Ecological significance of variation in *Themeda triandra* Forsk: A case of intra-specific divergence in life history strategies?

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"Themeda triandra is by far the most generally important of our grasses" Acocks (1990).

Submitted in fulfilment of the degree of
Master of Science

In the
Department of Botany
Faculty of Science
University of Cape Town, South Africa
2006

Declaration

I herby certify that the research work reported in this dissertation is the result of my own original investigation except where acknowledged.

Signed Signed by candidate

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Abstract

Rangelands are an important resource for commercial, subsistence and game enterprises. However, their variability poses a challenge for their effective management. This thesis was motivated by the need to contribute to a functional classification system for rangelands to guide managers in a way that adequately, yet simply, addresses ecological variation in South African rangelands. The approach was to investigate life history characteristics of rangelands at four sites representing climate extremes. These differed in the amount, and predictability, of rainfall and the incidence of frost. The approach was novel in that a single species, *Themeda triandra,* was used in an attempt to test predictions on sets of key traits associated with the different rainfall regimes. The underlying hypothesis was that density-dependent processes would be most important in mesic grasslands, requiring frequent defoliation by fire or grazing to maintain a productive *Themeda* sward. Climate variability would be the most important determinant of grass growth in semi-arid grasslands. Vegetative and reproductive traits of *Themeda* would be expected to have diverged in response to these different selection pressures in the different populations.

Observations were made on reproductive and vegetative traits in field populations in the four study areas and on plants grown from clonal material and seeds in a glasshouse to determine key axes of variation. Population responses to varying light and moisture levels were compared in a glasshouse experiment simulating the effects of different moisture regimes and competitive environments of source populations. Fecundity, seedbank characteristics, seedling numbers and population size structure were compared in field and glasshouse experiments. Production characteristics were compared in a clipping experiment conducted in the field.

Results showed that different populations of *Themeda* exhibit divergent life history characteristics associated with different rainfall and temperature regimes. These differences are evident in the morphology, allocation patterns, leaf traits, germination biology and phenology of populations. The ecological significance and implications of trait divergence were clearly evident in demographic characteristics of the populations, in experimental responses to watering and shading, and in divergent growth responses to clipping experiments. The results were consistent with classic life history theory. In low, unpredictable rainfall regions, populations have evolved r-selected strategies whereas populations from high and predictable rainfall are characterized by K-selected traits. However the incidence of frost is also a factor influencing growth form divergence.

The use of a single species name for a genetically and ecologically divergent grass has caused much confusion in rangeland literature. The ecologically divergent responses of *Themeda* from different environmental conditions means that experimental findings, and management recommendations based on them, have limited generality. Widely accepted generalisations on the properties of this preferred pasture grass only hold for particular genotypes growing in particular environmental circumstances. This study identifies key functional traits, and different functional forms of *Themeda* as a guide to recognising ecologically important forms. These in turn are useful for predicting key factors likely to influence grassland productivity and persistence in different regions.

Acknowledgements

This research was made possible with the financial assistance from the National Research Foundation

I would like to express my sincere thanks to the following people and institutions:

Prof. W.J. Bond, my supervisor, for his advice, encouragement and support.

Prof. W.D. Stock for his advice in the eco-physiological aspects of the work.

The University of Cape Town, particularly the Botany Department.

Sandy Smuts, of the Botany department, UCT, for administrative support and regular encouragement.

EKZN Wildlife, particularly Dave Balfour, for supporting the project.

The staff at Hluhluwe Research Centre for their logistical support and for keeping me safe from various dangers in the bush.

Dr. Dinny Howle, owner of Hillside farm, for her hospitality, keen interest in the work and assistance in finding suitable sites in the area to work on.

Flip Henning for making some of his land available for the study.

University of Natal, Pietermarizberg for allowing me to use Ukulinga Research farm as one of my study sites.

The staff at Ukulinga Research farm who always ensured my stays there were comfortable.

My parents, whose love and support through the years have made this opportunity possible.

