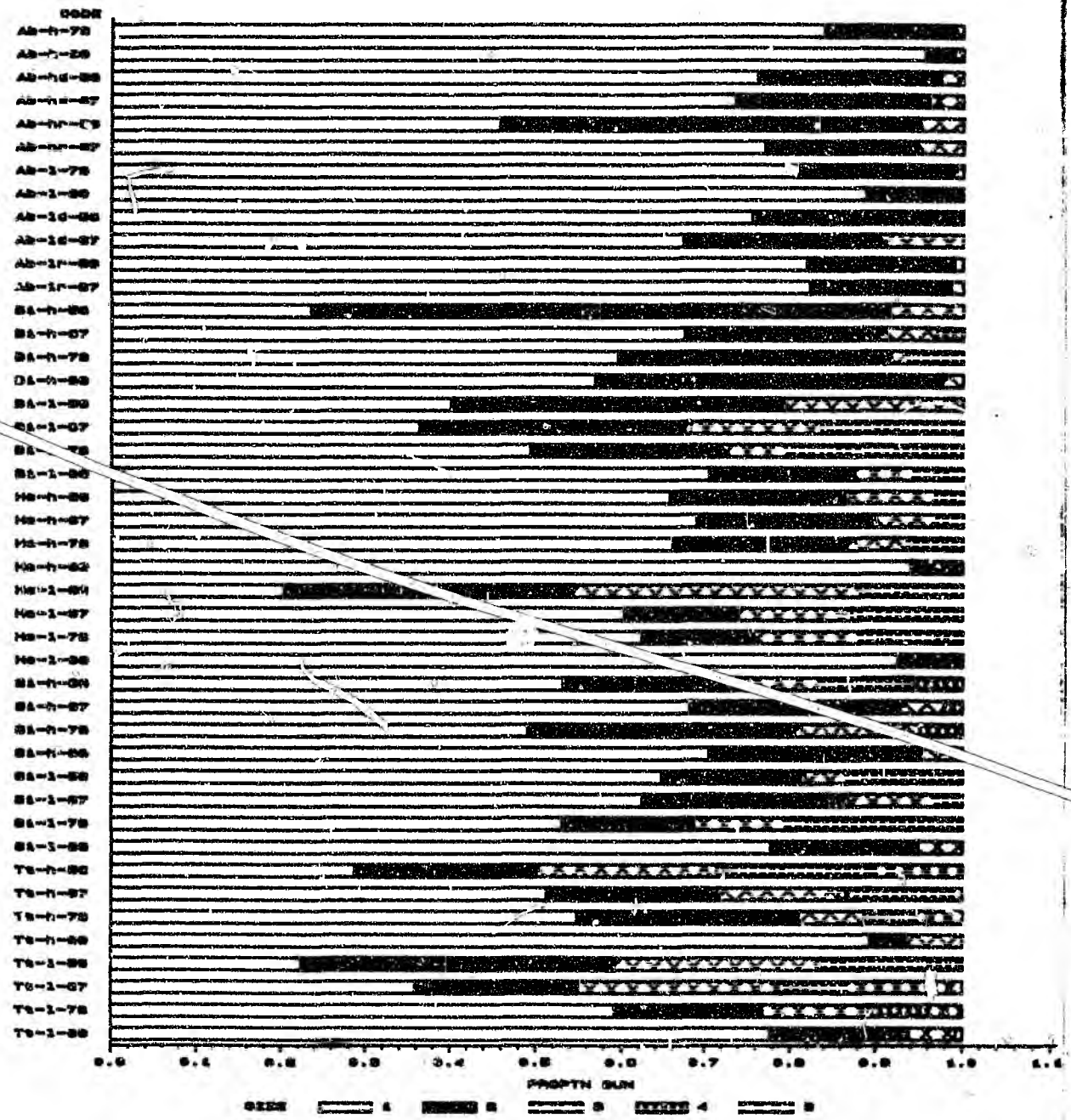
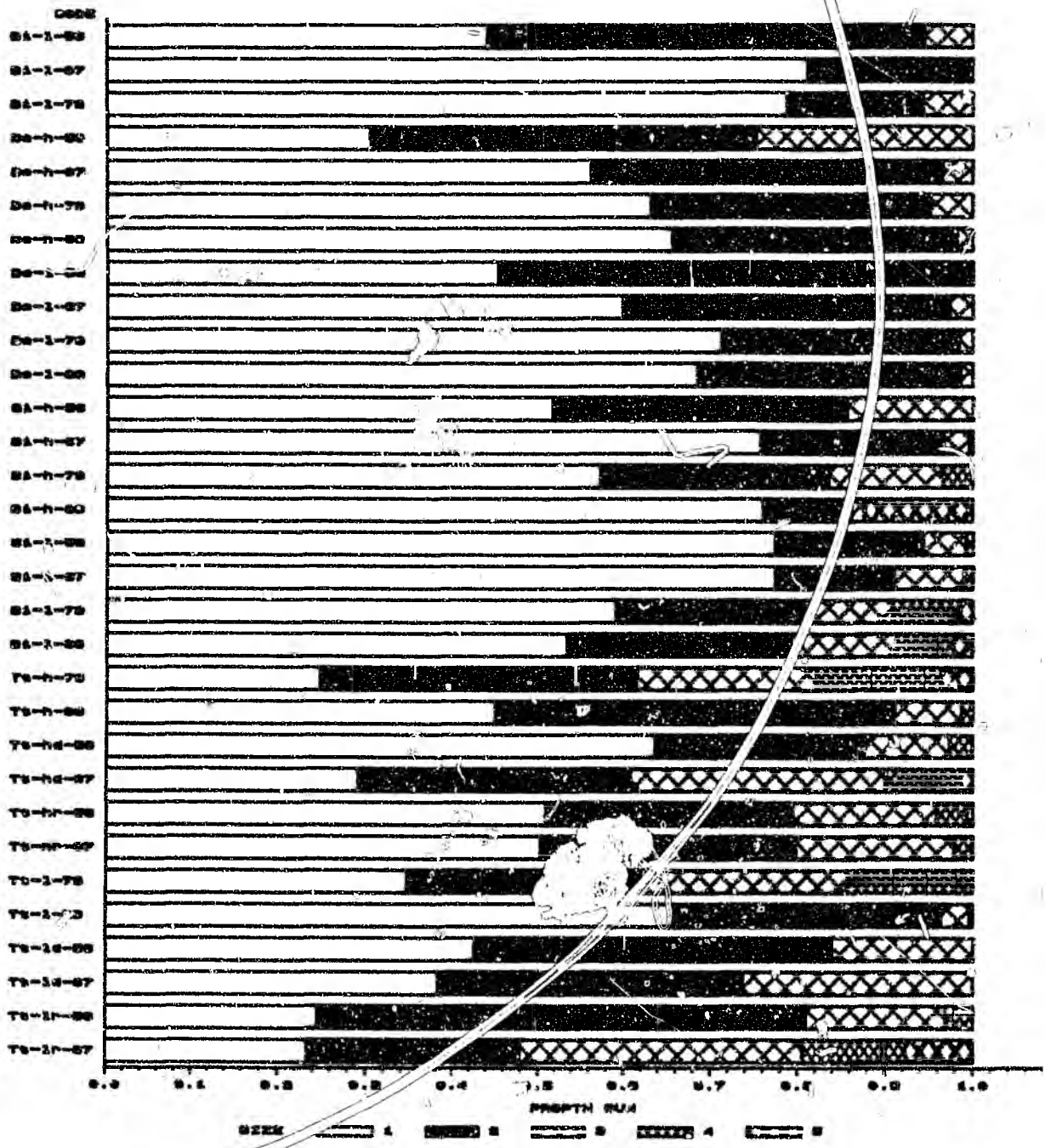

ORDER
PROPTN SUM
SIZE

Figure 9.2. The stable stage distribution of the most common perennial grasses of the Utha site. The first two letters of the code of each bar give the species, the following letter denotes the treatment, and the numerals denote the transition period. Notation for species: Bi - *Bothriochloa insculpta*, Di - *Digitaria eriantha*, Si - *Setaria incrassata*, Tt - *Themeda triandra*. Notation for treatment: h - heavy grazing; l - light grazing; hd - heavy grazing, rainfall interception; hr - heavy grazing, normal rainfall; ld - light grazing, rainfall interception; lr - light grazing, normal rainfall. Notation for transition period: the first numeral is the starting year (in May), the second numeral is the finishing year (in May), e.g. 56 is May 1985 to May 1986.


CODE
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
PROPTN RUN
SIZE

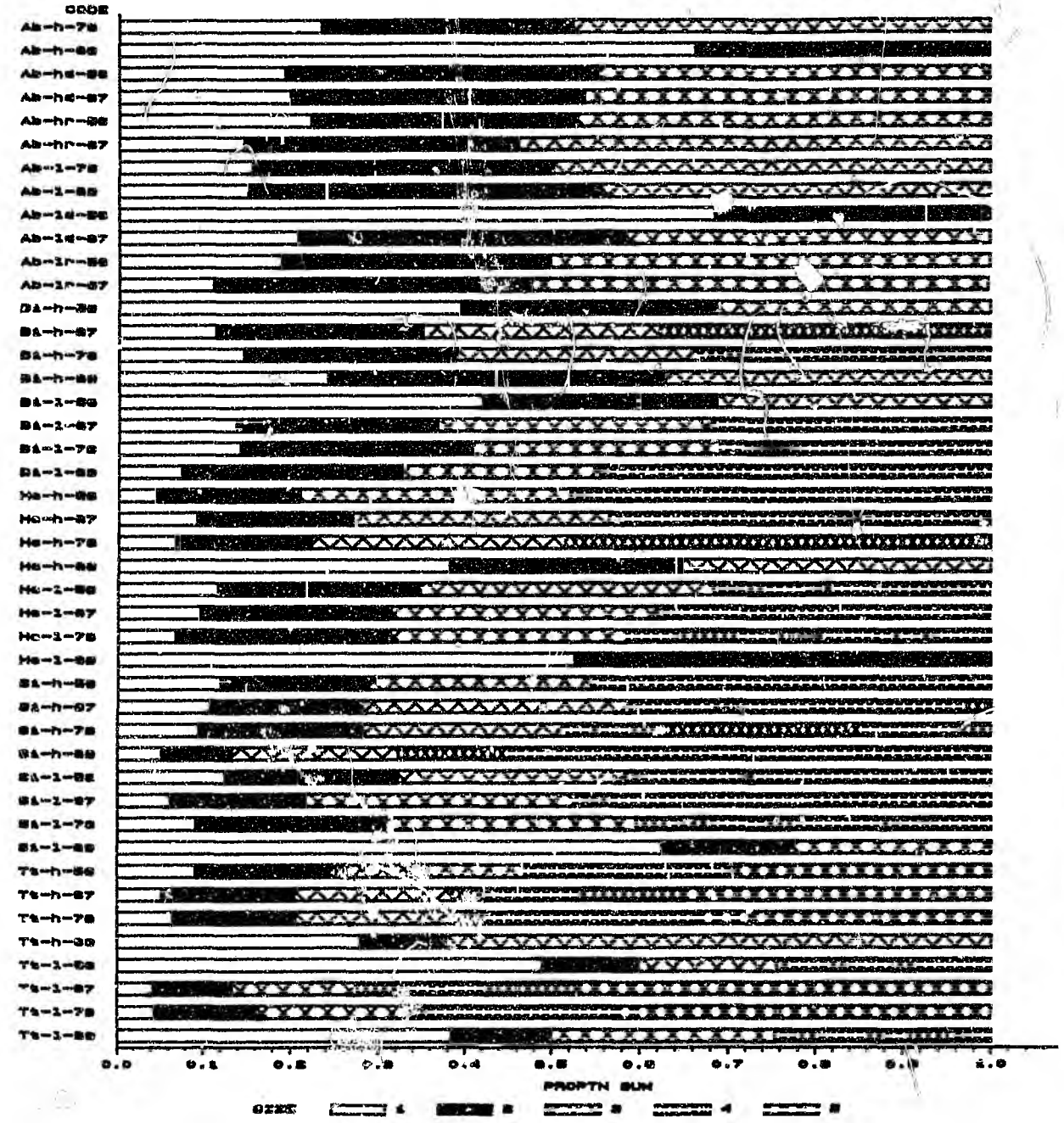


Figure 9.3. The distribution of reproductive value of the most common species of the Thlavekisa site. Notation as for Figure 9.1.

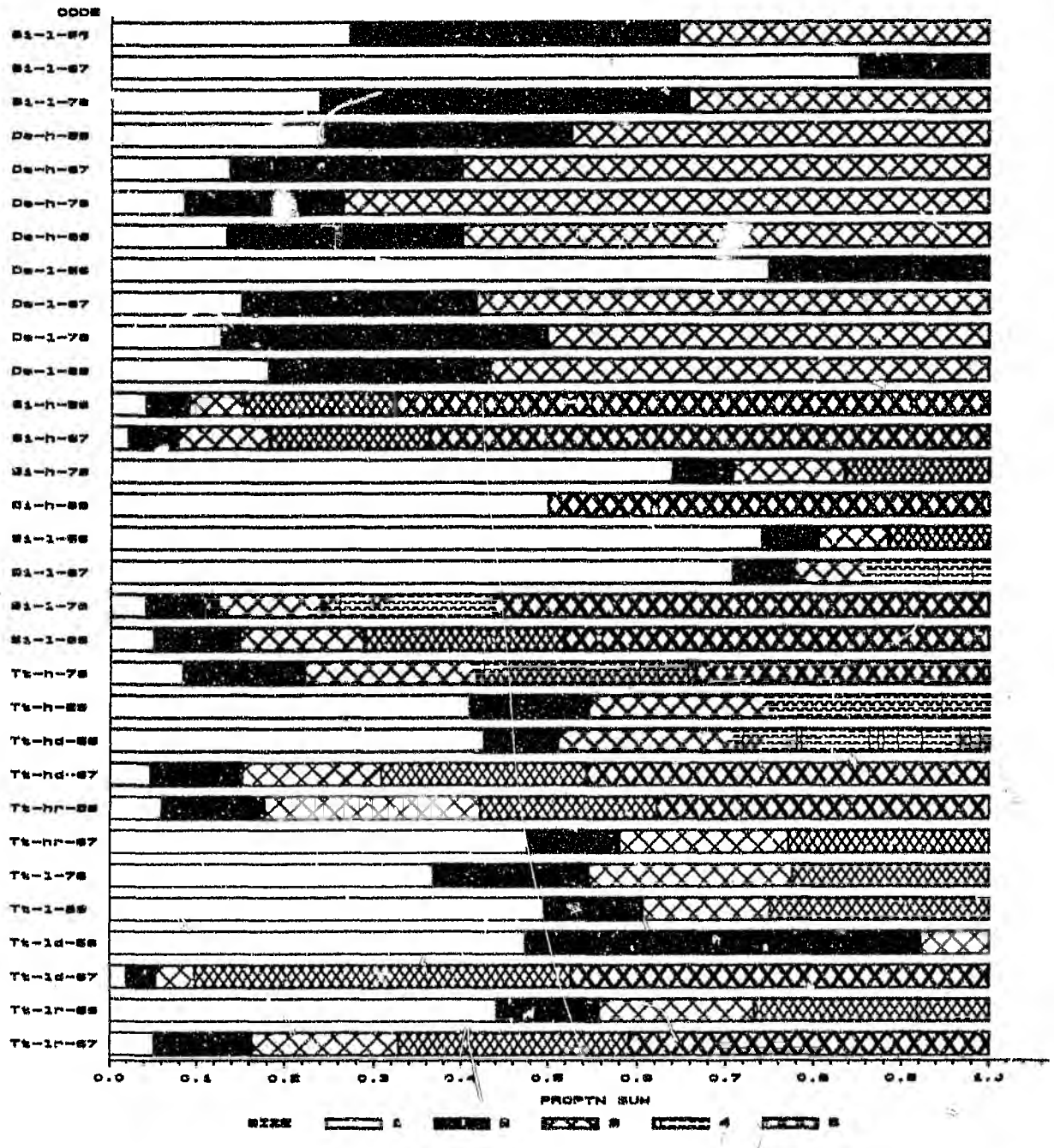


Figure 9.4. The distribution of reprcductive value of the most common species of the Utha site. Notation as for Figure 9.2.

($r=0.69$, $p=0.06$). The (arithmetic) mean duration of P_2 per species ranged from 8.6 to 27.5 (Table 9.4), but in no cases was P_2 correlated with λ_1 or with t_5. However, P_2 was significantly correlated with ρ for *Digitaria* ($r=0.93$, $p=0.0008$). The lack of correlations of P_2 are partly a result of 31 of the λ_2 having only a real component.

Elasticity Analyses

Two distinct patterns are apparent in the elasticity matrices (Table 9.5). In one pattern the transitions involving the smallest size classes, in particular the proportion surviving, were the most important contributors to the population growth rate, with often negligible contributions from the largest size classes. This pattern was associated with negative population growth rates ($\lambda_1<1$), or, if with a positive growth rate ($\lambda_1>1$), the largest size classes were collapsing because of tuft fragmentation and no or poor growth into them from smaller sizes. This pattern is exemplified by *Aristida* (with in most cases positive population growth but a collapsing largest size class) with up to 92%, and, except in one case, never less than 40% of the elasticity accounted for by the first entry of the matrix (predominantly the proportion of the smallest size class surviving - Table 9.2). Other examples include most of the elasticity matrices of *Digitaria*, *Bothriochloa* and *Setaria* for all years, and *Themeda* and *Heteropogon* for the dry 1988 to 1989 transition period when there was negative population growth.

In the second pattern the highest elasticity values were more equitably distributed along the main diagonal of the matrix (proportion surviving in each of the size classes), and with relatively high values for transitions to larger size classes. This was associated with relatively

Table 9.4. Summary statistics for the damping ratio (ρ), period of oscillation (P_2), and the time taken for the contribution of λ_1 to population growth to become five times greater than that of λ_2 (t_5).

Site, species	ρ			P_2			t_5		
	x	max	R	x	max	R	x	max	R
Thlavekisa									
Aristida	2.6	5.5	3.7	14.4	135	135	2.0	2.8	1.9
Bothriochloa	2.5	3.7	2.4	8.5	32	32	2.6	5.4	4.3
Heteropogon	3.4	11.5	9.9	17.4	45	45	2.2	3.3	2.7
Setaria	2.0	2.4	1.1	27.5	132	132	2.9	6.0	4.2
Themeda	1.6	2.1	1.1	13.3	60	60	6.6	26.9	24.8
Uth[illegible]									
Bothriochloa	2.1	2.8	1.6	15.7	47	47	4.6	10.2	8.6
Digitaria	2.6	4.7	3.6	12.4	50	50	3.1	12.9	11.9
Seta[illegible]a	1.4	1.7	0.5	7.5	60	60	5.5	9.7	6.8
Themeda	1.7	2.	1.6	12.8	87	87	5.2	16.9	15.3

high population growth rates and populations in which the largest size classes were maintained to some extent. This was the pattern for *Themeda*, *Heteropogon* and *Bothriochloa* (Thlavekisa - lightly grazed treatment) for most of the transition matrices of the first three years. *Setaria* (Thlavekisa - lightly grazed treatment) was somewhat anomalous with the highest elasticity value of the 1987 to 1988 transition period being the proportion of the largest size class surviving.

Table 9.5. Transition matrix elasticities (as percentages) for the populations of perennial grass species at two locations during four transition periods. Entries denoted by a line correspond to transition elements of zero. Notation for treatment: HD - heavy grazing with rainfall interception; HR - heavy grazing with normal rainfall; LD- light grazing with rainfall interception; LR - light grazing with normal rainfall; H - heavy grazing; L - light grazing.