Table of contents

Chapters

List of tables

List of Figures

1 General introduction, research questions and approach

1.1 General introduction

Rangelands

Grasses are a remarkable group of plants, occupying the greatest area of land on the earth's surface compared to other plant families (Bradshaw, 1998). They are rather uniform in their basic structure and yet exhibit extensive diversity in evolutionary adaptation, inter- and intra-specifically, thus providing opportunities for investigating the relationship between plants and their environment (Bradshaw, 1998). Grasses are not only interesting, their economic importance is well recognised (Bradshaw, 1998; Baxter, 1997), partly because they are the major component of the world's rangelands which span an array of climatic conditions and constitute a resource base of great ecological, agricultural, economic and conservation value (Knapp and Seastedt, 1998).

Research challenges for sustainable rangeland management

Consequently, rangelands have been intensively studied in order to refine management strategies so as to ensure biological and economic sustainability (Knapp and Seastedt, 1998). The focus of these studies has primarily been on the response of species to permutations of disturbance (fire and grazing), disturbance intensity and season, towards improving agricultural practice. The results of these are valuable but cumbersome when attempting comparisons and often weak in predicting general trends. This is compounded by the variability associated with rangelands. Ecological studies of rangelands are rare and there is growing recognition of the need for studies that take cognisance of and attempt to explain rangelands in terms of their ecology (Ndawula-Senyimba, 1972, Knapp and Seastedt, 1998). Several authors suggest efforts should be focused on developing functional classification systems that have an ecological basis instead of a taxonomic one in order to deal with the complexity of rangelands (Theunissen, 1992; Campbell, *et al.*, 1999, Duckworth, *et al.*, 2000).

Processes implicated as being important in influencing the ecology of grasslands and savannas include climate, fire, grazing (O'Connor, 1985) and, more recently, climatic variability (Ellis and Swift, 1988; Westoby *et al.*, 1989; O'Connor and Everson, 1998; Knapp and Seastedt, 1998; Epstein *et al.*, 1999), the relative importance of which may vary in space and time (O'Connor and Bredenkamp, 1997; Knapp and Seastedt, 1998). The challenge is to develop an understanding of the interplay among these processes and the consequent product reflected in ecology of rangelands. One approached potentially employed in such investigations is that of investigating the life history characteristics associated with sets of conditions.

Life history strategies: some conceptual frameworks

Various conceptual models attempt to predict what life history strategies will be selected for under certain permutations of stress and disturbance (e.g. Grime, 1979; Tilman, 1988, Westoby, 1998).

A number of studies have demonstrated that fast-growing species are generally found in high-resource environments (nutrient rich, high supply of light and water) whereas slow-growing species are commonly found in adverse environments with low availability of resources (see Poorter, 1990 and Lambers, *et al.*, 1998 for reviews). One view (Grime, 1979), suggests the advantage of fast growth to competitors is space occupation and thereby gaining a larger share of the resources (light and water) and, in disturbed habitats, fast growth assists in completing the life cycle in a short period of time. The advantages of slow growth are less clear and often debated (Poorter, 1990; Lambers, *et al.*, 1998). Lambers, *et al.* (1998) review several hypotheses that attempt to explain the advantages of slower relative growth rates (RGR) and end by proposing that the components linked to RGR are the traits selected for, rather then RGR itself. Lambers, *et al.* (1998) take this further by stating that short-lived, fast-growing species are more common in unpredictable but productive environments where disturbance such as fire occurs, whereas slow-growing, longer-lived species are more common in predictable environments with a low incidence of disturbance.

Another approach to describing plant strategies is that of r- and K-selection. In plant populations, K-selected strategies (plants allocate more to non-reproductive activities) are associated with populations that experience high density-dependant regulation, and r-selected strategies (allocate more resources to reproductive output) are associated with populations that experience mortality that is density independent (Gadgil and Solbrig, 1972). R-selected species occur with a higher frequency in variable environments where mortality is common, whereas in more stable, constant, predictable environments, species that are slower growers and longer lived (K-selected) predominate. Traits selected for in r-selected plants include rapid development, high growth rate and early reproduction, whereas competitive ability and delayed reproduction are traits associated with K-selected plants. It is generally agreed that short-lived species have fast growth rates, whereas long-lived species have slow growth rates (Lambers, *et al.*, 1998).

The various life history schemes that exist can be applied at various levels with varying degrees of success and focus primarily on plant traits, competitive ability and reproduction strategy in natural systems. Attempts have been made to characterise rangelands specifically, but due to the utilization potential of these systems and the impact of this utilization on the vegetation, the approach is somewhat different. They focus on the processes influencing productivity and vegetation dynamics, such as species response to grazing and fire regimes, rather then focusing on plant traits.

Rangeland dynamics

Westoby, *et al.* (1989) debate the relative merits of two models pertaining to rangeland ecology. The first, described as the "range succession model", is based on Clementsian ideas. This model sees rangelands as changing in composition though time such that, in the absence of grazing, there is a successional tendency to a single persistant state (the climax). Grazing reverses the successional trend tending to shift the community to a pioneer state. An equilibrium can be produced by maintaining stocking rates at a certain level which is equal and opposite to the successional processes (Westoby, *et al.*, 1989). Consequently, herbivore-stocking rates are considered to be the key tools for the management of such systems to maintain the rangelands at a favourable equilibrium. By simply adjusting stocking rates the desired rangeland state can be obtained.

This equilibrium paradigm has, until recently, been the dominant framework in which management strategies for rangelands have been formulated (Westoby, *et al.*, 1989, Wu and Loucks, 1995). However, the equilibrium models have been recognized as being weak with respect to predicting the dynamics of natural systems since equilibrium conditions are rare in nature, compounded by the fact that heterogeneity and scale multiplicity are inadequately expressed in quantitative expressions for stability pertaining to equilibrium systems (Wu and Loucks, 1995).

Ellis and Swift (1988) argue that semi-arid rangelands are non-equilibrium systems where animals have little effect on productivity and vegetation composition. The rationale is that because of the variation in rainfall in these systems, animal numbers seldom reach the levels where they would impact significantly on the vegetation. However, O'Connor (1995) contests this, recognizing that species shifts and abundance are influenced by rainfall, but demonstrating that there is a cumulative effect of grazing on vegetation dynamics in these systems.

Westoby, *et al.* (1989) state that episodic events, the influence of grazing and intrinsic vegetation change act intermittently (as opposed to a stable succession). They present the "state and transition model", arguing that this is more appropriate for dealing with "intermittent" systems. Here, instead of directional predictable succession, a set of states, transitions and transitional states are proposed to describe vegetation dynamics, suggesting that rangelands are essentially event driven and events (e.g. high rainfall years, droughts, fire management actions) trigger transitions between states.

What is evident is that there has been a general paradigm shift from the Clementsian view to one addressing event-driven dynamics and the basis of the current arguments emphasize the potential relationship between rainfall and vegetation dynamics (Bond, 1997). Specific studies exploring plant functional types in rangelands, however, focus primarily on the effect of fire and grazing, and not on rainfall. Briske, (1999) uses plant traits to develop an integrative plant function type model for predicting grazing resistance of mesic grasslands and consequential species compositional changes. Lavorel and McIntyre (1999) and McIntyre and Lavorel (2001) attempt to resolve functional types specifically in relation to disturbance response and grazing. Landsberg (1999) compares two approaches (functional response groups versus derived functional effect groups) to clarify overlap between functional groups with respect to their response to disturbance. A common functional classification of grasses is the increaser-decreaser status of the species, and it is still considered a useful tool for predicting plant response (Noy-Meir and Sternberg, 1999). Noy-Meir and Sternberg (1999) use the functional approach to review the response of species in Mediterranean grasslands to fire and grazing.

Campbell, *et al*. (1999) attempted to develop a rule-based functional model with enough resolution to predict the combined effects of human disturbance, climate and grazing livestock on vegetation structure which would enable managers to predict changes in rangelands. The best results from the modal were obtained for cases where there were extreme climates or management effects. Models were sensitive to the key plant functional attributes favoured by differing climates and disturbance regimes. The authors urged that a more explicit understanding of these is required (Campbell, *et al*., 1999).