Species & treatment	Size class	Transition period: 1985-1986					1986-1987									1988-1989				
		1	2	3	4	5	1	2	3	4	5	1	2			1	2	3	4	5
Thiaveksa																				
Aristida HD	1	48	13	2			45	12	3			70	10				5	0		
(Treatment=H	2	14	17	1			14	15	3			11	7	+			1	0		
for 1987/88,	3	—	2	3			1	5	1			—	1	+			—	—		
1988/89).																				
HR	1	16	17	4			45	8	4											
	2	21	31	2			11	15	3											
	3	—	6	2			2	5	8											
LD	1	71	16	0			40	8	4			50	13	2			62	12	1	
(Treatment=L	2	4	9	0			12	20	1			15	17	+			12	12	+	
for 1987/88,	3	—	—	0			—	5	10			—	2	1			—	1	+	
1988/89).																				
LR	1	62	10	1			46	10	1											
	2	11	13	1			11	23	3											
	3	—	1	1			—	4	3											
Bothriochloa	1	11	12	6	0		27	13	3	4		23	19	+	3		28	15	2	
H	2	12	47	3	—		16	13	4	+		22	12	1	6		17	34	1	
	3	—	7	2	—		4	6	2	—		—	3	—	—		—	3	—	
	4	—	—	—	0		—	2	2	3		—	7	2	3					
L	1	26	17	6	0		12	4	2	4		18	7	2	6		28	8	1	2
	2	15	13	3	0		8	18	2	5		12	11	2	3		11	14	3	5
	3	—	7	12	0		2	9	5	6		2	5	4			—	6	5	1
	4	—	—	—	0		—	2	13	8		—	5	4	20		—	4	5	8
Heteropogon H	1	14	5	3	3		33	8	4	2		23	3	2	7		86	9	1	0
	2	12	16	1	1		12	13	1	1		11	12	2	+		3	1	—	0
	3	—	9	19	1		2	6	8	1		1	10	3	2		—	+	—	0
	4	—	—	5	8		—	—	4	6		—	—	9	15		—	—	—	—
L	1	6	2	1	1		21	4	3	5		14	2	4	7		87	6	0	0
	2	4	21	5	1		7	4	4	2		13	4	2	2		5	2	0	0
	3	—	9	33	3		5	8	9	1		—	10	9	3		—	—	0	0
	4	—	—	5	9		—	—	8	20		—	4	8	19		—	—	—	0

Table 9.5 continued.

Species & treatment		Size class	Transition period 1985-1986					1986-1987					1987-1988					1988-1989				
			1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Setaria	H	1	22	2	3	5		33	14	3	2		16	7	2	3		36	13	1	+	
		2	10	5	2	1		19	8	3	1		12	17	5	2		14	8	3	2	
		3	—	10	3			—	8	2	+		—	8	11	3		—	6	4		
		4	—	—	6	31		—	—	3	3		—	4	3	7		—	—	3	10	
	L	1	34	2	1	7		19	7	4	3		11	2	3	9		78	11	3	0	
		2	10	6	—	1		7	17	4	2		8	8	—	1		1	3	1	0	
		3	—	2	5	1		6	7	14	1		4	6	5	2		—	1	1	0	
		4	—	7	2	21		—	—	5	6		2	1	9	29		—	—	—	0	
Themeda	H	1	5	3	3	2	2	10	4	1	5	1	14	7	2	2	4	75	3	7	0	0
		2	7	13	1	—	—	10	14	+	—	1	15	15	+	+	—	1	+	—	0	—
		3	3	5	15	2	—	2	7	11	1	+	—	9	4	1	—	—	1	13	—	—
		4	—	—	6	15	3	—	—	9	10	—	—	—	5	4	2	—	—	—	0	—
		5	—	—	—	5	11	—	—	—	2	2	—	—	1	5	9	—	—	—	—	0
	L	1	13	24	6	6	0	4	1	2	1	3	10	2	4	4	5	70	11	7	2	0
		2	6	10	1	—	—	6	3	1	1	—	12	6	—	1	—	2	3	+	+	0
		3	—	3	14	—	—	—	7	8	—	7	3	10	7	1	—	—	1	3	+	0
		4	—	—	1	17	—	—	—	11	2	—	—	1	10	4	1	—	—	+	+	0
		5	—	—	—	—	0	—	—	—	9	34	—	—	—	6	11	—	—	—	—	—
Utha Bothriochloa	L	1	18	15	3			86	10	0			58	9	2							
		2	12	43	3			2	2	0			6	15	3							
		3	6	—	—			—	—	0			5	—	2							
Digitaria	H	1	10	5	9			18	16	3			20	8	9			34	12	2		
		2	13	21	5			20	30	3			17	21	1			13	20	4		
		3	—	14	23			—	6	4			—	10	14			—	6	—		
	L	1	48	24	0			27	14	3			23	21	1			47	12	1		
		2	7	22	0			17	30	2			22	28	1			13	22	2		
		3	—	—	0			—	4	3			—	2	2			—	3	1		
Setaria	H	1	21	15	9	0	0	32	14	2	1	+	59	20	9	2	0	63	6	+	+	16
		2	24	9	3	0	0	17	19	1	+	+	2	2	1	+	0	0	0	0	0	—
		3	—	11	8	0	0	—	5	5	+	+	+	1	2	1	0	0	0	0	—	—
		4	—	—	—	0	0	—	—	2	+	+	—	—	1	1	0	—	—	0	—	—
		5	—	—	—	0	0	—	—	—	1	1	—	—	—	—	0	—	—	—	—	14
Setaria	L	1	84	11	1	1	0	77	12	6	2	0	20	5	2	2	2	19	7	1	1	+
		2	1	1	+	+	0	1	1	+	+	0	9	7	4	3	+	6	14	6	2	—
		3	—	+	+	+	0	+	+	+	+	0	1	9	5	+	+	2	5	5	4	—
		4	—	—	+	+	0	—	+	+	+	0	2	1	4	11	1	1	1	5	8	2
		5	—	—	—	—	0	—	—	—	—	0	—	—	—	4	6	—	—	—	2	9

Table 9.5 continued.

Species & treatment	Size class	Transition period 1985-1986					1986-1987					1987-1988					1988-1989				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Thomeda HD (Treatment=H for 1987/88, 1988/89).	1	73	2	7	3	0	7	1	2	1	+	4	4	3	2	1	47	18	3	1	0
	2	4	2	+	+	0	5	16	3	4	1	8	14	5	3	2	4	18	1	+	0
	3	—	3	2	+	0	—	9	25	3	1	+	13	8	3	1	—	3	3	+	0
	4	—	—	1	1	0	—	1	9	6	1	—	1	10	11	1	—	—	1	+	0
	5	—	—	—	—	0	—	—	—	3	2	—	—	—	4	4	—	—	—	—	0
HR	1	8	3	14	4	1	39	12	24	1	0										
	2	15	13	1	1	+	3	5	2	+	0										
	3	4	14	16	2	+	+	4	7	+	0										
	4	—	—	4	2	+	—	—	1	1	0										
	5	—	—	—	1	1	—	—	—	—	0										
LD (Treatment=L for 1987/88, 1988/89).	1	19	24	7	0	0	14	5	5	0	0	35	5	4	4	0	71	17	1	+	0
	2	18	26	2	—	0	11	20	7	—	0	3	13	2	+	0	2	7	+	+	0
	3	—	1	2	—	0	—	12	26	0	0	—	4	15	1	0	—	1	1	+	0
	4	—	—	—	0	0	—	—	—	0	0	—	—	2	10	0	—	—	+	+	0
	5	—	—	—	—	0	—	—	—	0	0	—	—	—	—	0	—	—	—	—	0
LR	1	19	17	11	5	0	4	1	2	1	+										
	2	7	21	3	—	0	4	10	3	—	1										
	3	—	6	6	1	0	—	7	22	1	4										
	4	—	—	2	2	0	—	—	7	12	1										
	5	—	—	—	—	0	—	—	—	6	14										

The influence of the reproductive terms on population growth were confounded with the effect of the contributions to the first size class by fragmentation or reduction in size of tufts. For obligate seed reproducing species, the latter process influences the value of the first two entries of the first row of the transition matrices quite markedly, whereas the first row entries of the larger size classes are predominantly formed by seedling recruitment (Table 9.2). However, few of the latter values account for more than 10% of the elasticity matrices (most <5%).

Relationship between species

At Thlavekisa, the population growth rates of *Aristida* were not correlated with those of any other species, but the growth rates of all other species were strongly correlated (Table 9.6). Only the growth rates of *Setaria* and *Themeda* at Utha were correlated ($r=0.738$, $p=0.036$). There were no differences between species at Thlavekisa in r, the damping ratio or t_s, but the species at Utha differed for both r ($F=8.03$, $p=0.0021$) and the damping ratio ($F=6.03$, $p=0.0076$). The population growth rate of *Setaria* was lower ($p<0.05$) than that of *Digitaria* or *Themeda*, while the damping ratio of *Digitaria* was higher ($p<0.05$) than that of *Setaria* or *Themeda*.

DISCUSSION

The population growth rates of the species studied varied substantially from year to year, with concomitant changes in the demographic processes which were important contributors to overall population growth, and a

Table 9.6. The Pearson's correlation coefficient (with the probability in parenthesis) between the population growth rates ($\ln(\lambda_1)$) of five grass species at Thlavekisa.

Species	Heteropogon contortus	Setaria incrassata	Themeda triandra
Bothriochloa insculpta	0.924 (.001)	0.929 (.0009)	0.989 (.0001)
Heteropogon contortus	———	0.803 (.016)	0.944 (.0004)
Setaria incrassata	———	———	0.912 (.0016)

slight directional change in the stable stage structure of these populations. A consistent feature across all species for the sequence of years studied was the collapse of the largest size classes due to the fragmentation of tufts, irrespective of whether the populations were declining or growing. This resulted in a dramatic change in the size structure of all populations in the field by the end of the study, with the majority of individuals to be found in the smallest size classes (Tables 7.1, 7.2), in partial correspondence with the predicted stable stage distributions. This pattern of change occurred independently of grazing regime, and is concluded to be associated with the directional pattern of rainfall which prevailed during the course of the study. The season in which baseline data were established (1984/85) and the preceding season were both relatively very wet years, the first two transition periods were successively drier, the third was wetter than these but not as wet as 1983/84 and 1984/85, and the final transition period was dry (Table 3.1). The initial two very wet years are considered to be responsible for the number of large tufts found at the start of the study. The increasingly xeric conditions over the course of this study could not

support the total basal area of grasses (Figures 6.3, 6.6), and the adjustments of basal area were effected through extensive fragmentation of tufts. Similar fragmentation of the caespitose *Schizachyrium scoparium* of the American prairies was noted during drought conditions (Butler & Briske 1988).

Despite the generally xeric conditions of three of the four transition periods, there was at least some seedling recruitment of the obligate seed reproducers in all of these years (Table 7.4; Table 8.2). The majority of *Bothriochloa* recruits were also seedlings, a few new genets of *Setaria* established, and there was vegetative recruitment of *Digitaria*. However, the elasticity analyses indicated that recruitment had little effect on population growth rates. Similarly, the most important demographic process contributing to the population growth of *Danthonia sericea* was the proportion of individuals surviving, particularly of the larger size classes (Moloney 1988). The species of this study to some extent match his conclusion that the reproductive success of an individual, because of high mortality of recruits and large losses of seed, depends upon being able to produce seed for several years. However, in contrast to the pattern of his populations, in this study it was usually the processes involving the smallest size classes which exerted the strongest influence on population growth. It does however appear to be a common characteristic of longer-lived, slower-growing species that reproduction contributes the least to population growth (Caswell 1986), based on elaticity analyses of the perennial herb *Arisaema triphyllum* (Bierzychudek 1982) and the shrub *Alnus incana* (Huenneke & Marks 1987).

Similar variability of asymptotic population growth rates of perennial grasses has been described for *Danthonia sericea* (Moloney 1988) and *Andropogon semiberbis* (Silva *et al*. 1991). The predicted growth rates for *Danthonia sericea* (λ_1) ranged from 0.6 to 1.43 over five closely spaced locations on a soil gradient over two years, but this variation

was not explicitly related to environmental factors. Fire was shown to be a primary determinant of the population abundance of *Andropogon semib bis*; burnt populations increased rapidly (λ_1=1.2524) whereas unburnt populations declined to extinction ((λ_1=0.2762). The results of this and the above described studies have provided a realistic foundation for a simulation study to assess which transitions the population growth rate of a perennial grass is most sensitive to.

The overall population decline of *Bothriochloa* and *Setaria*, and tendency for decline of *Themeda*, on the lightly grazed treatment at Utha is attributed to density-dependent effects. Heavy grazing had an initial positive effect on the population growth rate of *Themeda* at Utha, and *Aristida* at Thlavekisa, because of increased recruitment (Table 7.4), more rapid growth of established seedlings and differences in size transitions (Chapter 7), all possibly a result of reduction of biomass by grazing (Figure 4.2, 4.3). The population decline of *Aristida* under light grazing (1986 to 1987 transition) was possibly the effect of the fire.

Reproductive value has been found to increase with size in trees (Caswell 1986), herbs (Caswell & Werner 1978, Bierzychudek 1982) and shrubs (Huenneke & Marks 1987). Although in general the same result was found, there was marked annual variation in the distribution of reproductive value across size classes. A form of switching behaviour was apparent. In those populations in which the largest size class became extinct, the highest reproductive value was usually then found in the smallest size class, not the second largest size class.

The damping ratio (ρ), period of oscillation (P_2) and the time taken for the contribution of λ_1 to become five times greater than that of λ_2 (t_5) were of little value in elucidating general patterns in the stability (transient) behaviour of these populations. The generally small range

of λ_1 for each species (per site) probably had an influence, when the data for *Themeda* from the two sites was combined, which increased the range of λ_1, there was a significant correlation between λ_1 and ρ although this had not been the case for either site alone. A correlative approach to the transient behaviour of matrix transition models is therefore only likely to yield clearer insights when population responses to more extreme ranges of environmental conditions are described.

The dependence of mortality on age for the smallest size class of *Aristida* and *Heteropogon* at Thlavekisa (Chapter 7) suggests that transition models of these perennial grasses would be improved using both size and age. I am not in a position to evaluate this, and a prohibitive amount of effort would be required to monitor a population long enough until all individuals were of known cohorts, considering the slow rate of population turnover (Chapter 7). However, Caswell (1989) reanalysed the relative effects of both age and size on the fate of individuals of two monocarpic perennial plants and on the fate of ramets of a clonal shrub. Although both size and age had significant effects on demographic fate, size was a more important variable than age except for the clonal shrub. In contrast Law & Edley (1990) argue that the transient dynamics of a population classified by size and age rapidly collapse into an age dependent mode.

The strong positive correlations between the growth rates of four species at Thlavekisa, and *Themeda* and *Setaria* at Utha, indicate that there should be potential for strong interactions between these species. All correlation coefficients were positive (significant or not), indicating that all species were reacting in a similar direction to an extrinsic force. This is considered to be the increasingly xeric conditions which occurred. The lack of any negative correlations indicate that, under the range of environmental conditions sampled, no species had a consistent detrimental effect on the population growth of another. However, such a

negative effect might be anticipated over a greater range of rainfall, particularly for species which are spatially associated with one another, such as *Setaria* and *Themeda* at Thlavekisa (Chapter 4).

The finding that long-term population growth rates vary substantially with rainfall and grazing suggests a direction for future research. The population response to extreme levels of these environmental forces, others such as fire, and their contingency, needs to be investigated. A conspicuous gap in the present results is the effect of a succession of extremely wet years on population growth. The circumstantial evidence for density dependent effects from *Setaria* and *Themeda* at Utha are a further essential consideration for improved models. Elasticity analyses provide a focus for which population transitions should receive greater empirical attention. For example, factors influencing the survival of the smallest size classes are more important for declining populations, while reproductive output is of lesser importance, and the survival of larger size classes is important for stable populations. But these analytical insights themselves need to be evaluated in the light of all available empirical evidence, as the extinction of the seed bank may become the most important process under certain environmental conditions.

SUMMARY

Size-structured matrix models were developed for the most common species of the Thlavekisa and Utha sites, separately for four years. A consistent feature of all matrices was the collapse of the larger size classes due to the fragmentation of tufts. The population growth rate, given by the dominant eigenvalue of the matrix, varied widely between years and species, but in few instances were there marked differences between

grazing treatments. The variation in λ_1 was attributed to the directional trend of rainfall during the study from initially wet to successively drier, with most species showing negative population growth rates in the final dry year. The pattern of response of λ_1 to rainfall was the same for all species at each site. Parameters for the transient behaviour gave no clear indication of the stability of each species. Elasticity analysis of matrices identified that the proportion of the smallest size class surviving was the most important transition for declining populations, while the proportion either remaining in a size class or transferring to the next largest size class was the most important transition for stable or growing populations. Although individual reproductive output varied widely, it had little effect on population growth. In most cases the stable stage distribution was a reversed J, in accordance with the population size structure in the field. The distribution of reproductive value was generally J shaped, except it switched to a reversed J distribution if the larger size class had been eliminated.

CHAPTER 10

THE INFLUENCE OF GRAZING ON THE SEED PRODUCTION AND THE SEED BANKS OF TWO SAVANNA GRASSLANDS

INTRODUCTION

The compositional dynamics of the savanna grasslands of southern Africa are characteristically temporally variable, reflecting the variability of the annual rainfall (O'Connor 1985). Sustained heavy grazing in conjunction with drought can result in extensive grass mortality, which may ultimately lead to the local extinction of perennial grasses with "K-selected" life history attributes, and to the increase of invasive and unpalatable species (Chapter 2). The ability of savanna grasses to maintain their populations depends in part on the availability of vegetative or sexual propagules, for the recolonisation of gaps made available by drought and grazing. Even perennial grasses which propagate vegetatively rely on sexual reproduction at some stage (Silvertown 1982). The input of seeds is a function of the abundance of a species, and of the resource factors influencing seed production. Seed produced may be lost to ingestion by ungulates, pre- or post-dispersal predation, deep burial, decay or germination. However, no study could be found which had examined all the processes which determine the size of the seed bank of a perennial grass species.

There is a lack of correspondence between the composition of the seed bank and the composition of the vegetation for many perennial grasslands

(Thompson & Grime 1979, and references therein). Perennial grasses which are predominant in the vegetation, but posses transient seed banks may be absent, while species with abundant persistent seed banks may be absent from the established vegetation (Thompson & Grime 1979). Few established species of any community show random dispersion (Greig-Smith 1983), but the role of the seed bank in maintaining such pattern has been little investigated.

This chapter examines the influence of sustained heavy grazing on the production of viable seed, and the consequent representation in the seed bank, of the predominant perennial grass species of two savanna grasslands. A second objective was to examine the relationship of the composition of the seed bank to the composition of the vegetation. A third objective was to establish if the seed bank might influence the spatial pattern of population dynamics. A fourth objective was, by the use of a simple model, to investigate the importance of different processes for determining the size of the seed bank, and to assess if heavy grazing could eliminate a species from the bank.

The study was conducted at Thlavekisa and Utha.

METHODS

Reproductive output

Three plots were monitored per grazing treatment in 1985/86, and six in 1986/87. The tagged tufts closest to 52 randomly located points were

used. The number of reproductive culms (irrespective of stage of development) of each tuft was recorded at approximately monthly intervals throughout the 1985/86 and 1986/87 growing seasons, and usually preceding and following grazing. The basal circumference of each tuft was measured to the nearest cm at the end of each growing season.