Bond (1997) proposes a functional classification of vegetation properties for South African systems specifically in relation to rainfall, in which mesic rangeland (> 650 mm) dynamics are driven by competitive interactions, where productivity is a function of density-dependent processes (self shading), seedlings are rare and propagation is primarily vegetative. In the absence of fire these systems would behave in the classical successional manner, progressing to a thicket or forest. Vegetation dynamics in the semi-arid and arid areas (< 650 mm) would be driven by rainfall, mortality of grass plants may be relatively high, and propagation through seed would be more common. The aim of the work presented in this thesis was to test these ideas, but the approach used was novel in that a single species, *Themeda triandra* Forsk., was used. The rationale for this approach lies in the distribution and abundance of this species, combined with its apparent versatility and variation in morphology. Furthermore, disturbance is disregarded, with the focus rather being on processes important to selecting for certain traits that are related to productivity and population persistence.

Abundance and distribution of *Themeda triandra* Forsk.

Themeda triandra is a tufted C_4 perennial grass belonging to the Andropogoneae tribe of the sub-family Panicoideae (Clayton and Renvoize, 1986) and is the only representative of the *Themeda* genus in Africa (Ndawula-Senyimba, 1972). Common names for *Themeda* include: Rooigras, Kangaroo grass (Groves, 1975) and Blaugras (Bews and Beyer, 1931).

Themeda triandra (henceforth referred to as *Themeda*) has a widespread distribution in southern and central Africa (Brown and Emery, 1957; Lock and Milburn, 1971; Ndawula-Senyimba, 1972; Theunissen, 1992; O'Connor and Bredenkamp, 1997) and in Asia (Clayton and Renvoize, 1986; Gibbs Russel, *et al.*, 1990). It is also one of a few species described as having "a pan-Australian distribution" (Woodland, 1964) which extends from New Guinea, through all the states of Australia and down to Tasmania (Woodland, 1964; Evans and Knox, 1969; Clayton and Renvoize, 1986; Gibbs Russel, *et al.*, 1990). Its geographical distribution within these areas is wide (Brown and Emery, 1957; Evans and Knox, 1969; Lock and Milburn, 1971; Ndawula-Senyimba, 1972; Clayton and Renvoize, 1986; Gibbs Russel, *et al.*, 1990; Theunissen, 1992a), incorporating a broad range of latitudes (Evans and Knox, 1969), longitudes, altitudes and geomorphology (Groves, *et al.*, 1982; O'Connor and Bredenkamp, 1997). As a result, *Themeda* populations occur over a range, and often at extremes of environmental and climatic gradients including rainfall, temperature, moisture availability, frost and soil types.

Within this distribution, *Themeda* is represented in a number of habitat types (Acocks, 1975), for example: temporal, tropical (Evans and Knox, 1969), sub-humid temperate grasslands in Australia (Moore and Perry, 1970, In Groves, 1975), arid and mesic grasslands and savannas (O'Connor and Everson, 1998), fynbos and Nama karoo (Gibbs Russell, 1987).

Themeda not only persists over this range of conditions, it is often abundant within its distribution and dominant within grassland and savanna communities in Australia and Africa (Lock and Milburn, 1971; Ndawula-Senyimba, 1972; Mott, 1978; Clayton and Renvoize, 1986; O'Connor 1985; Theunissen, 1992a; O'Connor and Bredenkamp, 1997). Referring to its distribution in Africa, Theunissen (1992a) describes *Themeda* as "one of the most common grass species south of the equator". Within its pan-Australian distribution it is considered as one of the more dominant species in both temperate and tropical grasslands (Evans and Knox, 1969).

Uses and importance

"*Themeda triandra* is probably the best grazing grass found in South Africa" Phillips (1931)

Themeda is a palatable species, utilised as a natural forage grass for domestic and indigenous animals, (Bews, 1931; Acocks, 1990; Meredith, 1955; Tainton, 1984; Ndawula-Senyimba, 1972; O'Reagain, *et al.,* 1995), sometimes cut and used for hay (Bews and Bayer, 1931). In some tropical environments, where it can grow to a height of 1.5 m, *Themeda* is also used as a thatching grass (pers. obs.). One report even states that it was used to indicate ground suitable for pineapple cultivation (Phillips, 1931). Of great relevance to this thesis is the fact that *Themeda* is considered to be a useful indicator species, its abundance within grasslands and savannas being attributed to sound veld management (Tainton, 1984). It is also often used to characterize various vegetation types (Ndawula-Senyimba, 1972; Downing and Marshall, 1980, see O'Connor and Bredenkamp 1997).