The number of viable seeds ha^{-1} was estimated from the basal area, the number of reproductive culms produced per unit basal area, the numbers of seeds produced per culm, and the percentage of viable seed. The number of seeds per culm was assessed in 1986/87 for for each grazing treatment for *Themeda*, *Heteropogon*, *Setaria* and *Digitaria*, by collecting all the mature reproductive culms in 15 random 1 m square quadrats per treatment. Collections of *Aristida* and *Bothriochloa* from different treatments were combined. The number of seeds (disseminules) per culm of *Themeda*, *Setaria*, *Digitaria* and *Aristida* can easily be determined even if they have been shed, but the number of seeds per culm of *Heteropogon* and *Bothriochloa* were determined from fresh culms. Ripe seed of each species was collected in 1986 and 1987 for seed viability tests by shaking out inflorescences into bags. Seeds (n>400) were considered to be viable if they contained both an embryo and endosperm, determined by microscopic examination following imbibition and dissection. To test for innate dormancy, ±100 apparently viable seeds of each major species, which had been stored in the dark, were placed on filter paper in petri dishes and kept moist for 14 days at <1 mo and 12 mo after collection. Seeds which did not germinate were dissected to determine their viability.

An index of the seed production of a species, independent of its abundance, is the number of seeds produced per unit of summed basal area of tufts. An index of the vulnerability of the seed production of a species to grazing is the ratio of the number of culms per unit basal area to the number of seeds per culm.

Seed bank

Twenty four (9.6 x 9.6 x 5 cm) soil cores per treatment were collected in May 1987 at the end of the growing season. This was a higher intensity of sampling than most studies (Bigwood & Inouye 1988) to overcome the problem of contagion in grassland seedbanks (Johnson & Anderson 1986; Thompson 1986). The litter and the upper 2 cm of soil of each core were collected separately from the lower 3 cm of soil. The soil was allowed to air-dry, then sieved into fractions of <212 um, 212 um - 2 mm, and >2 mm. The first fraction was placed in dishes and kept moistened for 2 mo in an attempt to germinate any seeds present, but none were recovered. The latter two fractions were visually searched (X10), coarse litter was discarded and all seeds were extracted. Subsequently, all organic matter was extracted from the 212 um - 2 mm soil fraction (Smucker *et al.* 1982), microscopically searched again, and kept moist for 4 months. The condition of non-viable grass seeds was recorded as either empty (no embryo or endosperm), parasitized (a circular hole bored through the palea or lemma), broken (floret shredded), or rotten (embryo and/or endosperm liquid or darkened in colour). The seeds of the perennial *Urochloa mosambicensis* and the annual *U.* cf *trichopus* are indistinguishable, and combined figures are given.

Spatial patterns of the seed bank

The compositional variation of seed cores was described with reciprocal averaging (Hill 1979). The overall difference between species in their frequency of occurrence in soil cores was tested with a G-test, on the assumption that species had an equal probability of occurrence. Unplanned

pairwise comparisons were tested against the appropriate X^2 value (Sokal & Rohlf 1981, p728). The degree of dispersion of the seeds of each species was tested with Morisita's (1959 - in Greig-Smith 1983) index. The index tends to unity for random distribution, is below one for regular distribution, and ranges from one to the sample size (24) for contagious distribution. The association between pairs of species in the seed bank was examined with Hurlbert's (1969) coefficient of association, which is based on presence or absence. The coefficient is not effective if the value of one of the species tends to unity or zero. Therefore, a correlation (Spearmans) was also sought between the numbers of seeds of each species, but only using those cores in which both species occurred together (for $n>10$). To examine if the dispersion of the seed bank is related to the pattern of the vegetation, correlations were sought between the seed number recovered from a sample and the abundance of the established population in the area surrounding the sample point.

Statistical analyses

The partitioning of each site into two grazing treatments is an example of pseudo-replication (Hurlbert 1984), in whi differences between the treatments may only reflect differences in location. However, statistical tests have been undertaken to detect differences between grazing treatments (i.e. locality), and inferences concerning the effects of grazing are obviously external to the statistical analyses. Despite the relatively high sampling intensity, most of the counts of seeds were skewed, even after transformation, hence non-parametric statistics have been employed. Tests for differences between species were restricted to the commoner perennial grasses; forbs were excluded. Differences in the number of seeds between species within a treatment were examined with

Kruskal-Wallis 1-way ANOVA's, with pairwise tests between species (Wilcoxon 2-sample test, tested at 0.05/number of pairwise comparisons). The G-test was used to examine if the pattern of difference between species was independent of locality (grazing). The difference in the number of seeds for each species between grazing treatments was examined with Wilcoxons 2-sample test (with 0.05 continuity correction).

Modelling of seed bank dynamics

A model of the seed bank dynamics of each species (Figure 10.1) was examined for different parameter inputs. The bank is assumed to consist of seeds of only two age classes (at the end of the growing season), because seeds of perennial grasses do not persist for more than three years if in a state of enforced or induced dormancy (Chapter 2). The number of seeds which persist in the bank is determined by the proportion lost to germination or to decay (or alternatively the intrinsic capacity of survival of seeds which do not germinate). The bank therefore consists of seeds produced in that growing season, or seeds which have persisted from the previous growing season. A small proportion of seeds produced two growing seasons previously may enter the bank, but these will either all decay or germinate.

One scenario assumed no predation, germination or decay, and 100% viability, whereas a more severe scenario assumed 5% seed viability, 95% predation, 90% germinability, and 90% decay. The size of the seed bank is the outcome of a sequence of processes which are assumed to be linearly related and therefore computed by simple multiplication.

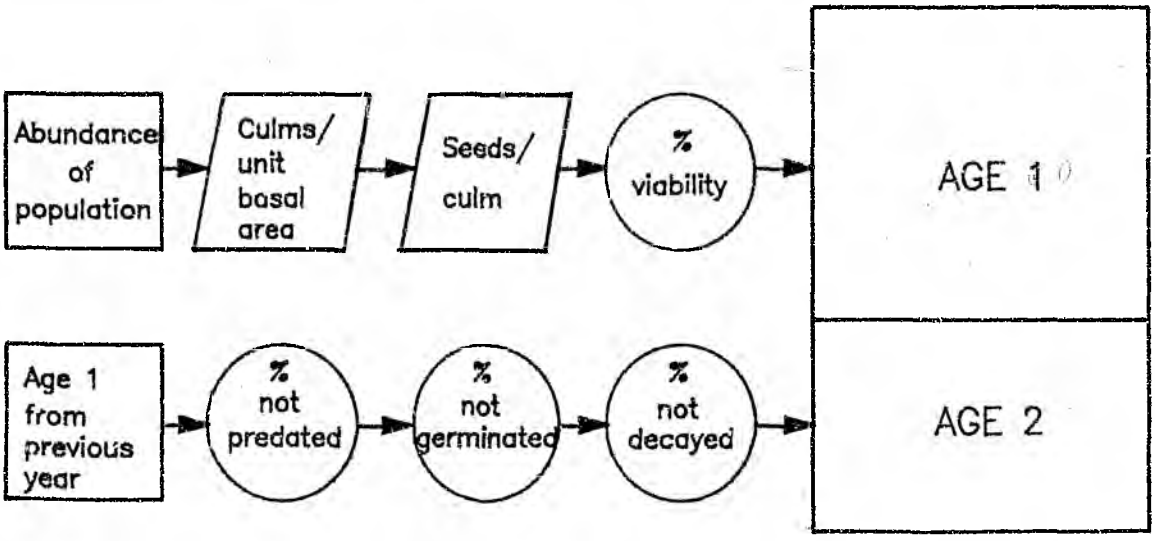


Figure 10.1. The processes determining the size of the seed bank of a perennial grass species. Only two age classes of seeds are assumed (see text).

RESULTS

Reproductive output of species

The differences between species in seed output (assuming 100% viability) are striking (Figures 10.2, 10.3). For example, in 1986/87 under light grazing at Thlavekisa (Figure 10.2), seed output ($x10^2$ m^{-2}) was 106 for *Aristida*, 41 for *Setaria*, 7 for *Hetropogon* and *Digitaria*, 6 for *Bothriochloa*, 5 for *Themeda*, and <3 each for *Urochloa mosambicensis* and *Eragrostis*. Under light grazing at Utha in 1986/87, seed output ($x10^2$ m^{-2}) varied between 13 for *Setaria*, 4 for *Themeda*, and 3 each for

Figure 10.2. The field pattern at Thlavekisa of a) grazing (number of cattle for a ±0.81 ha area), b) rainfall, and the number of seeds (assuming 100% viability) produced over the 1985/86 and 1986/87 growing seasons for c)1985/86: *Setaria incrassata* (----), *Aristida bipartita* (____), *Bothriochloa insculpta* (....), and for 1986/87 only *Setaria* and *Aristida*, and d) *Digitaria eriantha* (....), *Heteropogon contortus* (long hyphen), and *Themeda triandra* (____), plus *Bothriochloa* (short hyphen) in 1986/87. The lightly and heavily grazed treatments are represented by the open and closed circles respectively.

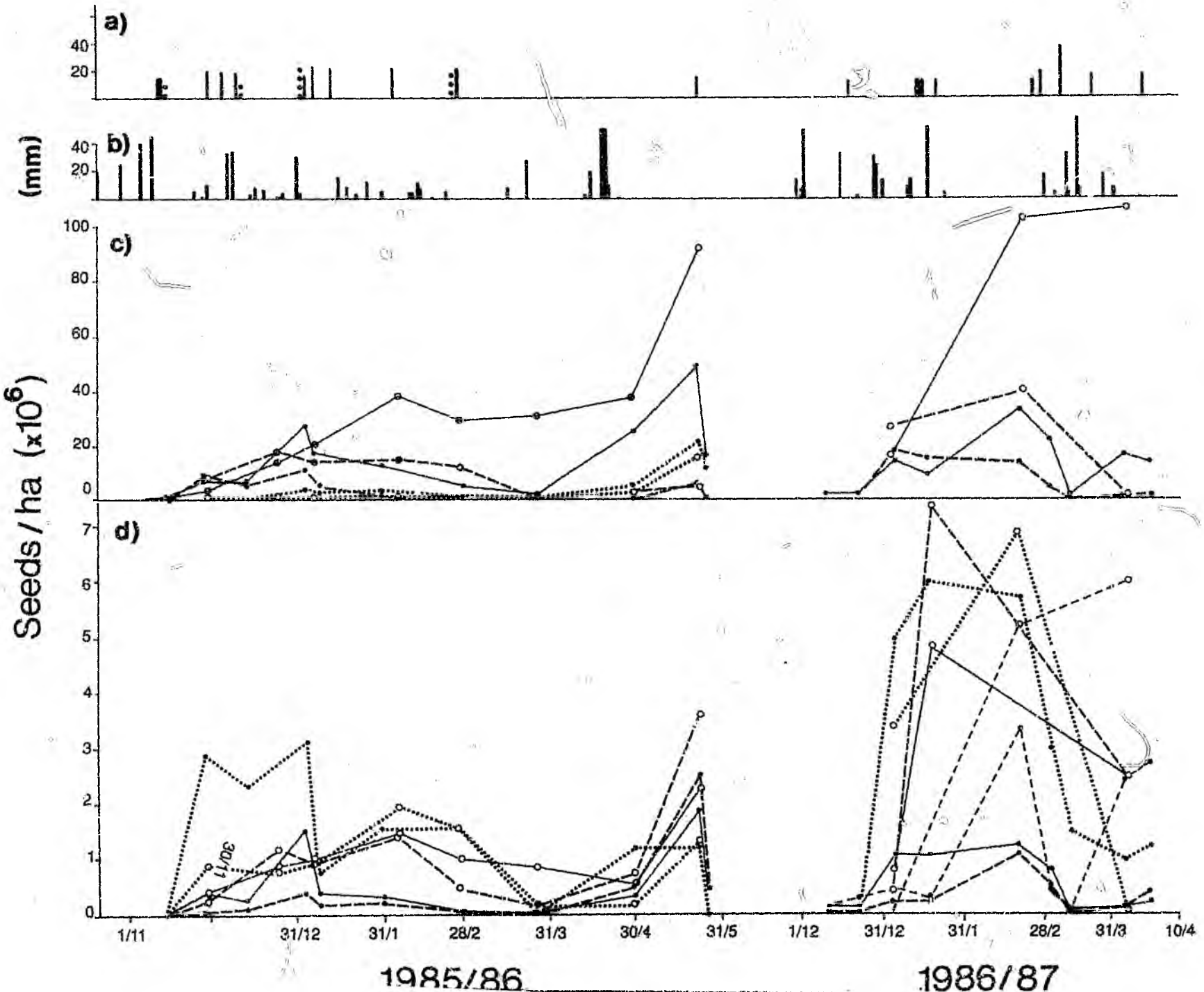

a)
b)
(mm)
40
20
c)
d)
Seeds / ha (x10^6)
100
80
60
40
20
0
7
6
5
4
3
2
1
0
30/11
1/11
31/12
31/1
28/2
31/3
30/4
31/5
1/12
31/12
31/1
28/2
31/3
10/4
1985/86
1986/87

Figure 10.3. The field pattern at Utha of a) grazing (0.95 ha area), b) rainfall, and c) the number of seeds of *Setaria* (____), *Themeda* (----), and *Bothriochloa* (....), for the 1985/86 and 1986/87 growing seasons. The notation is the same as for Figure 10.2.

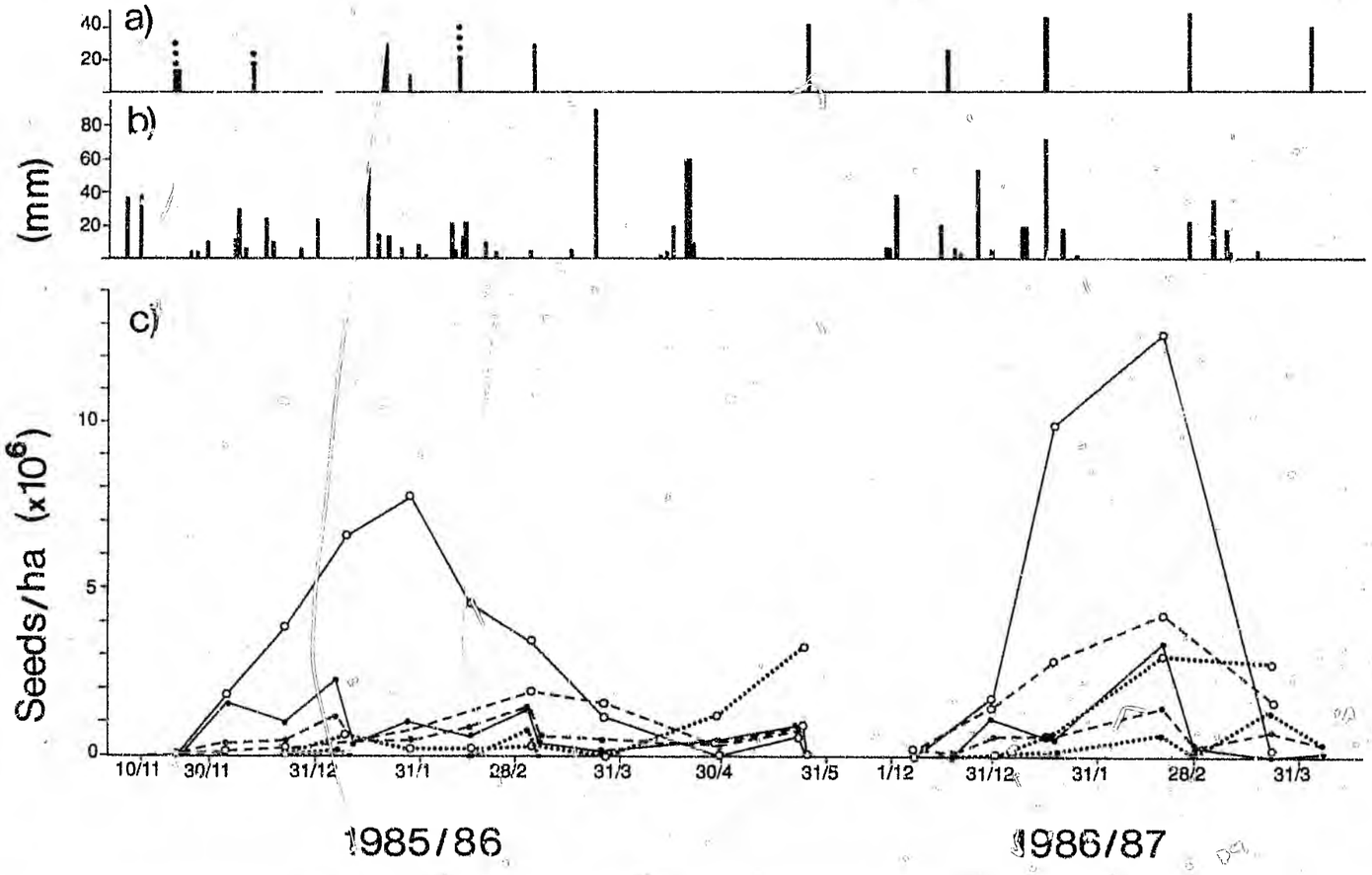

a)
40
20
b)
80
60
40
20
(mm)
c)
10
5
0
Seeds/ha (x10^6)
10/11
30/11
31/12
31/1
28/2
31/3
30/4
31/5
1/12
31/12
31/1
28/2
31/3
1985/86
1986/87

Table 10.1. The reproductive output of the major perennial grass species of Utha (U) and Thlavekisa (T) under both heavy grazing (H) and light grazing (L).

Species	Treatment	Seeds per culm Mean	Seeds per culm Median	Number of culms / m^2 basal area	Number of seeds / m^2 basal area	% Viability[1]
Aristida bipartita	TH	51	45	33336	1696802	30
	TL			38998	1973300	
Bothriochloa insculpta	TH	118	108	3631	428458	19, 43
	TL			7644	901992	
Digitaria eriantha	UH	215	186	288	61920	
	UL	280	271	180	50400	
	TH	210	218	293	61530	
	TL	174	169	441	76734	0, 4
Heteropogon contortus	TH/86	9.4	9	1923	18076	
	TH/87	9.6	10			
	TL/86	8.5	8	5483	52089	33
	TL/87	10.6	10			77
Setaria incrassata	UH	115	109	113	13545	26, 68
	UL	151	154	139	20989	
	TH	186	177	227	42222	
	TL	170	182	414	70380	
Themeda triandra	UH	12.2	9	533	6503	
	UL	12.7	10	1771	22495	19-49
	TH	11.6	9	2024	23478	
	TL	23.4	20	8715	106033	29, 38
Urochloa mosambicensis	TL	116	106	1340	155440	86

[1] pairs of figures denote two samples.

Digitaria and *Bothriochloa* (Figure 10.3). The species order of the number of seeds m^{-2} basal area under light grazing at Thlavekisa is *Aristida*, *Bothriochloa*, *Urochloa*, *Digitaria*, *Themeda*, *Setaria* and *Heteropogon* (Table 10.1). This pattern depends on both the number of seeds per culm and culm density. For example, *Aristida* has the most prolific seed output, but a relatively moderate number of seeds per culm. *Setaria* and *Digitaria* produce the greatest number of seeds per culm. *Heteropogon* and *Themeda* not only have a low number of seeds per culm, but also produce the lowest number of seeds.

Rainfall was higher in 1985/86 than in 1986/87, and the distribution of this rainfall affected seed production. The 1986/87 season was attenuated, but favourable moisture conditions existed for 4 months (Figures 10.2, 10.3). Accordingly peak seed production was attained by early February. Following the short mid-season drought, a second pulse of production, most evident on the heavily grazed plots, occurred for most species as in 1986 (Figures 10.2, 10.3). *Aristida* and *Themeda* responded rapidly to the first major storm of the season, and seed production continued throughout the season if there was sufficient rainfall. Seed production of *Bothriochloa* was bimodal in accordance with the rainfall pattern, but most seed production ocurred towards the end of the season. *Heteropogon* shared this pattern at Thlavekisa in 1985/86, but not in the following year. Most of the seed output of *Setaria* occurred in the first part of the growing season.