The combination of *Themeda*'s widespread distribution, abundance and its value as a forage grass makes it one of the most important forage resources for game and livestock (Bosch, 1989). O'Connor and Everson (1998) describe the perennial grasslands of sub-Saharan Africa (true and savanna), of which *Themeda* is a major component, as "the heart of pastoral enterprise which directly supports a greater human population then any other pastoral enterprise in the world", demonstrating that the correct management of *Themeda* is vital to the livelihood of many, including subsistence farmers, commercial farmers and conservation areas. Its economic importance is therefore well recognized (Baxter, 1997).

Due to *Themeda*'s importance, it has long been appreciated that it is essential to improve the knowledge and understanding of the growth and development of *Themeda* in order to make advances in veld management practices and ensure its sound and sustainable utilization (Ndawula-Senyimba, 1972; Snyman, *et al.*, 1997). Much research has been undertaken on *Themeda* in the hope of contributing towards such an understanding. These studies include various aspects of the cytology (Gluckman, 1951; Birari, 1981; Liebenberg, 1986; Fossey and Liebenberg, 1987; Spies and Gibbs Russel, 1988a&b; Liebenberg, 1990; Fossey and Liebenberg, 1992; Liebenberg, *et al.*, 1993), reproductive biology (Brown and Emery, 1957; Evans and Knox, 1969; Cresswell and Nelson 1971; Cresswell and Nelson, 1972; 1973; Hagon, 1976; Martin, 1975; Birari, 1980; Groves, et al., 1982; Adams and Tainton, 1990;

Capon and O'Connor, 1990; Sindel, 1993; Everson, 1994; Baxter, *et al.*, 1995; Baxter, 1997), demography (Carter and O'Connor, 1991; Everson, 1994), growth and development (Scott and Rabie, 1956; Groves, 1965; Ndawula-Senyimba, 1972; Downing and Marshall, 1980; Groves, 1975; Downing and Groves, 1985; Dankwerts, 1987; Moore, 1989) and physiology (in relation to water stress) (Dankwerts, 1988; Dankwerts and Stuart-Hill, 1988; Snyman, *et al.*, 1997). Studies predominantly relevant to the management of *Themeda* veld investigate the response of *Themeda* itself, and sometimes in conjunction with vegetation communities, to various permutations of fire, grazing and rainfall (Coetsee, 1975; Brown, 1985; Drewers and Tainton, 1981; Coughenour, *et al.*, 1985; Barnes, 1989; Dankwerts and Nel, 1989; Barnes, 1990a; 1990b; Morris and Tainton, 1993; Adams, 1996).

Increasing demand on a declining resource

A source of great concern, therefore, is that *Themeda* is disappearing from certain areas in grasslands and savannas, (Danckwerts, *et. al.*, 1984; Baxter, 1997), particularly the semi-arid areas (Bosch, 1989) and sometimes rapidly (Danckwerts, *et al.*, 1984). This decline is often attributed to over-grazing (Evans and Knox, 1969), sensitivity to heavy grazing (O'Connor and Picket, 1992), poor agricultural practice and land degradation (Baxter, 1997). In work done in savannas, O'Connor (1994) found that both *Themeda* populations and their presence in the seedbank are eliminated through a combination of drought and heavy grazing, highlighting the potential for *Themeda* to become locally extinct in these areas. Similarly, Everson (1994) found that *Themeda* from montane grassland is prone to extinction under continuous grazing. This author demonstrated that certain fire regimes, for example, fire exclusion or summer burns, could also have a detrimental effect on the population of *Themeda*.