The influence of a single grazing event on seed production is dramatic, and grazing markedly lowered the seasonal output of seeds (Figures 10.2, 10.3; Table 10.1). For example, there was a 71% reduction in the number of reproductive culms for all species following grazing at Thlavekisa in May. The seed production figures for grazed treatments are overestimates, because it is assumed that all culms are mature and all seeds borne are ripe, but it takes approximately five weeks from the initiation of a culm

until the first seeds ripen. This is longer than some of the intervals between grazing.

The effects of grazing on seed production are indicated by the ratio of the number of seeds produced per unit basal area for the two treatments (Table 10.1). For example, the ratio for *Themeda* at Thlavekisa is 0.22, indicating the great extent of culm consumption by cattle. This ratio is in favour of lightly than heavily grazed treatments, with the exception of *Digitaria* (Utha) (Table 10.1). Species with a low density of reproductive culms per unit basal area, each culm carrying a large number of seeds, are particularly vulnerable to grazing. The species order from most to least vulnerable (from Table 10.1) is *Digitaria*, *Setaria*, *Urochloa*, *Bothriochloa*, *Themeda*, *Heteropogon* and *Aristida*. That is, the obligate seed reproducers were the least vulnerable.

Seed viability varied markedly between species, between years, and within a growing season (Table 10.1). *Digitaria* produced no viable seeds in 1986, and only 4% in 1987, whereas 33% and 77% of *Heteropogon* seeds were viable in 1986 and 1987 respectively. Seed viability of *Themeda* (24, 29, 42, 49%) and *Setaria* (26, 68%) varied through the 1986/87 growing season, attributed to changes in soil moisture (Figures 10.2, 10.3). More than 90% of the non-viable seeds had failed to form an embryo or an endosperm, <10% had been parasitised (e.g. 4.3% for *Themeda*) or had decayed (e.g. *Heteropogon* 2.6%). Pre-dispersal predation was mainly confined to *Themeda* and *Setaria*, with large seeds. The percentage germinability of five species was 0-10% for seeds < 1 mo old, and 56-87% for seeds approximately one year old (Table 10.2).

Table 10.2. The percentage germinability of freshly collected seed (< 1 mo) and 12 mo old dry stored seed of five grass species (n in parentheses).

Species	< 1 mo	12 mo
Aristida bipartita	10 (115)	84 (184)
Bothriochloa insculpta	<1 (472)	62 (74)
Heteropogon contortus	<1 (109)	87 (189)
Setaria incrassata	0 (256)	-
Themeda triandra	9 (87)	56 (96)

- not tested

Composition of the seed bank

About 90% of the grass seeds occurred within the uppermost 2 (of 5) cm of soil (and litter), although the forb *Phyllanthus maderaspatensis* was more evenly distributed (Table 10.3). Ten grass and at least six forb species were found in the seed bank at Thlavekisa (Table 10.4), while seven species each of grass and forbs occurred at Utha (Table 10.5). Seed densities were 430 seeds m^{-2} on the heavily grazed Utha treatment, 908 seeds m^{-2} on the Utha lightly grazed treatment, 2832 seeds m^{-2} on the Thlavekisa heavily grazed treatment, and 4320 seeds m^{-2} on the Thlavekisa lightly grazed treatment. Perennial grasses constituted 95% and 85% of the Thlavekisa and Utha seed banks respectively.

Table 10.3. The percentage of viable seeds of the predominant species found in the uppermost 2 cm of soil (plus litter) of 24 5 cm deep soil cores, at Thlavekisa (T) and Utha (U), for heavy (H) and light (L) grazing treatments.

Species	TH	TL	UH	UL
Grasses				
Aristida bipartita	93.7	97.0	-	-
Bothriochloa insculpta	86.7	96.6	-	100.0
Digitaria eriantha	75.0	-	-	100.0
Eragrostis superba	82.4	71.7	100.0	-
Heteropogon contortus	84.6	94.3	-	-
Setaria incrassata	90.9	96.0	93.6	85.6
Themeda triandra	90.9	86.4	100.0	95.8
Tragus berteronianus	93.0	-	-	-
Urochloa spp.	90.0	80.0	-	-
Total of grasses	91.2	94.9	95.4	88.7
Forbs				
Cassia mimosoides	100.0	95.2	-	-
Phyllanthus maderaspatensis	86.4	46.2	83.3	60.0

- number of seeds sampled too low for a meaningful figure.

The seed bank densities of the perennial grasses differed significantly ($p<0.0001$) for both the heavily and the lightly grazed treatments at Thlavekisa. *Aristida* dominated the seed bank, and *Setaria* was the second most prominent constituent, in both grazing treatments (Table 10.4). *Bothriochloa* and *Heteropogon* were significantly more prolific on the

lightly grazed treatment than the other four species (Table 10.4). Likewise, at Utha the seed bank densities of the perennial grasses differed ($p<0.0001$) for both the heavily and the lightly grazed treatments. *Setaria* was the principal constituent, and together with *Themeda* accounted for >70% of the seed bank (Table 10.5). *Cassia mimosoides* and *Phyllanthus madaraspatensis* were the only forb species which were well represented in the seed banks of both sites (Tables 10.4, 10.5). Few viable seeds were recovered of the common species of forbs at Utha. No forb refuge species or tree species were found.

Grazing slightly reduces the size of the seed bank. At Thlavekisa, the lightly grazed treatment had more seeds for seven of the eight perennial species (*Urochloa* excluded) (Table 10.4). At Utha, there were more seeds of *Bothriochloa*, *Setaria*, *Themeda* and *Digitaria* in the lightly than heavily grazed treatments (Table 10.5).

Correspondence of seed bank and vegetation

There was a correlation ($p<0.01$) between the abundance of grass species in the vegetation and in the seed bank for the light ($r_s=0.77$) but not for the heavy grazing treatment at Thlavekisa. The grasses of the light grazing treatment at Utha were also correlated with the seed bank ($r_s=0.88$, $p<0.05$). *Setaria* comprised 63% of the basal cover and 68% of the seed bank, and together with *Themeda* and *Bothriochloa* comprised 91% of basal area and 95% of the seed bank. The pattern for the heavily grazed treatment at Utha was similar but not significant. Although *Setaria* and *Themeda* had an equivalent basal area there were four times as many *Setaria* seeds. The correlations between seed production and the seed bank for the heavily grazed treatments at Thlavekisa and Utha, and the lightly

Table 10 4. The contribution of species to the above ground vegetation and their seed bank density (m^{-2}) for Thlavekisa in 1987. Species with the same subscript are not significantly different at the 0.05 level. Species without a subscript were not included in the analysis.

	Heavy grazing			Light grazing		
Species	% of basal area	Viable seeds/ m^2	% of viable seeds	% of basal area	Viable seeds/ m^2	% of viable seeds
Grasses						
Aristida bipartita	9.0	1465a	51.7	10.2	2672a	61.9
Bothriochloa insculpta	4.4	68b	2.4	6.5	262b	6.1
Cymbopogon plurinodis	0	0	0	1.1	0	0
Digitaria eriantha	10.5	36b	1.3	4.7	81c	1.9
Eragrostis superba	4.3	77b	2.7	2.6	208bc	4.8
Heteropogon contortus	14.2	118b	4.2	25.7	158bc	3.7
Setaria incrassata	45.1	448a	15.8	38.3	561b	13.0
Themeda triandra	10.4	50b	1.8	9.9	99bc	2.3
Tragus berteronianus	+	321	11.3	0	41	0.9
Urochloa spp.	2.0	90b	3.2	0.9	45c	1.0
Forbs						
Cassia mimosoides	+	23	0.8	+	95	2.2
Plexipus hederaceus	+	0	0	+	9	0.2
Hibiscus pusillus	+	14	0.5	+	9	0.2
Phyllanthus maderaspatensis	+	99	3.5	+	59	1.4
Tephrosia burchellii	+	9	0.3	+	9	0.2
Indigofera sp.	+	5	0.2	+	0	0
Unidentified	+	9	0.3	+	12	0.3
Total		2832			4320	

Table 10.5. The contribution of species to the above ground vegetation and their seed bank density (m^{-2}) for Utha in 1987. Species with the same subscript are not significantly different at the 0.05 level. Species without a subscript were not included in the analysis.

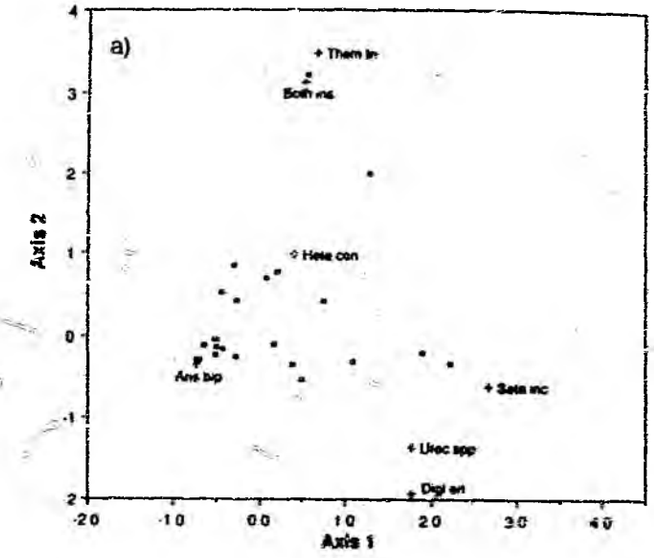
	Heavy grazing			Light grazing		
Species	% of basal area	Viable seeds/ m^2	% of viable seeds	% of basal area	Viable seeds/ m^2	% of viable seeds
Grasses						
Aristida bipartita	0.1	9	2.1	+	18	2.0
Bothriochloa insculpta	0.9	5c	1.2	2.3	99bc	10.9
Digitaria eriantha	7.9	14bc	3.3	8.4	23c	2.5
Eragrostis superba	0.2	27	6.3	0.0	0	0.0
Elionurus muticus	+	9	2.1	+	0	0.0
Heteropogon contortus	9.6	0	0.0	2.7	0	0.0
Setaria incrassata	40.4	235a	54.7	63.2	533a	58.7
Themeda triandra	40.6	81ab	18.8	25.8	109b	12.1
Forbs						
Cassia mimosoides	+	14	3.3	+	32	3.5
Plexipus hederaceus	+	0	0	+	5	0.6
Hibiscus pusillus	+	0	0	+	5	0.6
Phyllanthus maderaspatensis	+	27	6.3	+	45	5.0
Tephrosia burchellii	+	0	0	+	18	2.0
Unidentified	+	9	2.1	+	12	1.3
Total		430			908	

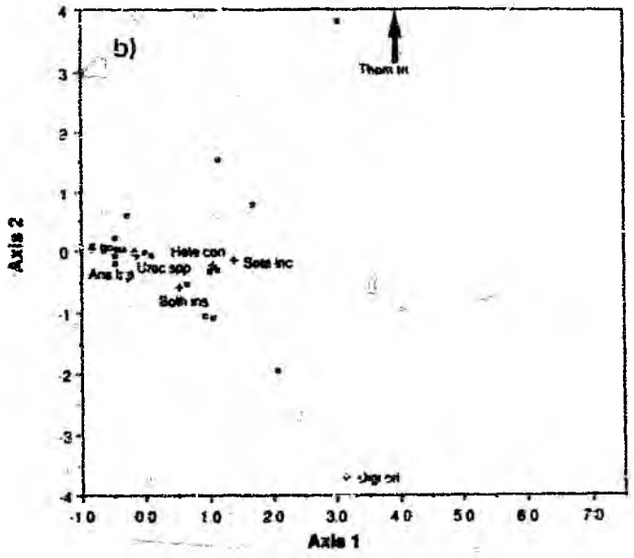
grazed treatment at Utha, were slightly improved, but were still not significant.

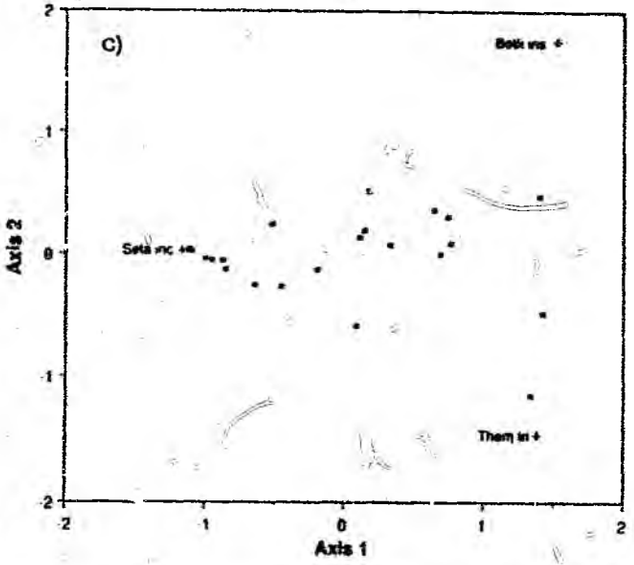
Spatial and community patterns of the seed bank

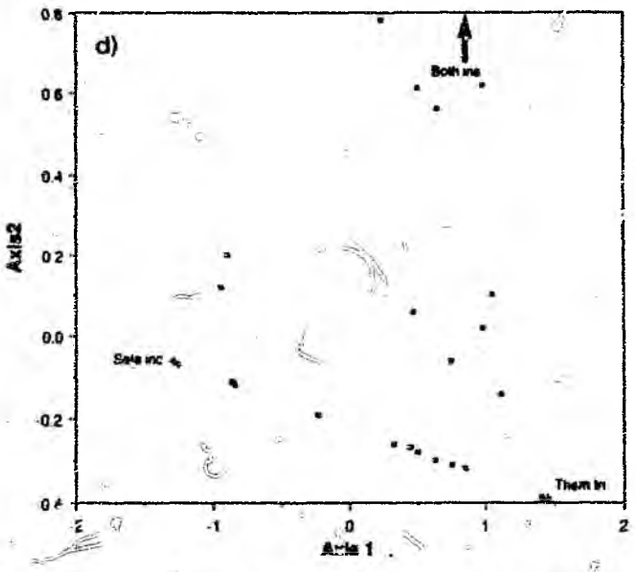
A varying degree of spatial patterning of the seed bank was evident at both sites. At Thlavekisa this was partially disguised by the abundance of *Aristida* in most of the cores (Figures 10.4a, 10.4b). For the lightly grazed plot, the first axis of reciprocal averaging (eigenvalue=0.354) described a gradient from the majority of the cores dominated by *Aristida* and *Heteropogon* through to a few cores with *Setaria* as a predominant compoment. The second axis (eigenvalue=0.191) identified two distinct samples dominated by *Themeda* and *Bothriochloa*. The ordination for the heavily grazed plot principally reflected the range in abundance of *Aristida* (Figure 10.4b). The first axis (eigenvalue=0.387) described a gradient from a large number of cores with a high abundance of *Aristida* through to a few cores with *Setaria* and *Heteropogon* as the predominant components. The second axis (eigenvalue=0.317) distinguished cores on the basis of species other than *Aristida* or *Setaria*. The outlier position of *Themeda* reflected the rarity of this species in the bank. The ordinations of the seed bank at Utha (Figure 10.4c, 10.4d) reflected the spatial patterning of the vegetation. For the heavily grazed plot, the first axis (eigenvalue=0.434) described a gradient from cores dominated by *Setaria* to cores dominated by *Themeda*. while the second axis accounted for a minor amount of variation (eigenvalue=0.076) probably associated with the uncommon species *Bothriochloa*. The first axis (eigenvalue=0.382) of the ordination of the seed bank of the lightly grazed plot described a similar gradient from cores dominated by *Setaria* to cores dominated by *Themeda* and *Bothriochloa*. The second axis

Figure 10.4. The first two axes of the ordination by reciprocal averaging of the composition of the seed bank for a) the lightly grazed treatment at Thlavekisa (eigenvalues: axis 1=0.354, axis 2=0.191), b) the heavily grazed treatment at Thlavekisa (eigenvalues: axis 1=0.387, axis 2=0.317), c) the lightly grazed treatment at Utha (eigenvalues: axis 1=0.382, axis 2=0.095), and d) the heavily grazed treatment at Utha (eigenvalues: axis 1=0.434, axis 2=0.076).


a)
Them in
Both ins
Hete con
Ans bip
Seta inc
Urec spp
Digi ori
Axis 2
Axis 1


b)
Them in
Hete con
Seta inc
Urec spp
Both ins
Axis 2
Axis 1


c)
Both ins
Seta inc
Them in
Axis 2
Axis 1


d)
Both ins
Seta inc
Them in
Axis2
Axis 1

(eigenvalue=0.095) distinguished some small variation due to the predominance of either *Themeda* or *Bothriochloa* in cores dominated by these species.

The number of cores with seeds differed significantly between species for the Thlavekisa lightly grazed treatment (G_{adj}=23.14, n=8, p<0.01), the Thlavekisa heavily grazed treatment (G_{adj}=24.0, n=8, p<0.001), the Utha lightly grazed treatment (G_{adj}=26.9, n=6, p<0.001) and the Utha heavily grazed treatment (G_{adj}=25.5, n=6, p<0.001). The seeds of *Setaria* and *Themeda* were more widespread in both treatments at Utha than any of the other species (Table 10.6). For Thlavekisa, *Aristida* was the most widespread species, *Setaria* was also widely distributed, as was *Bothriochloa* on the lightly grazed plot, *Digitaria*, *Urochloa* and *Eragrostis* were poorly distributed, and the remaining species were moderately distributed, except for *Themeda* on the heavily grazed plot. The differences between species were independent of grazing regime. There were no significant differences between grazing treatments in the number of cores occupied by a species.

The seed banks of most species exhibited some degree of contagion, with the exceptions of *Themeda* on the lightly grazed plot at Utha, and *Bothriochloa* on the heavily grazed plot at Thlavekisa (Table 10.7). *Cassia mimosoides* was randomly dispersed on the lightly grazed plot at Thlavekisa. At Thlavekisa, *Urochloa* spp., *Tragus*, *Eragrostis* and *Digitaria* exhibited pronounced contagion relative to the other species (Table 10.7).

For the heavily grazed Thlavekisa treatment, *Aristida* was significantly negatively associated with *Themeda* (C_s=-1, p<0.01), and was usually positively or negatively, but non-significantly, associated with the other species. *Heteropogon* was positively associated with *Bothriochloa* (C_s=0.45, p<0.05), *Digitaria* (C_s=0.68, p<0.05), and *Setaria* (C_s=1.0,

Table 10.6. The number of cores occupied by seeds of eight species at two sites. Species with the same subscript are not significantly different at the 0.05 level (i.e. comparisons within a column only).

	Thlavekisa		Utha	
Species	Lightly grazed	Heavily grazed	Lightly grazed	Heavily grazed
Aristida bipartita	22a	22a	4bc	2bc
Bothriochloa insculpta	18ab	11abc	7bc	1c
Digitaria eriantha	5c	5c	3bc	3bc
Eragrostis superba	5c	8abc	-	3bc
Heteropogon contortus	11abc	9abc	-	-
Setaria incrassata	16abc	19ab	21a	18a
Themeda triandra	12abc	5c	14b	10ab
Urochloa spp.	7bc	7bc	2c	0

$p<0.05$). On the lightly grazed plot at Thlavekisa, *Bothriochloa* was positively associated with *Setaria* ($C_s=0.5$, $p<0.05$), negatively associated with *Eragrostis* ($C_s=-0.43$, $p<0.05$), and positively correlated with *Themeda* ($r_s=0.67$, $p=0.016$, $n=11$). There were no significant associations or correlations between any of the species at Utha, although *Setaria* and *Themeda* were non-significantly negatively associated ($C_s=-1$) on the lightly grazed treatment.

The relationship between seed density and the vegetation immediately surrounding the sample point varied between species (Table 10.8). There were significant correlations for *Aristida* on all treatments, whereas

Table 10.7. Morisita's (1959 - in Greig-Smith 1983) index of dispersion for the viable seeds of the major grasses for each grazing regime, for both sites.

	Thlavekisa		Utha	
Species	Heavily Grazed	Lightly Grazed	Heavily Grazed	Lightly Grazed
Aristida bipartita	1.79 ***	1.67 ***		
Bothriochloa insculpta	1.14 ns	2.06 ***		
Digitaria eriantha	3.43 *	6.75 ***		
Eragrostis superba	3.18 ***	9.65 ***		
Heteropogon contortus	3.54 ***	2.94 ***		
Setaria incrassata	1.67 ***	2.73 ***	2.96 ***	1.61 ***
Themeda triandra	4.80 ***	1.87 *	1.88 *	1.48 ns
Tragus berteronianus	11.35 ***	3.73 **		
Urochloa spp	5.43 ***	3.20 **		

ns - not significant, * - $p<0.05$, ** - $p<0.01$, *** - $p<0.001$.

Heteropogon showed no relationship, and the other species varied between grazing treatments mainly (Table 10.8).

Table 10.8. The Kendall correlation coefficient between the abundance of the vegetation and the abundance of the seed bank of the major perennial grass species. Refer to the text for an explanation of how the abundance of the vegetation and the seed bank was measured.

	Thlavekisa				Utha			
	Heavily grazed		Lightly grazed		Heavily grazed		Lightly grazed	
Species	r	p	r	p	r	p	r	p
Aristida bipartita	.444	.0037	.591	.0002				
Bothriochloa insculpta	-.076	.6943	.415	.0256	-.079	.7055	.343	.0702
Digitaria eriantha	.805	.0000	.648	.0019	.216	.2681	.187	.3184
Eragrostis superba	.105	.5838	.534	.0081				
Heteropogon contortus	.059	.7269	.287	.1061				
Setaria incrassata	.429	.00	.079	.6507	.297	.0689	.166	.2796
Themeda triandra	.291	.1065	.428	.0241	.246	.1426	.300	.0824
Urochloa spp.	.034	.8603	.326	.1285				

Modelling of seed bank dynamics

The seed output for a benign and a severe scenario for both heavy and light grazing is shown, and the differences between species are stark (Table 10.9). For the heavily grazed scenarios the relationship between the species is *Aristida* >> (a lot greater than) *Bothriochloa* >> *Urochloa* >> *Digitaria* >> *Heteropogon* >> *Themeda* = *Setaria*. For the lightly grazed

scenarios *Themeda* is ranked fourth after *Urochloa*. The decrease in seed production with heavy grazing for either the benign or severe scenarios (Table 10.9) indicates that the effect of heavy grazing on culm production is far more deleterious for the seed production of *Setaria* and *Themeda* than of *Aristida* or *Bothriochloa*.

DISCUSSION

Comparison with other grasslands

The largest number of seeds produced, 18 000 seeds m^{-2}, was on the lightly grazed Thlavekisa site, which is comparable with the 19 700 seeds m^{-2} estimated for a Missouri prairie (Rabinowitz & Rapp 1980). The sizes of the seed banks sampled in this study (430 to 4320 seeds m^{-2}) are of the same order of magnitude as prairie grasslands in Illinois (2019 seeds m^{-2} - Johnson & Anderson 1986), Alberta (204 to 12 342 m^{-2} - Jonnston *et al*. 1969), Missouri (6470 m^{-2} - Rabinowitz 1981), and British pastures (1400 to 3600 m^{-2} - Howe & Chancellor 1983).

Factors influencing the seed bank

The influence of rainfall on the reproductive output of semi-arid or mesic perennial grasslands is characteristic (Weaver & Mueller 1942; Brown 1943; Cornelius 1950; Knapp 1984; Dye & Walker 1987). The within season

Table 10.9 The simulated size of the seed bank ($x10^6$ ha^{-1}) of the perennial grasses of this study for various parameter values. The high and low number of culms reflect site derived values for lightly and heavily grazed conditions respectively. The maximum size of the seed bank assumes 100% viability, and no predation, germination or decay. The low size of the seed bank assumes 5% viability, 95% predation, 90% germinability and 90% decay. All computations are for populations which constitute 50% of a total basal cover of 8% (approximate site value).

	Number of culms/m^2		Maximum size of seed bank		Low size of seed bank	
Species	High	Low	High	Low	High	Low
Aristida bipartita	40000	20000	1632	816	20.4	4.1
iochloa insculpta	8000	4000	755	378	9.4	1.9
taria eriantha	500	200	70	28	0.7	0.1
Heteropogon contortus	5500	2000	40	14	0.4	0.1
Setaria incrassata	400	50	37	5	0.1	
Themeda triandra	9000	500	86	5	0.1	
Urochloa mosambicensis	1300	600	121	56	1.4	0.2

range in seed viability (Table 10.1) was possibly a result of the influence of the intra-seasonal pattern of rainfall. For the grasses of Kansas, the rainfall in the period preceding and following flowering was an important influence on seed production (Cornelius 1950). Sustained grazing during the growing season has commonly resulted in the near total consumption of infloresences (Brown 1943; Tainton & Booysen 1964; Ambasht & Maurya 1970; Rethman *et al.* 1971). *Aristida* maintained relatively

prolific seed production under grazing, while the seed production of the more palatable, long-lived species *Themeda*, *Setaria* and *Heteropogon*, diminished greatly (Figures 10.2, 10.3). *Themeda* had one of the lowest reproductive capacities (seventeen seeds a plant and 0% viability) of twenty species in a South African grassland (Jones 1968). High levels of pre-dispersal infestation of seeds were not found, but have been recorded for *Themeda* (Lock & Milburn 1970).

The reduction in the seed bank of grasses by grazing (Tables 10.4, 10.5) was also reported for Alberta prairies (Johnston *et al.* 1969). There was not a marked difference between grazing treatments in the size of the seed banks of individual species after two years of heavy grazing (Tables 10.4, 10.5), although grazing had a pronounced impact on seed production (Figures 10.2, 10.3). The extremely high levels of post-dispersal seed predation - up to 90% within five days (Capon & O'Connor 1990) - may have reduced the difference in seed density between treatments.

The age structure of the seed population will be regulated by dormancy mechanisms. All species tested had a period of innate dormancy (Table 10.2), characteristic of grasses in a seasonal rainfall environment (Lock & Milburn 1970; Mott 1978; Brown 1982; Hacker 1984; Frasier *et al.* 1987; Hacker & Radcliff 1989). This is generally interpreted as an adaptive germination mechanism to ensure the survival of the seed through the inhospitable dry season (Angevine & Chabot 1979). A major deficiency in the current understanding of the dynamics of savanna grass seed banks is the fate of seeds when released from plants, specifically the proportion readily germinable or incorporated into the bank. Most grass seeds appear to germinate readily once a period of innate dormancy is past, or have a limited intrinsic capacity for survival if in a state of secondary dormancy (Coukos 1944; Madsen 1962; Winkworth 1963; Lock & Milburn 1970; Williams 1983), because most succumb through germination while buried too deep to emerge (Schafer & Chilcote 1967). The prevalence of induced

dormancy mechanisms in these species is unknown, but the light requirement of some species (e.g. *Themeda* - Lock & Milburn 1970) suggests enforced dormancy may be operative. Seed longevity depends on the intrinsic capacity for survival of the seed, while in a state of induced or enforced dormancy.

The composition of the grass seed bank was partly correlated with the composition of the vegetation, in contrast to many grasslands (e.g. Thompson & Grime 1979). There were no refuge or ruderal dicotyledenous species in the seed bank, as is often found in many grasslands (e.g. Weaver & Mueller 1942). The only refuge species were the annual grasses *Tragus berteronianus* and *Urochloa* sp., both commonly associated with heavily grazed areas. The seed banks of the perennial grasses of this study are most similar to the Type II transient seed bank (Thompson & Grime 1979), in which winter dormancy is followed by germination, except that a proportion of these seeds are >1 year old, and the species possess large seeds often with elongated structures and long awns. These tropical species are best described as possessing 'delayed' transient seed banks to accommodate the extended period of innate dormancy. The annual grasses and the annual legume *Cassia mimosoides* undoubtedly form persistent seed banks.

There are definite patterns of compositional variation within the seed bank (Figure 10.4), with marked contagion of nearly all species (Table 10.7), and in some cases significant co-occurrence of species. These patterns are partly caused by the influence of the surrounding vegetation on the seed bank of a point sample (Table 10.8). Seed banks will therefore play some role in the maintenance of spatial pattern in the established vegetation. The well-defined two-phase vegetation mosaic on the lightly grazed treatment at Utha (Carter & O'Connor 1991) corresponds with a similar pattern of dispersion and association in the seed bank.

Implications for vegetation dynamics

The modelling of seed bank dynamics illustrates that the size of the seed bank of perennial grasses is primarily dependent on the amount of seed produced in the prior growing season, because seeds do not survive for longer than two years. Seed production depends on the abundance of the species in the established vegetation. If the population is halved, the seed bank is halved. Halving the number of culms per unit basal area (e.g. heavy grazing) will halve the seed output, but this may be partially compensated by an increase in the number of seeds per culm (see *Themeda* in Table 10.1). If no seeds ripen (e.g. mid-season drought) then the seed bank is a function of the proportion of seeds transferred from the previous growing season, which is a combination of the proportion not predated in the dry season, or not germinating or decaying in the growing season.

What is the role of the seed bank in the response of these species to heavy grazing? In Chapter 2 I defined an extinction prone perennial grass which is a palatable, obligate seed reproducer, which characteristically produces smaller numbers of larger seeds, with limited dispersal capabilities. Such a species can become locally extinct in a temporally varying rainfall environment if the established population is eliminated during a drought period in conjunction with heavy grazing. If this happens there will be rapid attrition of the seed bank, because there is no seed production *in situ*, the seeds present last only two to three years, and dispersal is poor.

Examples from this study are *Themeda* and *Heteropogon*; obligate seed reproducers which produce a low number (Table 10.1, Figures 10.3, 10.4) of larger seeds (Capon & O'Connor 1990). Corroboration of this model was provided by a gradient study of areas with a lenient to a severe grazing

history (Pickett 1987). Sustained heavy grazing had eliminated *Themeda* and *Heteropogon* from both the established vegetation and the seed bank. In contrast, the abundance of the unpalatable *Aristida* increased along this gradient, and also increased on the heavily but not the lightly grazed plots of this study (Chapter 6). This increase is partly due to the prolific seed production of the species even under heavy grazing (Figure 10.2, Table 10.1), and its consequent representation in the seed bank (Tables 10.4, 10.5). The prolific seed production of *Aristida* species is considered to promote its invasiveness in Australian rangelands (Harradine & Whalley 1980; Brown 1985). Although *Digitaria* produced little viable seed (Table 10.1, Figures 10.2, 10.3) and was poorly represented in the seed bank (Tables 10.4, 10.5), *D. eriantha* var *pentzii* at Utha could, under heavy grazing, successfully colonise bare patches because of extensive recruitment from stoloniferous growth (Chapter 110). The compact rhizomes of *D. eriantha* var *eriantha* (at Thlavekisa) afford protection from grazing, but there was no recruitment (Chapter 7). *Setaria* has an extensive rhizome system (Carter & O'Connor 1991) which allows clonal expansion, but was also well represented in the seed bank (Tables 10.4, 10.5) and emergence of seedlings occurred (Chapter 7). Thus the array of growth strategies in this assemblage determines the response to heavy grazing, but the availability of seed is of paramount importance for at least three of the species.

SUMMARY

The influence of sustained heavy grazing by cattle on the seed production, and consequent species representation in the seed bank, of the major perennial grasses of two mesic savanna grasslands was studied for two growing seasons. The potential reproductive output of each species was

estimated by monitoring the density and size of tufts, the number of reproductive culms of tufts of known sizes, the number of seeds produced per culm, and the percentage viability of seeds. The density of viable seeds in the seed bank was determined from microscopic examination of soil cores. The pattern of production of reproductive culms varied within and between seasons in accordance with rainfall patterns. Intra-seasonal drought decreased seed production. The seeds produced m^{-2} of tuft basal area (assuming 100% viability) ranged from 21000 for *Setaria* to 1.9 million for *Aristida*. Annual seed output ha^{-1} ($x10^6$) under light grazing at Thlavekisa was <4 for *Themeda* and *Heteropogon*, 40 for *Setaria*, and >100 for *Aristida*. At Utha, annual seed output ha^{-1} ($x10^6$) under light grazing was 3 for *Bothriochloa*, 4 for *Themeda* and 13 for *Setaria*. Grazing decreased reproductive output by up to 70%, but *Aristida* maintained high levels of seed production. Seed viability varied from zero for *Digitaria* to 68% for *Setaria*. Seed viability varied within a season for *Themeda* (24-65%) and *Setaria* (26-68%). The seeds of all species tested possessed a period of innate dormancy of <12 mo.

Ten grass and at least six forb species were found in the seed bank at Thlavekisa, while seven species each of grass and forbs occurred at Utha. Perennial grasses constituted 95% and 85% of the seed bank at Thlavekisa and Utha respectively, with >90% of all seeds occurring in the top 2 (of 5) cm of soil. Seed density differed markedly between sites and grazing treatments; heavily grazed Utha site (430 m^{-2}), lightly grazed Utha site (908 m^{-2}), heavily grazed Thlavekisa site (2832 m^{-2}), lightly grazed Thlavekisa site (4320 m^{-2}). The predominant components of the seed bank of the heavily and lightly grazed treatments respectively for Thlavekisa were *Aristida* (52%, 62%) and *Setaria* (16%, 13%); and for Utha were *Setaria* (55%, 59%) and *Themeda* (19%, 12%). Grazing slightly reduced the seed density of perennial grasses. The seeds of most species showed some degree of contagion. The Thlavekisa samples displayed a gradient from cores predominated by *Aristida bipartita* through to cores with high

numbers of *Setaria incrassata*. At Utha, there was a gradient with cores of predominantly *Setaria* or *Themeda*, which corresponded with a pronounced two-phase vegetation mosaic. There was some correlation between the abundance of the perennial grasses in the seed bank with their abundance in the vegetation.

A model of the seed bank dynamics of perennial grasses illustrates that, because seeds germinate readily and have a limited intrinsic capacity for survival, the size of the seed bank is determined primarily by the abundance of the species in the vegetation. Thus the seed bank of species which produce low amounts of larger seeds (*Themeda*, *Heteropogon*) can easily be eliminated by sustained grazing.

CHAPTER 11

PATCH COLONISATION IN A SAVANNA GRASSLAND

INTRODUCTION

The factors which influence the species which will come to occupy available space include the availability of propagules (vegetative or seed), dormancy mechanisms germination and seedling establishment conditions (Grubb 1977), and species may differ in their response to these factors. For example, species in a grassland community usually have different growth forms (e.g. Silva & Ataroff 1985), the abundance of species in the seed bank often corresponds poorly with their abundance in the vegetation (Thompson & Grime 1979 and references therein), different dormancy mechanisms can be operative (Harper 1977), differential germination responses between species can occur in response to different levels of the same environmental factor (e.g. soil moisture - Watt 1982). In addition, light (Harper 1977; Angevine & Chabot 1979) and substrate conditions (litter cover - Werner 1975; Fowler 1986b, 1988) can influence germination and seedling establishment, while heavy grazing can also prevent seedling establishment (Wright & van Dyne 1976, Salihi & Norton 1987).

The objective of this part of the study was to examine the influence of heavy grazing by cattle and litter cover on the plant colonisers of available patches in a savanna grassland whose species exhibited a diversity of growth patterns.

METHODS

The experiment was conducted at the Utha site. At 12 randomly located locations in each grazing treatment, a pair of 1 m diameter circular areas (2 m apart) were cleared of all living vegetation before the 1985/86 wet season. Dicotyledons and the crowns of grass tufts were cut at ground level, keeping soil disturbance to a minimum. However, regeneration from rhizomes of *Setaria* necessitated a second clearing before the 1986/87 wet season. Some soil disturbance was necessary for the extraction of *Setaria* rhizomes. Thereafter the cleared circles were monitored closely to ensure that no further regeneration from rhizomes occurred (the pattern of growth is easily distinguished from seedling growth), but growth into the patch from the outside (e.g. by *Setaria* rhizomes or *Digitaria* stolons) was not prevented. One circle of each pair was randomly assigned a litter cover of 1-cm thick stem and leaf material of grasses (devoid of seeds), harvested nearby; this was placed over the cleared circle at the beginning of the 1986/87 wet season, and thereafter not removed. The cover of litter remaining after the first season was 57% on the heavily and 71% on the lightly grazed treatment. The open circles were bare. The four treatments are hereafter referred to as HL - heavily grazed with litter cover, HO - heavily grazed without litter cover, LL - lightly grazed with litter cover, and LO - lightly grazed without litter cover.

The circles were monitored for three seasons. Only a diameter of 0.6 m was monitored, to minimise the edge effect of standing vegetation. All individuals alive at the end of each growing season were tagged and charted, and the basal circumference measured (in cm). Each rooted node of stolons of *Digitaria* growing into the patch was counted as an individual. Density is defined as all apparently physiologically independent individuals, and includes both seedlings and ramets. In the 1986/87 season, all emergent seedlings following most major rainfall

events were marked with coloured pins. A cohort of seedlings is defined as all new seedlings present at the time of monitoring. The establishment phase commences when the plant begins to assimilate external reserves, and ceases for present purposes at the end of the first growing season.

The composition of the vegetation in a radius of 0.5 m surrounding each circle was described by ranking the aerial cover of each species (Walker 1976). The surrounding vegetation of each grazing treatment was described by the permanently located quadrats. Because the experiment was initiated two seasons after grazing treatments were initiated, the leaf height, aerial cover and proportion of moribund material (Walker 1976) of the grazing treatments differed at the start of the experiment (Table 11.1).

Analysis

Correspondence analysis, with detrending by 3rd order polynomials (ter Braak 1988) was used to summarise the compositional differences (by basal area - $\log_e(x+1)$ transformed) that had arisen between the 48 circles by the last year monitored. Species which occurred only once or twice were deleted. The patch scores of the first three ordination axes were entered into a classificatory discriminant analysis to identify distinct patch types. Differences between patch types on each axis were separately tested with one-way ANOVA, with Tukey's studentised range test for differences between means. The analysis of changes in total basal area or total density were based on untransformed values, because these met assumptions of normality (unless otherwise indicated). Even after transformation, the basal areas of individual species did not meet the assumption of normality.

Table 11.1. The number of cattle grazing days and the number of grazing events (in parenthesis) per growing season, for the heavily (0.95 ha) and the lightly (0.85 ha) grazed treatments, the annual (July to June) rainfall, and the structure of the vegetation (mean ±1 S.E.) at the start of the experiment (1986/87).

	Grazing days (events)		
	Heavily grazed	Lightly grazed	Rainfall (mm)
Season			
1984/85	224 (4)	85 (3)	665
1985/86	196 (7)	47 (3)	768
1986/87	168 (5)	35 (1)	438
1987/88	255 (6)	24 (1)	663
1988/89	n.r.	0	400
Vegetation structure			
Leaf height (cm)	37 ±2.9	36 ±3.5	
Aerial cover (%)	35 ±0.8	69 ±2.0	
Moribund grass (%)	10 ±0.8	24 ±3.3	

n.r. - not recorded

The dependence of the colonisation success of a species on the abundance of the species in the adjacent vegetation was e[illegible]ed with Hurlbert's (1969) coefficient of association, because of th[illegible] large number of zero values of the abundance of most species in the adjacent vegetation. There

is an increased probability of a Type I error resulting from 24 different *a posteriori* tests of association, which has an upper bound of p=0.7. The coefficient cannot be used if the frequency of a species in either the vegetation or the patches is zero or approaches unity, and Kendall's tau correlation coefficient for species which occurred in both the circle and the vegetation for n>6 was also used. A Komolgorov-Smirnov goodness of fit test examined whether the proportional contribution to the basal area of patches by each species (for each treatment) accorded with their proportional contribution to the basal area of the surrounding vegetation.