Variation in *Themeda* and rangeland management

Themeda, described as having a "ubiquitous nature" (Ndawula-Senyimba, 1972), is remarkably variable in terms of its morphology (Woodland, 1964; Evans and Knox, 1969; Downing and Marshall, 1980; Gibbs Russell and Spies, 1988; Baxter, 1997), cytology (Gluckman, 1951; Birari, 1981; Liebenberg, 1986; Fossey and Liebenberg, 1987; Liebenberg, 1990; 1992; Liebenberg, *et al.*, 1993), and seed biology (Groves, *et al.*, 1982; Baxter, *et al.*, 1993). Variation has also been documented in terms of its phenological development (Hayman, 1960, Rethman, 1971; Dankwerts, et al., 1984) and, more recently, the population biology of *Themeda* from different regions (O'Connor and Everson, 1998). However, the nature and extent of variation in *Themeda* has as yet not been described within a comprehensive ecological framework. Furthermore, *Themeda's* variability is seldom acknowledged in the body of literature dealing with the effect of management strategies (permutations of fire, grazing and rainfall) on the response of *Themeda*. Some authors have suggested that *Themeda* populations may vary in their response to certain management regimes or treatments, depending on the type of environment from which they originate (Wooldland, 1964; Evans and Knox, 1969; Ndalula-Senimba, 1972; Danckwerts, *et al.*, 1984; Downing and Marshall, 1980). A small number of studies provide evidence to support this notion (Retheman, 1971; Ndalula-Senimba, 1972; Tainton, *et al.*, 1977; Danckwerts, *et al.*, 1984) and caution that results from work on the response of *Themeda* originating from one area may not be generally applicable to other areas. However the full extent of the variation in the response of Themeda to various management strategies and its implications is not known.

The cause of variability in *Themeda* is generally ascribed to some degree of ecological differentiation that may be expected among populations, due to their broad geographic range (Evans and Knox, 1969; Ndawula-Senyimba, 1972). This implies that variation observed in *Themeda* has ecological significance and several authors recognize and refer to "ecological races" of *Themeda* (Wooldland, 1964; Evans and Knox, 1969; Ndawula-Senyimba, 1972). Different chromosome races occur in different frequencies in different vegetation types across climatic gradients, indicating that some races are more suited to specific conditions then others (De Wet, 1960). Originally, at least four variants of *Themeda* were recognized and the Australian form was classified as a different species (*T. australis*) (De Wet, 1960), but later these were combined (Simon 1985). Groves et al., (1982), working on dormancy and germination in *Themeda australis*, noted that *T. triandra* and *T. austrilis* are "closely related, if not identical". Later Simon (1985) reviewed the nomenclature of *T. australis* and *T. triandra* concluded that there was not enough distinguishable difference between the two to warrant the split. In Australian literature, some still refer to *T. triandra* as *T. australis* but generally the species is referred to as "*Themeda triandra* Forssk. Syn *T. austrailis* (R.Br) straf. Theunissen (1992a) highlights the fact that the present taxonomic classification of *Themeda* and other grasses is "unsuitable for critical use by ecologists" as it underestimates the variation and ecological importance of such variation. This indicates that a more ecological classification, taking the causes of variation into account, may be more appropriate. However, a few studies have been attempted, without much success, to resolve which selection processes have been important in producing variation in *Themeda* (see Evans and Knox, 1969; Groves, 1975). The causes of variation in *Themeda* and their ecological significance are therefore not yet understood and in the rangeland science literature, it is still generally treated without distinction as a single taxonomic entity.

Compounding the issue is that although numerous investigations have been conducted on *Themeda*, these studies have been carried out in a few areas that may not necessarily incorporate or represent the broad range of climatic and environmental conditions in which *Themeda* occurs. Ndalula-Senimba (1972) pointed out that the majority of work on the behaviour and ecology of *Themeda* (in different plant associations) had been carried out in only a few localities such as South Africa and Zimbabwe. Within South Africa, research on the development and behavioural responses of *Themeda* has received considerable attention but this work has been particularly concentrated in the humid parts of the country, whereas such studies are lacking in the sweet grassveld of the Eastern Cape (Danckwerts, *et al*., 1984). This results in a situation where research results from a few areas are often broadly and perhaps inappropriately applied.

The current decline of *Themeda* in certain areas may be partly a function of the lack of appreciation and understanding regarding the extent, nature, causes, implications and ecological significance of variation in *Themeda*, coupled with the broad application of research results drawn from only a few selected areas. A new framework needs to be developed, which takes the variation in *Themeda* into account within the context of the processes important in producing this variation.