The proportional establishment of grass and forb seedlings for the litter and open patches of the heavily grazed treatment was examined with a two-way ANOVA (arcsine transformed data). The lightly grazed treatment was not tested because no grass seedlings established on open patches.

RESULTS

Compositional change

Correspondence analysis summarised the compositional differences between the 48 patches which existed at the end of the third year. The eigenvalues of the first three axes were 0.586, 0.426 and 0.287. There were differences between patch types on the first axis (F=3.19, p=0.033), due to a difference between the HO and LL patches, but there were no significant differences on the second or third axes. The classificatory discriminant analysis also showed that the HO and LL patches were the most

dissimilar, while the LL and HL patches were the most similar (Table 11.2). But overall the patches classified poorly, with, for each group of twelve, only eight of the HO, seven of the LL, four of the LO, and two of the HL correctly classified. The first axis describes a gradient from patches predominated by *Aristida* and *Digitaria*, through patches predominated by *Themeda*, to patches predominated by *Setaria* (Figure 11.1). The second axis describes a gradient from patches with *Heteropogon* as a major constituent through to patches with the perennial forb *Chaetacanthus burchellii* as a prominent species. The range for patches of the first axis is 4 s.d., and of the second axis 5 s.d., indicating that patches from the ends of these axes had almost no species in common.

Eight of 12 HO patches form a major part of the grouping associated with *Aristida* and *Digitaria*, and are partly separated from the HL patches. Many of these are associated with *Themeda*, with a gradation to patches associated with *Digitaria* and *Aristida*. Many of the LL patches are associated with *Setaria* or *Themeda*, while LO patches are scattered across the ordination (Figure 11.1). The third and fourth axes displayed no clear pattern.

Relationship of patches to surrounding vegetation

There was a positive association ($p<0.05$) between the presence of a species on a patch and its presence in the surrounding vegetation for *Aristida* (HL, LL and LO treatments), *Digitaria* (HO and LL treatments), *Heteropogon* (HL and LL treatments) and *Themeda* (LL treatment). When the number of patches occupied by a species is compared with the presence of the species in the vegetation (Table 11.3), *Themeda* and *Setaria* tended to have greater colonisation success on patches with litter cover. Of

Table 11.2. The generalised square distance between four treatments of a classificatory discriminant analysis; (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter).

	HO	LL	LO
HL	0.89	0.11	0.29
HO	0.00	1.41	1.21
LL	____	0.00	0.36

the five instances (for n>6) tested, only *Themeda* on the HL treatment had a correlation (Kendall tau B = 0.485, p=0.044, n=12) between cover of the patch and the surrounding vegetation.

Treatment effects

The extent of change of total basal cover and density on the HL treatment over three years was 3-10 times that of the other treatments (Figure 11.2). The cover of the HL treatment was higher than the cover of the HO treatment after three years (t=3.7418, p=0.0011, untransformed data), and there was a tendency for a higher cover on the LL than on the LO treatment (t=1.9277, p=0.067, $\log_e(x+1)$ transformed data). Similarly the density of the HL treatment was significantly higher than the density of the HO treatment (t=2.6146, p=0.0158, square root (x+0.5) transform -

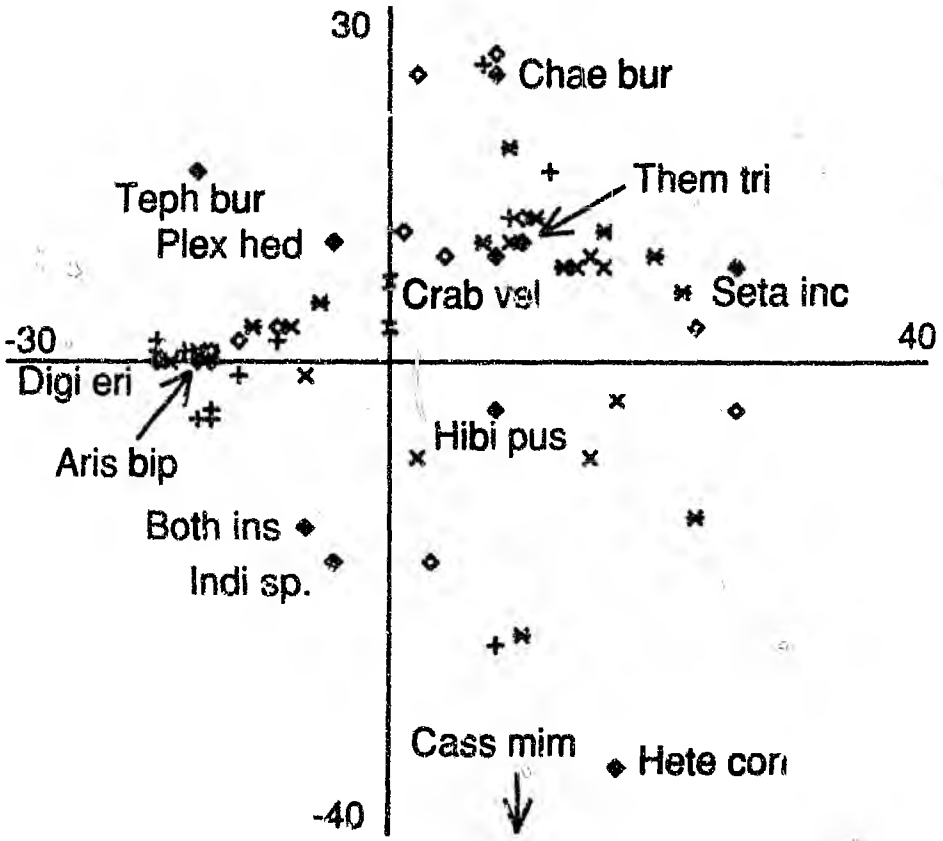


Figure 11.1. A joint plot of the patches and species of the detrended correspondence analysis of the 48 individual patches; 12 patches each of the HL(X), HO (+), LL (*) and LO (◇) treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter). Eigenvalues; axis 1 = 0.586, axis 2 = 0.426. Species (◆) abbreviations are: Aris bip = *Aristida bipartita*; Both ins = Bothriochloa insculpta; Cass mim = *Cassia mimosoides* ; Chae bur = *Chaetacanthus burchellii*; Crab vel = *Crabbea velutina*; Digi eri = *Digitaria eriantha*; Hete con = *Heteropogon contortus*; Hibi pus = *Hibiscus pusillus*; Indi sp. = *Indigofera* species; Plex hed = *Plexipus hederaceus*; Seta inc = *Setaria incrassata*, Teph bur = *Tephrosia burchellii*; Them tri = *Themeda triandra*.

Table 11.3. The frequency of occurrence of the major perennial grasses in 12 cleared patches after three years of colonisation, and in the immediately adjacent vegetation of 0.5 m radius of the patch (in parenthesis), for four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter).

Species	HL	HO	LL	LO
Aristida bipartita	6 (3)	4 (3)	4 (4)	4 (3)
Bothriochloa insculpta	3 (9)	6 (10)	1 (4)	0 (5)
Digitaria eriantha	7 (10)	8 (10)	4 (6)	3 (7)
Heteropogon contortus	3 (3)	1 (4)	2 (3)	1 (2)
Setaria incrassata	8 (7)	2 (10)	7 (10)	4 (11)
Themeda triandra	12 (12)	2 (12)	8 (10)	6 (11)

Sokal & Rohlf 1981, p421), but there was no difference ($p>0.05$) between the LL and LO treatments. The basal area/m^2 of colonising individuals of the HL treatment was lower than the basal area of the surrounding vegetation ($t=3.7057$, $df=25$, $p=0.001$, untransformed data), and similarly for the LL treatment ($t=6.8893$, $df=25$, $p=0.0001$, $\log_e(x+1)$ transformed data).

Total basal cover after the first season of colonisation ranged from 5.84 cm^2m^{-2} (HL) to 0.46 cm^2m^{-2} (LO). The poor establishment in the first year (1986/1987) was attributed to the poor rainfall season (Table 11.1). The increase in cover between the first and second seasons was associated with an increase in total density (Figure 11.2b). The favourable rainfall season of 1987/88 is considered responsible for the successful establishment in this season. The rainfall of the final season monitored

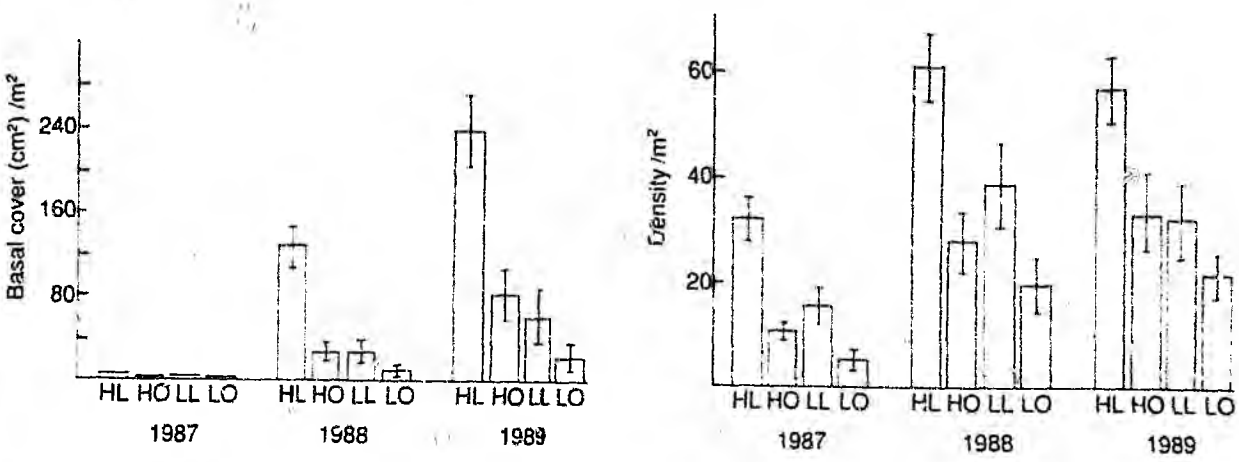


Figure 11.2. The mean basal cover and the mean density (of all individuals collectively) per m^2 at the end of the growing season over three years for each of the four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter). Vertical bars represent ± 1 S.E. (data untransformed).

(1988/1989) was low, and there was limited new establishment, but established individuals expanded further, hence there was an increase in cover but only a slight increase in density.

The changes in the basal cover of *Aristida*, *Digitaria* and *Themeda* in part reflect the changes in total basal cover (Figure 11.3). *Aristida* was absent from the HL and LO treatments in the first season, but had established on all treatments by the second season, and expanded substantially in the third season. *Digitaria* established on all

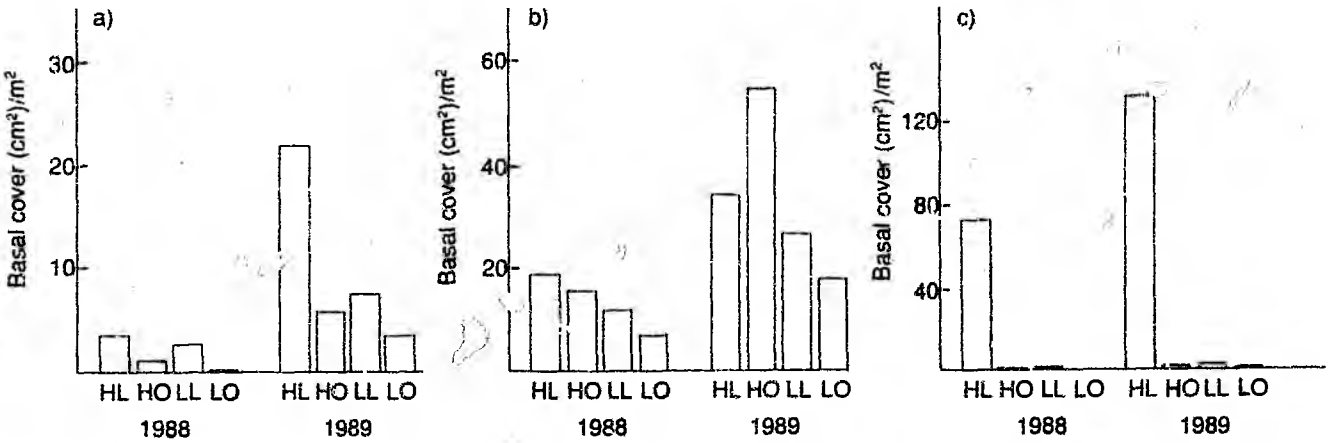


Figure 11.3. The changes over two years in the mean basal cover per m^2 of a) *Aristida bipartita*, b) *Digitaria eriantha* and c) *Themeda triandra*; for four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter).

treatments in the first season, and substantially colonised each of these by the third year. *Themeda* successfully colonised the HL treatment, but only marginally established on the other treatments.

The changes in total basal cover were accompanied by a change in the proportional contribution by each species (Table 11.4). *Digitaria* formed 10% and 30% of the basal cover of the HO and LO treatments respectively in the first year, but this increased to 67% and 72% by the third year. The proportional contribution to cover by *Aristida* increased from <2% in the first year to between 7-16% in the third year. Forbs were a major

component of each treatment in the first year, contributing from 14% to 70% of basal cover, but their contribution declined dramatically as grasses established (Table 11.4).

The proportional representation of grass species within the patch communities in 1989 was different ($p<0.05$) to their representation within the surrounding vegetation (Table 11.5), but the pattern was generally consistent over all treatments (Table 11.4). *Aristida* and *Heteropogon* were absent or sparse in the sampled surrounding vegetation, but *Aristida* and *Heteropogon* established well on all patches (except *Heteropogon* on the LO patches). The basal cover of *Digitaria* on patches was well in excess of its proportion in the surrounding vegetation, while the cover of *Setaria* and *Themeda* (except on HL treatment) on patches was far less than their representation in the surrounding vegetation.

Population Basis Of Compositional Change

Seedling dynamics

A far higher density of grass and forb seedlings emerged on patches with litter, with the highest number on the HL treatment (Figure 11.4). The number of grass, but not forb, seedlings establishing in the first season maintained this pattern. There was a tendency for a higher proportional establishment of forbs on open patches (interaction effect of litter cover and plant group - $F=3.88$, $df=1$, $p=0.055$).

Table 11.4. The percentage contribution of the common grasses and herbaceous dicotyledons to the total basal area of the vegetation of the cleared circles and of the surrounding vegetation for the three growing seasons monitored, for four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter).

	HL			HO			Surrounding vegetation heavily grazed			LL			LO			Surrounding vegetation lightly grazed		
	87	88	89	87	88	89	87	88	89	87	88	89	87	88	89	87	88	89
Grasses																		
Aristida bipartita	0	3	9	2	4	7	<1	<1	<1	1	10	13	0	3	16	0	0	0
Bothriochloa insculpta	4	2	3	0	4	7	<1	<1	<1	4	1	0	0	0	0	2	2	<1
Digitaria eriantha	6	15	14	10	60	67	8	12	13	39	45	44	30	88	72	8	9	11
Heteropogon contortus	13	13	10	26	25	14	10	8	6	11	30	27	0	0	1	<1	<1	<1
Setaria incrassata	9	7	7	0	0	<1	40	26	28	13	4	8	0	<1	3	63	62	66
Themeda triandra	54	59	56	20	4	3	41	55	52	10	6	5	0	3	5	26	27	21
Total grasses	86	99	99	57	97	99	99	99	99	77	97	97	30	94	97	99	99	99
Forbs																		
Chaetacanthus burchellii	<1	<1	<1	2	<1	<1	<1	<1	<1	5	2	2	10	2	1	<1	<1	<1
Crabbea velutina	2	<1	<1	0	<1	<1	<1	<1	<1	7	1	1	10	<1	0	<1	<1	<1
Hibiscus pusillus	2	<1	<1	25	1	<1	<1	<1	<1	2	<1	<1	0	<1	<1	<1	<1	<1
Plexipus hederaceus	<1	<1	<1	11	1	<1	<1	<1	<1	2	<1	<1	20	1	1	<1	<1	<1
Total forbs	14	1	1	43	3	1	<1	<1	1	23	3	3	70	6	3	<1	<1	<1

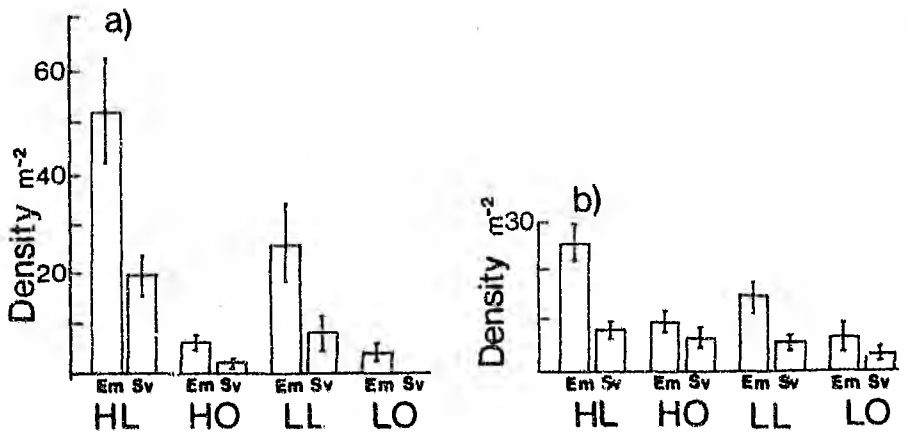


Figure 11.4. The total number of a) grass and b) forb seedlings emerging (Em) in the 1986/87 season and surviving (Sv) until May 1987, for the four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter). Vertical bars represent ± 1 S.E. (data untransformed).

The majority of grass and forb seedlings emerged in two cohorts at the beginning of the wet season (Figure 11.5). There was initially ca. 50% mortality of grass seedlings, but mortality thereafter was low. There were no prominent refuge species which appeared, only a few individuals of *Tragus berteronianus* and *Urochloa* cf. *trichopus*, annual grasses characteristic of disturbed sites, germinated. The common dicotyledons species, which are listed in Table 11.3 (uncommon species are not shown), established successfully.