1.2 Thesis aims and predictions

The aims of this thesis were:

- To investigate the nature, extent and ecological significance of variation in *Themeda.*
- Determine the key factors that lead to variation.

- Assess the feasibility of using different forms of *Themeda* as indicators of processes important in regulating grassland dynamics.

I explore the following hypotheses:

- Populations of *Themeda* have evolved adaptations to their local environment, reflected as differences in life history strategies.
- Plant density-dependent processes and rainfall (amount and predictability) are the key factors resulting in the ecological adaptations of populations of *Themeda* but the relative importance of these processes differs depending on the climatic regime of the given area.
- Density-dependent processes will be more influential in predictable and/or high-rainfall environments.
- Rainfall will be more important in areas with low and/or unpredictable rainfall, typified by a high co-efficient of variation in rainfall.
- Populations in predictable high-rainfall regions will be characterized by K-selected strategies, with population structure primarily maintained through vegetative propagation. Productivity will mostly be a function of density-dependant processes (self-shading).
- Populations in low/unpredictable rainfall regions will be characterized by r-selected strategies, with greater dependence on propagation by seed to maintain population structure. Here productivity will be a function of rainfall.
- These different strategies will be reflected as variability in the allocation patterns, morphology, life history attributes, population biology and ecology of populations occurring over environmental gradients.
- Variation observed among *Themeda* populations is genetically based.

1.3 Thesis layout

Site descriptions are given in Chapter 2.

Chapters 3, 4, 5 and 6 each deal with the research conducted to test the above hypotheses. Each of these chapters provides a brief literature review, more specific predictions, methodology, presentation of results and discussion of the relevant aspects investigated within that chapter.

In Chapter 3, the nature and extent of morphological and phenological variations of *Themeda* from the four field populations were investigated. Clonally propagated plants and plants propagated from seed, and grown under controlled conditions, were used to verify a genetic basis for the variation recorded from field populations.

Chapter 4 surveys allocation patterns of four *Themeda* populations in terms of reproductive and vegetative effort and phenology. Growth analyses were conducted on plants grown from seed to determine whether observed differences in allocation in field populations had an inherent genetic basis. Analysis of some of the leaf traits of the seedlings complemented these results.

Chapter 5 addresses the question of the ecological significance of the variation in morphology and allocation patterns determined in Chapters 2 and 3. This was done by testing the relative importance of rainfall, shading and carry-over effects in determining productivity in greenhouse and field experiments.

Chapter 6 deals with the population biology of *Themeda*. Here, population structure, seedbank dynamics and seed biology were investigated to test whether differences in allocation patterns had ecological significance in terms of population demography and persistence.

Chapter 7 provides a synthesis of the results from the preceding chapters within the context of the broader aims of the thesis, and discusses the management implications of the results.

2 Description of study areas

Four study areas in South Africa were selected on the basis of three main criteria: rainfall, coefficient of variation in rainfall and *Themeda* dominance. The sites chosen were representative of a rainfall gradient from low unpredictable rainfall to high predictable rainfall. These areas were: Trompsberg (low, unpredictable rainfall, droughts common), Hluhluwe-Umfolozi Park (HUP) (variable rainfall, inter-annual wet/dry cycles; periodic droughts); Ukulinga (moderately mesic, predictable rainfall); Kamberg Nature Reserve, (mesic, predictable rainfall) Figure 2.1. Descriptions of each of these areas are given below. The relevant location, veld types and climatic data is summarised in Table 2.1