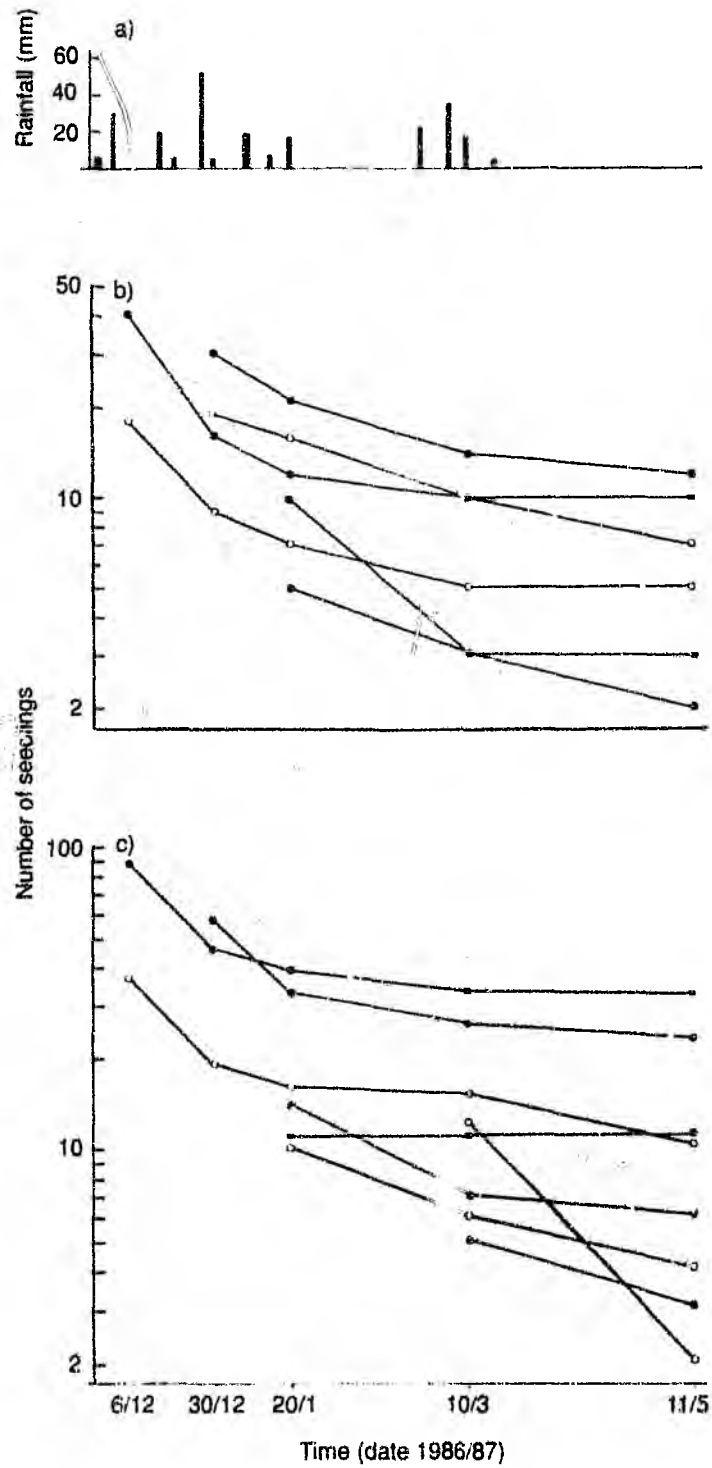


Figure 11.5. The pattern through the 1986/87 season of a) rainfall, and of seedling survival of the seedling cohorts (defined in text) of all grasses combined (closed circles) and all forbs combined (open circles) for b) litter cover and lightly grazed and c) litter cover and heavily grazed treatments. Values represent the total number of seedlings for all patches (n=12) of each treatment.

Establishment and subsequent survival

The number of individuals which established in any one year, and survived in following years, varied both between years for each species and between species within a year (Table 11.5). The consistent direction of differences between years for each of the major species across treatments suggests the importance of rainfall for establishment success, although patterns differ between species. *Setaria*, *Themeda*, *Heteropogon* and *Hibiscus pusillus* established comparatively well in 1986/87, while *Aristida*, *Digitaria* and *Bothriochloa* established well during the high rainfall season of 1987/88, with further establishment success of *Setaria* and *Themeda*.

The grazing and litter treatments influenced the establishment and survival patterns of individual species (Table 11.5). *Aristida*, *Heteropogon*, *Setaria*, *Themeda*, and the forbs *Plexipus hederaceus* and *Crabbea velutina*, fared well on patches with litter cover compared to patches without litter, for both grazing treatments. However, the proportion of *Setaria* and *Themeda* individuals surviving on litter patches was higher for the heavily than the lightly grazed treatment. *Heteropogon*, *Setaria* and *Themeda* had poor establishment and survival on the patches without litter, but this effect was not apparent for *Aristida*.

Only six (of 140) of the *Digitaria* individuals which established germinated from seed, the remainder grew from nodes of stolons in contact with the soil surface which rooted. The source of *Digitaria* stolons were established individuals in the surrounding vegetation. *Digitaria* tufts sent out stolons >1 m in length (max=175 cm, $\bar{x}$=44 cm, n=16), with up to eight rooted nodes within 50 cm of stolon. Of the 34 individuals of *Setaria* which established on the lightly grazed treatment, three grew in

Table 11.5. Establishment and survival of the major species of each of four treatments (HL - heavily grazed with litter, HO - heavily grazed without litter, LL - lightly grazed with litter, LO - lightly grazed without litter). Columns headed 87/89 (88/89) indicate the number of individuals (seedlings plus ramets) establishing in 1987 (1988) (listed as the first figure in the column) and surviving to 1989. The column headed 89 is the number of individuals establishing in 1989.

	HL			HO			LL			LO		
Species	87/89	88/89	89	87/89	88/89	89	87/89	88/89	89	87/89	88/89	89
Grasses												
Aristida bipartita	0	35/38	0	1/1	13/13	11	1/1	22/27	4	0	10/10	4
Bothriochloa insculpta	1/2	5/5	0	0	5/7	1	0/1	0	0	0	0	0
Digitaria eriantha	7/8	16/17	10	2/3	25/34	16	3/4	8/15	3	1/3	23/27	0
Heteropogon contortus	4/8	0	1	1/1	0	0	6/8	4/7	10	0	0	0
Setaria incrassata	11/17	8/17	1	0	0	3	2/13	3/13	4	0	0/1	3
Themeda triandra	33/36	28/32	4	1/4	1/1	1	3/4	12/22	0	0	4/6	2
Forbs												
Chaetacanthus burchellii	1/1	0	0	1/1	2/2	0	5/5	2/7	4	2/2	4/5	5
Hibiscus pusillus	6/6	2/2	0	14/15	2/2	0	2/2	0	0	0	1/1	0
Plectipus hederaceus	1/1	0	0	6/7	0	0	1/2	2/2	1	4/4	0	0

from the outside, and three were rooted nodes of stems of adjacent plants which had collapsed onto the patch. All *Setaria* individuals which established on the heavily grazed treatment were new genets. A few *Chaetacanthus* individuals similarly established from prostrate branches which rooted and later separated from the parent plant.

DISCUSSION

A consideration of the regeneration phase has assisted in the prediction of the likely course of compositional change of sown pastures (Howe & Chancellor 1983). Such considerations alone will not suffice for a diverse grassland of long-lived perennial species, growth subsequent to establishment and how this is influenced by rainfall and grazing have to be considered, but certain general predictions based on gap dynamics present themselves.

An obvious constraint is the availability of propagules. A gap is liable to be filled by a species already present in the community (which includes refuge species in the seed bank). The colonisation success of *Digitaria* on all treatments was due to its stoloniferous growth habit, which promoted more rapid and effective colonisation of available space than seed recruitment. The initial size and leaf area of a rooted node of *Digitaria* is much greater than that of an emergent seedling, which allows more rapid initial growth than a seedling. The colonisation success of *D. macroblephara* in the Serengeti was also due to stoloniferous growth (Belsky 1986c). *Setaria* had begun to colonise the lightly grazed patches by rhizomatous growth in the second and the third seasons, and the representation of this species is expected to increase in following years as this growth continues, although clonal expansion by rhizomatous growth

appears slow. *D. scalarum* was a successful colonizer of disturbed patches in the Serengeti because of rhizomatous growth (Belsky 1986c).

The majority of the colonising individuals were seedlings, which was also observed in the Serengeti grasslands (Belsky 1986b). The colonisation success of seed reproducing species did not correspond well with their presence in the seed bank. The seed bank of both grazing treatments was comprised predominantly of *Setaria* (235 (55%) and 533 (59%) seeds/m^2 for heavily and lightly grazed respectively) and *Themeda* (81 (19%) and 109 (12%) seeds/m^2 for heavily and lightly grazed respectively), while *Bothriochloa* (1% and 11% for heavily and lightly grazed respectively) was represented but *Aristida* (2%) and *Heteropogon* (0% sampled) were almost absent (Chapter 10). Yet *Aristida* and *Heteropogon* colonised very successfully, and *Setaria* had poor colonisation success. *Themeda* colonised the HL treatment (and the LL treatment to some extent) successfully, and *Bothriochloa* established on the heavily grazed patches. Although few viable seeds of forbs were present, the prominent forb species of the community were successful in colonisation. Similar to the Serengeti (Belsky 1987), there was no colonisation by weedy species. The importance of the availability of seeds is suggested by the significant association between presence on a patch and presence in the adjacent vegetation for the uncommon obligate seed reproducing species *Aristida* and *Heteropogon*, and the correlation for the HL treatment of the abundance of *Themeda* on the patches and in the surrounding vegetation. The successful colonisation by *Aristida* is attributable to the prolific seed production of a few nearby individuals and possibly to its dispersal capabilities (see Rice *et al.* 1960), despite the low abundance of the species in the surrounding vegetation and in the seed bank. Although *Heteropogon* was a successful coloniser in this study, the species did not colonise disturbed patches in the Serengeti although it was present in the vegetation (Belsky 1986c). Nearly all the species which established on the patches were present prior to the treatments. This was recorded

for the comparable Serengeti grassland, where the most abundant colonising species were the most abundant species in the vegetation (Belsky 1986b). The generally weak relationship between seed availability and colonisation success raises the following question, which I speculate on for future study.

Could dormancy mechanisms or germination requirements have influenced colonisation patterns? Tropical grasses in seasonal environments have a period of innate dormancy (Lock & Milburn 1970; Mott 1978; Brown 1982; Hacker 1984, 1989; Frasier *et al.* 1987) which is an adaptive germination syndrome to ensure the survival of the seed through the dry season (Angevine & Chabot 1979). Innate dormancy is broken by a cumulative effect of the increase of temperature towards the end of the dry season, which ensures that germination occurs at the onset of the rainy season (Mott 1978; Hacker 1984, 1989). The proximate cues are the availability of soil moisture, and for some species there is a light or temperature requirement (Mott 1978; Watt 1982; Cox 1984; McKeon 1985; Pande & Singh 1984; Frasier *et al.* 1987). The treatments of this study would affect the moisture, light and temperature regimes of the seed bed. The open patches would be hot and xeric environments because of the high temperatures which occur and the dark colour (high absorptivity) of the soil. Litter cover would reduce light intensity and temperature in the first season when the cover was intact, reduce evaporation, and may effect germination and recruitment (Werner 1975; Gross 1984; Fowler 1986b, 1988). However, optimal germination levels of musk thistle *Carduus nutans* occurred in micro-habitats with reduced evaporation, one of which was a light ± 1 cm cover of litter (Hamrick & Lee 1987). The greater number of seedlings which emerged on litter patches (Figure 11.4) might be attributed to improved soil moisture conditions or to the entrapment of seeds by litter. The compositional differences between the litter and bare patches of each grazing treatment (Figure 11.1) and the poor development of seed reproducing species on lightly grazed patches

indicates that the nature of gaps can influence the germination environment, although this study does not indicate how.

Although intra-seasonal drought has a deleterious effect on establishment (Albertson & Weaver 1942; Pratt 1963, 1964; Ndawula-Senyimba 1972), the mid-season drought of 1986/87 had no discernible effect on seedling establishment (Figure 11.5). The pattern of seedling establishment was rather a classical concave survivorship curve indicating a period of high risk early in the life of the plant (Cook 1979). A number of seedlings of the lightly grazed patches died from being smothered by collapsed surrounding vegetation. Livestock trampling can reduce establishment (Wright & van Dyne 1976; Salihi & Norton 1986), but notably this did not occur. Orr (1980a) similarly found that the number of *Astrebla* seedlings was independent of grazing regime.

The nature of compositional change will depend on the number and size distribution of available patches (McConnaughay & Bazzaz 1987). The poor degree of colonisation of lightly grazed patches suggests that gaps smaller than these have little chance of being colonised under lightly grazed conditions. There was in fact little recruitment on the lightly grazed treatment over four years (Chapter 7). The dense mat of grass and moribund material which develops under lightly grazed conditions represses both germination and seedling establishment, especially for *Themeda* (Harrington & Ross 1974), and correspondingly there can be extensive stands of seedlings in *Themeda* grasslands when they are burnt (Ndawula-Senyimba 1972). The dispersal abilities of colonising species would be more significant for larger patches, and vegetative propagation would be limited (e.g. Coffin & Lauenroth 1989). *Aristida* species would be at an advantage because their seeds can be rolled by the wind (Rice *et al*. 1960).

The species which will come to colonise an available gap in these or similar grasslands can therefore be partly predicted from a consideration of the factors which determine colonisation success. Propagules need to be available, and vegetative propagules arising from stoloniferous growth (*Digitaria*) were overall the most successful for colonisation. In contrast, the slow vegetative expansion of *Setaria* by rhizomatous growth results in slow colonisation. Successful colonisation by seed reproducing species requires not only that seeds be present in the seed bank, but that the appropriate environmental conditions for germination are met. The optimal germination requirements of savanna grasses are poorly understood. The prevailing environmental conditions will also determine the establishment success of emergent seedlings or new ramets, and their subsequent survival.

SUMMARY

Patches (1 m diameter) were cleared in a heavily and a lightly grazed plot, and half were covered with a 1-cm thick layer of grass litter. The greatest extent of colonisation over three years occurred on heavily grazed patches which initially had a litter cover, the least on lightly grazed patches without a litter cover. Annual rainfall affected the rate of colonisation. The basal cover of patches was lower than the basal cover of the surrounding vegetation. The composition of the patch communities was weakly affected by treament, and was partly related to the composition of adjacent vegetation, but the proportional representation of species on patches was different to their proportional representation in the surrounding vegetation. The stoloniferous *Digitaria* and the obligate seed reproducers *Aristida* and *Heteropogon* were major components of all patch communities but were uncommon in the

surrounding vegetation and poorly represented in the seed bank. *Setaria* and *Themeda* were the predominant components of the surrounding vegetation and of the seed bank, but *Setaria* established very poorly and *Themeda* established well only on heavily grazed patches with litter. The differences between treatments in the extent of colonisation were mirrored by the differences in seedling emergence and establishment of grasses and forbs in the first year. Most seedlings emerged at the beginning of the wet season, with *ca.* 50% seedling mortality soon after emergence.

The identity of a colonising species can be at least partly predicted through an understanding of the (sequential) factors determining colonisation success. These are availability of propagules (vegetative or seed), dormancy mechanisms and germination requirements, emergence and establishment success, and subsequent growth.

CHAPTER 12

DISCUSSION

A model of local extinction

A primary objective of this study was to evaluate the concept that a palatable, long-lived, obligate seed-reproducing grass species is extinction prone under sustained heavy grazing (Chapter 2). The most appropriate test would have been to continue the experiment for the time period appropriate to judge if local extinction has occurred, which is the time taken for a complete turnover of all individuals in the population, including the seed bank (i.e. 10-20 years for *Themeda* and *Heteropogon* - Mott *et al.* 1985). Obviously this ideal could not be currently realised. The concept of local extinction is judged from consideration of whether the processes leading to extinction responded as predicted under heavy grazing, and from an independent gradient study of similar areas which had experienced a twenty year grazing history of either light or sustained heavy grazing (Pickett 1987).

This study indicated that *Themeda* and *Heteropogon* could become locally extinct. Local extinction requires that the established population and seed bank are eliminated, and there is inadequate immigration of seed for successful recruitment. As predicted, there was pronounced population decline due to increased mortality in the final dry year in conjunction with heavy grazing. In the earlier drier seasons there had been partial mortality of these species because of the die-back of large tufts. The

asymptotic rate of population growth showed that the populations were in decline in the final year. The number of seeds produced per plant was low. Seed production was dramatically reduced because of the direct ingestion of inflorescences by grazing cattle, and the low viability of seed in dry years. Intense seed predation further compounded this effect (Capon & O'Connor 1990). The result was a reduced seed density of *Themeda* and *Heteropogon* in the seed bank, with a progressive decline of recruitment under heavy grazing. The seed bank is not believed to persist for greater than two or three years if there is no fresh input (Chapter 9 - a major deficiency in knowledge), and the maintenance of a seed bank by the immigration of seed is discounted (Chapter 2). The dispersal abilities of these species was not addressed by this study, but has to be considered. *Themeda* culms were quite extensively consumed and seeds may be dispersed through the gut of cattle, but this was not found on the Transvaal highveld (Jones 1964). Both *Themeda* and *Heteropogon* experience incidental epizoochory (Chapter 2; Milton *et al.* 1990), but the question is whether there would be sufficient recruitment from seeds introduced in this fashion to maintain the population. The patch colonisation experiment illustrated that *Heteropogon* could successfully establish when space was available for a range of environmental conditions, despite being uncommon in the vegetation, whereas *Themeda* successfully established in only one of four environments, but not on the heavily grazed and open patches which is likely to be the environment most commonly available in heavily grazed situations. Dispersal and its role in vegetation dynamics is a long neglected field of study, because of obvious practical difficulties, but requires future attention. A first experiment would be to establish what rate of seed supply and rainfall, dependent on grazing, are needed to promote recruitment of *Themeda* in areas from which it has been eliminated.

Independent corroboration of the model of local extinction was provided from a study of the herbaceous composition, population structure and seed

banks of the main perennial grasses of nine sites on a similar soil type ranging in grazing history from sustained heavy grazing (>20 yrs) to light grazing (Pickett 1987). The first axis of a detrended canonical correspondence analysis of herbaceous composition identified a gradient of grazing history independent of soil variation. Lightly grazed sites were characterised by *Themeda*, *Heteropogon*, *Bothriochloa* and *Digitaria*, which were absent or scarce on the heavily grazed sites, as were their seed banks. Mean tuft size of these key grasses declined across the gradient of increased grazing pressure, which was also recorded in this study (Chapter 7).

The Thlavekisa site will be a future test case for the concept of local extinction. Because of the influx of refugees into the area, the populations of towns such as Hluvukani and Thlavekisa were judged to have doubled in the space of only a few years, a considerably increased area has been brought under cultivation, and there has been no concomitant reduction in livestock density. Grazing pressure in the region has therefore increased, paticularly on the study site which is now directly adjacent to human settlement and is grazed heavily every day by cattle en route to or returning from foraging. This grazing intensity is difficult to quantify, but far exceeds any level that could be achieved experimentally.

Life history patterns and vegetation dynamics

The extinction prone species were vulnerable under sustained heavy grazing as a consequence of their life history characteristics. I now postulate how species with different life history characteristics will respond to heavy grazing and variable rainfall, that is, identify their

vital attributes (Noble & Slatyer 1980). The antithesis of an extinction prone perennial species is a shorter-lived, relatively unpalatable perennial, of which *Aristida bipartita* is an example. *Aristida bipartita* showed both an absolute and a relative increase under heavy grazing at both clay soil sites, except for an absolute decline at Thlavekisa in the dry 1988/89 season. The species is capable of prolific seed production, even under heavy grazing, because it is not heavily grazed by cattle, and has a high seed output per plant. *Aristida* species have enhanced dispersal capabilities (see Rice *et al.* 1960), which probably promoted the successful colonisation of available patches by this species although it was poorly represented in the surrounding vegetation (Chapter 11). The high seed production, and resultant relatively high recruitment, even during the drier seasons of 1985/86, 1986/87 and 1988/89, resulted in the highest population growth rates. Even with persistent heavy grazing the species was well represented in the seed bank, and was one of the predominant species associated with sites with a history of heavy grazing (Pickett 1987). *Aristida bipartita* showed no appreciable decrease at Thlavekisa after four years of light grazing (it was not present in the sampled vegetation of the Utha lightly grazed treatment), but I speculate that a decrease in the abundance of this species is dependent upon being outshaded by taller species such as *Themeda* and *Setaria* (Chapter 4).

An important finding was the ability of species with stoloniferous growth to maintain or increase their populations under heavy grazing. These species include *Digitaria eriantha* var *stolonifera* on the sandveld, *D. eriantha* var *pentzii* at Utha, and to a lesser extent *Bothriochloa*. The value of stoloniferous growth is demonstrated by the rapid colonisation of available patches by *D. eriantha* var *pentzii* at Utha (Chapter 11). Without stoloniferous growth *D. eriantha* var *pentzii* would probably decline under heavy grazing, because of extremely low production of viable seed in some years (Chapter 10), and negligible recruitment from seed (Chapter 7). However, the ability to persist under grazing probably

depends on the grazing intensity, as *D. eriantha* was absent from sites with a history of heavy grazing (Pickett 1987). *Digitaria eriantha* also has a low leaf table height, and may be susceptible to elimination from shading effects by tall species (Chapter 4).

The highly palatable *Setaria* is the only example of a rhizomatous species. The extensive rhizome network (Carter & O'Connor 1991) was expected to provide protection against grazing, but this species appeared sensitive to grazing. Although producing quite prolific amounts of seed, and being well represented in the seed bank, *Setaria* was relatively ineffective in the colonisation of available patches by seed. The low asymptotic population growth rates over four years for both grazing treatments suggests that soil moisture has a primary effect on the abundance of this species. The size of *Setaria* clones (Carter 1987) indicate that the species is extremely long-lived, and this longevity probably buffers individuals against the vicissitudes of environmental variability.

All the main species of the herbaceous stratum of the clay soil sites were perennial grasses - annual grasses and herbaceous dicotyledons were scarce. The most common of the annual grasses was *Tragus berteronianus*, an epizoochorous species (Milton *et al.* 1990) with seeds which can persist in the seed bank (Chapter 10), and generally recognised as an indicator of heavily grazed conditions. The herbaceous dicotyledons found on both sites included annuals (e.g. *Cassia mimosoides*, *Enicoséma hyssopifolium*) and longer-lived perennials. *Chaetacanthus burchellii* and *Crabbea velutina*, the most common long-lived perennials at Utha, were not associated with heavy grazing but were most common within well-developed vegetation, although open spaces were needed for recruitment (Chapter 11).

The study has therefore defined some of the differences between perennial grasses which are both palatable and unpalatable obligate seed reproducers, or species capable of stoloniferous or rhizomatous growth.

Relation to other models of vegetation change

Concepts pertaining to the dynamics of vegetation communities have been a prominent field of theoretical development since the inspiring contribution of F.E. Clements early in the century (for a lucid review see McIntosh 1988, pp 76-85). One type of model develops universal generalisations concerning the processes responsible for plant community dynamics, exemplified by the three primary plant strategies defined by Grime (1977, 1979) and the models of Tilman (1982, 1988), linking resource competition, plant strategies and the dynamics and structure of plant communities. They share a common emphasis on the importance of life history patterns and of resource competition, differ between themselves in specifics such as the importance of stress, and differ from previous attempts at generalisations, for example Connell & Slatyer's (1977) precis of successional concepts, in the greater emphasis laid on life history patterns.

Tilman (1988) provides a mechanistically based explanation for broad scale patterns of differentiation among terrestrial plants, based on equilibrium conditions with constant process rates for a given scenario. While the model may be of great utility for comparisons along the rainfall and soil gradients of southern African savannas, which is beyond the scope of this discussion, its application to individual savannas is constrained by the poor predictability of environmental variation and the extreme variability of processes such as loss rates due to fire or herbivory,

which can range from 0-100%. Grime (1977, 1979) distinguishes three primary strategies of plants; ruderal, stress tolerant and competitive, from which predictions are made on the pattern of successional change of different environments. For example, in a productive habitat such as the clay soils of this study the change should be from ruderal species, through competitive species, ending with stress-tolerant species. Although a general categorisation of the species of this study could be made according to Grime's groupings, for example *Tragus berteronianus* is a classical ruderal species and *Themeda* an example of a competitive species, the fit is poor. *Aristida* is one of the starting species of a grazing succession, and therefore should by Grime's definition be capable of sustaining severe disturbance (removal of biomass) yet it is never heavily grazed. Both Grime and Tilman assume directional change for succession, which limits the applicability of their models to semi-arid and savanna areas (see Westoby *et al*. 1989).

The vital attributes model (Noble & Slatyer 1980) emphasises how population mechanisms interact with disturbance type to determine vegetation change. In this model each major species of a community is categorised into a species type on the basis of a small number of life history (vital) attributes, which are the means whereby a species responds to disturbance. Replacement sequences of species following disturbance are derived from the interaction of the different life history types. This study has been a first pass at defining the vital attributes of some of the main species. A conceptual model similar to the vital attributes model is the state and transition model of Westoby *et al*. (1989), which explicitly recognises the importance of the contingency of environmental events in forcing vegetation change. and is discussed below.

Constraints of an experimental approach

Ecologists are chastised for not pursuing an experimental approach for the study of the organisation of herbaceous communities and their change with time (e.g. Hairston 1989), but two aspects bedevil such an approach in savannas. The role of the contingency of driving forces for community organisation in the Serengeti was described by McNaughton (1983) as the "proximate mechanisms regulating species abundances are many weak forces acting probabilistically, so that the cumulative effects are large, but the individual effects are minor, interactive and uncertain." In addition, the population response (e.g. mortality) to both individual factors and their interaction is probably markedly non-linear and therefore non-additive (Figure 12.1). Therefore the interactive effects of, for example rainfall and grazing, will vary markedly depending on the levels of the main factors.

It may emerge that a stronger hierarchical order exists amongst these variables than McNaughton suspects (an implication of O'Neill *et al.* (1986) concept of hierarchical ordering within ecosystems). This is in fact the suggested relationship between rainfall and grazing from this study. But until this emerges, and because of the importance of interactive effects, an adequate experiment investigating the organisation and change of savanna communities would have to include all driving variables which are currently recognised to be important. To date most experiments have investigated the influence of a single driving variable such as grazing or fire (see O'Connor 1985), but their interpretation has been confounded by the effects of, for example, rainfall variability and soil type. An adequate experiment would have to include rainfall, grazing and fire, define substrata for between and beneath tree canopies, and be conducted separately for different soil types (clay versus sand) and for different climatic regimes (semi-arid,

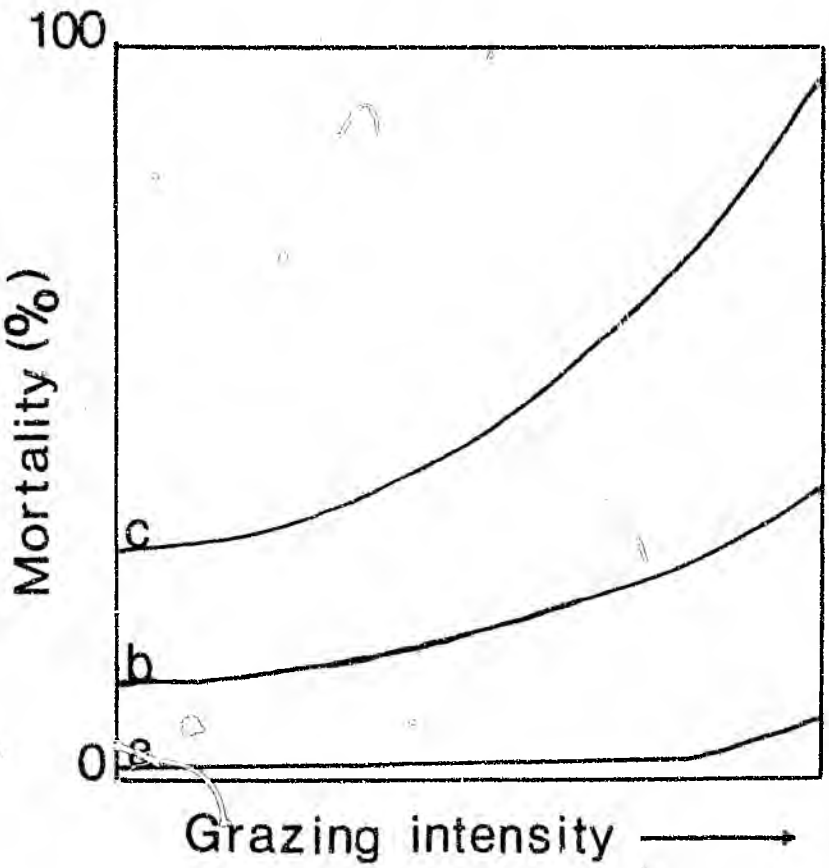


Figure 12.1. The hypothesised relationship between the percentage mortality of a perennial species and grazing intensity for a) high rainfall conditions, b) drought, and c) two sequential years of drought.

mesic, moist). A further complexity is that rainfall, grazing and fire are compound variables, each has an intensity and a frequency cum sequence component. To distinguish sequence and frequency, a drought year every third year would possibly have less effect on compositional change over nine years than three consistent years of drought. There is also a seasonal component which is ignored for present purposes. Therefore, an experiment with only two different levels of rainfall and grazing for two different sequences, and two fire frequencies, with only two replicates per treatment, would require 64 experimental units for each stratum and

each location. (The anticipated non-linear responses would in any event render two levels per treatment unacceptable.) There are also

$$k! / [(m+1)! (k-m-1)!]$$

m th order interactions in a *k* factor factorial to deal with to complete the nightmare. For example, with six main effects, there are twenty second order, fifteen third order, six fourth order and one fifth order interaction. The size of experimental units would depend on the spatial pattern of the vegetation, but with the number of units involved there is a likelihood of not only non-homoscedasticity of units, but that end spatial points would transgress into different soil and vegetation types. This occurred in the Kruger National Park fire trials on sandveld (van Wyk 1972) which invalidated comparisons for the effects of fire on the herbaceous stratum.

Finally, journal editors have a pre-occupation with Type I and Type II statistical error, but there is little recognition of "inference error". Although an explicit definition of the population of inference should be made prior to the experiment (Brown & Waller 1986; Stroup *et al.* 1986), the pronounced variation of southern African savannas over distances of <1 km renders this a text book concept. Experiments are conducted only over a small range of the variables involved, yet the conclusions will inevitably be applied far more widely. How much error is induced when the conclusions from an impeccably executed field experiment are extrapolated to a situation with, for example, 60 mm less rainfall, a slightly higher stocking density, and slightly different soil texture, etc., even if many of the plant species are the same? Further, an experimental approach does not directly translate into a predictive ability of what will happen to a defined piece of land which is subjected to a defined management action. Yet managers, be they pastoralists or nature conservators, require site and time specific predictions. I therefore consider below an embellished version of the state and

transition model (Westoby *et al.* 1989) which may offer a partial resolution of these problems.

Modelling approaches

The state and transition model (Westoby *et al.* 1989) was developed as a conceptual alternative to the classical range succession model for the organisation of research and management of (particularly semi-arid) rangelands. The model describes rangelands by means of catalogues of alternative states and catalogues of possible transitions between states. The definition of states was to recognise the possibility of alternative stable states and irreversible transitions. Transitions between states are a response to natural events (e.g. drought) or management actions (e.g. stocking rate) or a combination of the two.

I propose that an amended form of the model will serve the purposes of both scientific inquiry and predictive management of southern African savannas. The amendment is that individual species are considered as the state variables. The rationale for this departure is illustrated by the example of the Tall Grassveld in Natal that they offer, "to show how a state-and-transition formulation can be used even when there are uncertainties and disagreements as to what states should be recognised and what processes lead to transitions between them." Functional groups such as perennials, palatable perennials, large coarse perennials and unpalatable perennials are defined, with the further implicit assumption that all species of the same functional group will respond in the same way. This study refutes that belief, *Setaria*, *Themeda* and *Heteropogon* are palatable perennials but diverged in their responses to extrinsic influences. As much is obscured as is clarified by attempts to define

functional species or states. The argument that an individual species approach cannot cope with the extreme diversity of southern African rangeland is misleading, the majority of these rangelands are dominated by one or a few species (e.g. Chapter 4), most of which enjoy a wide geographic distribution. (Functional groupings for the purpose of inter-regional or inter-continental comparisons, in which no species are shared, is a different issue.)

The objective is therefore to provide scenarios of the possible future composition of a savanna herbaceous community, for relevant management time intervals. This is termed tactical prediction. Failure of the model predictions to be matched in the real world indicate that the model is lacking one or more of the principal transitions, or that those included are too simplistically formulated. If composition is not the variable of interest (e.g. production) then an alternative approach (e.g. systems analysis) is required.

Development of the model

An appropriate time horison has to be defined, as this can influence the number of transitions to be defined. If changes over twenty years are to be predicted, the change in the woody canopy has to be considered, as the effects of these are postulated to override all other effects. But if changes over only five years are to be considered, woody canopy effects can be ignored. Preliminary development of the model involves defining a currency (e.g. basal area as an absolute measure or as classes), and an iteration period (e.g. 1 year). Rainfall and grazing are continuous variables, but have to be decomposed into discrete class variables to develop a tractable model. In defining environmental classes a compromise

is needed between states which are too coarse to reflect the essential dynamics of the system and defining too many states for which estimates can be derived. The complexity of the model can be developed as additional information accrues. A starting point for the present example was to define three states of rainfall intensity (drought, moderate, wet). The range of the rainfall classes would be derived from probability analyses of rainfall records. The influence of the seasonal pattern of distribution is ignored. The response of all species to a sequence of years of average rainfall was treated as an additive effect of a single year, as pronounced compositional changes appear to be related to sequences of drought or of heavy rainfall.

The only two grazing states defined are heavy and light; the former corresponds to continually high stocking densities throughout the growing season, such as occurs on the communally grazed areas. Although complete exclusion can lead to pronounced compositional change in the longer term (±20 yr - O'Connor 1985), it is an option which can be ignored for almost all southern African savannas. The effect of a year or two of rest is treated as an additive effect which is the same as light grazing. The effect of sustained heavy grazing for a given rainfall scenario will not be additive. There is no general evidence that fire *per se* can result in pronounced compositional changes, but that the effect of fire (assumed to occur in the dry season or early spring) will depend on whether it is followed by a drought year with or without heavy grazing (O'Connor 1985). The effect of changes of other species on the species of interest can be included as rule based changes depending on the asymmetry of competition between the two species and the abundance of each. For example, although shading by *Themeda* might depress *Aristida* during high rainfall, low grazing conditions, this effect has to be scaled according to the abundance of *Themeda* and *Aristida*.

Themeda and *Aristida* were chosen as examples, and the transitions for each of these species for the perceived important environmental conditions have been catalogued (Box 12.1). This catalogue makes a first hypothesis about the relationship of the driving variables to one another, that is, the contingency effects of grazing, rainfall and fire have been transformed into a monotonic relationship.

Box 12.1 is an incomplete illustrative example only, derived from this study. Some transitions are almost certainly too simplistic, for example transition 9 of *Themeda* covers a wide range of contingencies. Further development would draw on all the available knowledge, such as the Matopos experiments which are a comparable climatic regime and soil type. Adjustments would need to be made for sequences of environmental states, but with present knowledge estimates would be limited to only a few years. Additional rules would become readily apparent if the heuristic exercise of developing a set of transition rules is undertaken.

Application of the model

In terms of scientific inquiry, understanding can be continually improved without having to wait for certain climatic sequences to occur. For example, predictions can be made for x sites on the change in the abundance of a species from one to n number of years, over a range of environmental conditions. A measure of statistical rigour is possible by *a posteriori* testing of the model predictions against outcome. Failure of the predictions to be within some predefined level would indicate that either the model is lacking one or more principal transitions, or that those included are too simplistically formulated. With each projection new insights are gained which are then incorporated into the set of

Box 12.1. Rules for the annual transition in abundance of A - *Themeda* and B = *Aristida*.

I. Hierarchy of effects

The following transitions are ranked in order (1=most) of the resulting decrease of a species.

A - *Themeda*
1. Drought and heavy grazing, following fire.
2. Drought and heavy grazing.
3. Drought and light grazing, with or without fire.
4. Moderate rainfall and heavy grazing, following fire.
5. Moderate rainfall and heavy grazing.
6. Moderate rainfall and light grazing, with or without fire.
7. High rainfall, light or heavy grazing, with or without fire.

B. - *Aristida*
1. Drought and light grazing, following fire.
2. Drought and heavy grazing, following fire.
3. Drought and light grazing.
4. Drought and heavy grazing.
5. High rainfall, light grazing, following fire.
6. High rainfall and light grazing.
7. Moderate rainfall and light grazing, following fire.
8. Moderate or high rainfall and heavy grazing, following fire.
9. Moderate rainfall and light grazing.
10. Moderate rainfall and heavy grazing.
11. High rainfall and heavy grazing.

The transitions for *Aristida* are dependent on the density of taller species such as *Themeda* and its own density (see discussion).

II. Adjustments for time effects

The effect of a sequence of years of any of the above transitions would be non-additive, as their effects on population change are non-linear. New transitions are defined for particular sequences. For example, drought and heavy grazing following fire can only occur for one year, as there would be insufficient fuel load in following years. Therefore an extra transition is added for each set of years considered (i.e. two, three, four or five year sequences). For example, for three years for *Themeda* the rankings in order of the resultant decrease are:
1. Transition 1 above followed by two years of transition two.
2. Three years of transition 2 above; etc.

For *Aristida*, the rankings may be considerably altered. It is conjectured that fire followed by light grazing, with a high abundance of tall species would result in the greatest decrease of *Aristida* Therefore ranking 1 would be the annual burning with high rainfall and light grazing.

III. Additional rules

Certain transitions could only take place if preconditions were satisfied. A fire could not occur if heavy grazing had occurred in the preceding season. The amount of change depends on the abundance of the species, because there is an upper limit to the total basal area of a site. If a species is eliminated from a site, it cannot be assumed to increase with improved conditions.

transition rules. Consistently correct predictions impart confidence that the proposed transitions are the most important. The approach obviates the need for a complex experimental design and overcomes the extrapolation error referred to earlier, by greater reliance on the inductive method for the development of concepts (Mentis 1988). The tactical approach should not however be seen as a surrogate for experimentation, but an approach to identify both the appropriate variables and their appropriate levels for rigorous experimentation (see also Brown & Waller 1986). Monitoring is a widespread activity in southern African savannas, yet it is difficult to find any evidence of insight extracted from most of this effort. The proposed approach is considered to be suited to extracting greater returns from monitoring exercises. In terms of application to management, baseline conditions are assessed, a projection period (e.g. one year) is chosen, the possible range of management actions and climatic sequences is defined, the transition rules are consulted to establish the range of possible transitions, which may influence the management action taken.

The fallibility of this proposed approach is easily tested. Box 12.1 could be easily developed for implementation, and the other species of this study could be similarly treated.

CONCLUSION

This study set out to differentiate the effect of rainfall and grazing on the compositional change of the herbaceous stratum of southern African savannas, and to explain these changes in terms of the life history patterns and population dynamics of the constituent species. To meet this end what is believed to be an original and universal concept of vegetation

dynamics was proposed. In any event detailed information was collected on the population dynamics of the main species, an approach which has hitherto all but been ignored in southern Africa. For example, I know of no published information on either the seed banks of southern African savannas or of seed predation in African savannas, or of the application of matrix modelling techniques to African grasses. While some facets of population dynamics such as mortality have received peripheral attention, I know of no study of savanna grasses in Africa which has systematically covered all the important population processes. The necessity of a population based approach to range dynamics is almost axiomatic in similar environments elsewhere in the world, the ample Australian and American literature cited bears testament to this. I feel the study provides evidence that it would be fruitful to pursue this avenue further in southern African savannas.

While the study could not clearly differentiate the effects of rainfall and grazing on compositional change , due to the breakdown of the experiment for reasons beyond my control, the data at least are a meticulous record from which conclusions could be drawn because of the associated information on population dynamics. Criticism could be levelled that the objectives were not attained because the study was too broadly based. My perception is that the scope of work was accomplished easily enough (substantially more work was undertaken than has been presented) but studies of this nature should be undertaken at an established research site with appropriate logistical support, but the precondition that work under the aegis of the funding body of this study should not transgress into the research activities of applied research departments constrained options.

In closing I would suggest, considering the proposed importance of rainfall variability and grazing for compositional change, that an expanded version of this experiment should be repeated provided that a

range of rainfall regimes (drought, average, high) can be maintained (based on smaller manipulations) over a range of soil and climate types. The difference would be to test an explicit suite of hypotheses (e.g. Frost *et al.* 1986 and some derived from this study) which cannot be reliably addressed by short term studies, and specifically to avoid the degeneration of experiments into monitoring exercises which at best address a vague question of whether or not change has occurred. The rationale guiding the long term ecological research programme in North America (Franklin *et al.* 1990; Magnuson 1990; Swanson & Sparks 1990) should be adopted, on sites with well established baseline data.

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