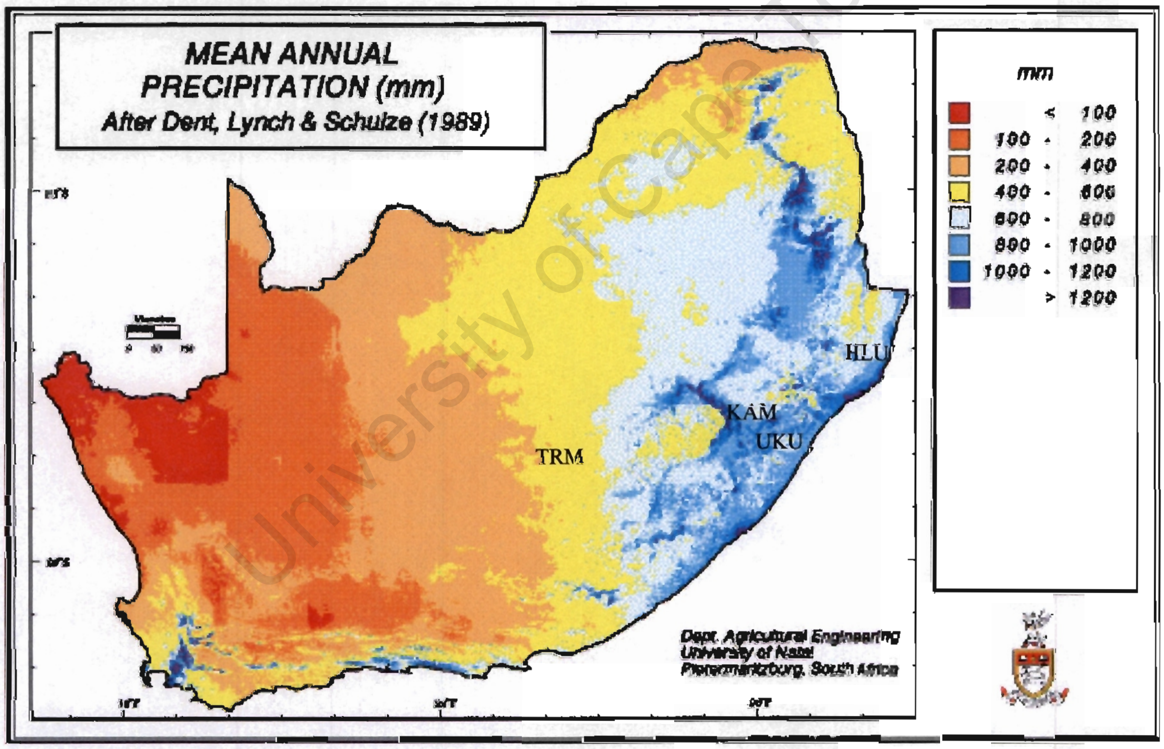

Figure 2.1 Precipitation map of South Africa taken from Dent et al., (1989) showing the position of the study areas. TRM=Trompsberg (semi arid, droughts common); HLU=Hluhluwe (tropical, variable rainfall, periodic drought); UKU=Ukulinga (moderately mesic, predictable rainfall); KAM= Kamberg (mesic, cold winters).

Methodologies employed required the sampling of different aged swards of *Themeda* at each study area. Where possible, these sites were adjacent to each other, but in some cases this was not possible.

Trompsberg: Semi arid

The Trompsberg area is semi arid to arid, with high inter-annual variation in rainfall and droughts being relatively common. The majority of rainfall occurs in late summer (February). Seasonal temperature fluctuations are marked, with hot summers and cold winters, associated with a high incidence of frost, Table 2.1. Fires are considered disastrous by the farming community and are avoided at all costs. The main sources of fire in the area are those started on the road verges by passing travellers (cigarettes and glass). When fires do start, every effort is made to put them out. The landscape is generally flat, interspersed with occasional "koppies"(hills), Figure 2.2.

The work conducted in the Trompsberg area took place on 2 farms, both of which produce sheep and cattle. It was necessary to use two farms due to the rarity of recently burnt sites in this area. Hillside farm is owned by Dinny Howell and is situated to the south of Trompsberg, just off the N1. Dinnie's late father, a close friend of Acocks, introduced a high-density rapid rotation grazing in the mid 1900's. The strategy, based on the principles of non selective grazing, involves many small paddocks where animals are moved about every three weeks and the return time to a grazed paddock is preferably more then 7 months and is strongly advocated by the owners (see Tainton, 1972). The site used on this farm had last been burnt in 1939, but had been heavily grazed prior to the commencement of the study. Flip Henning owned the other farm, situated a few kilometres (~10) north of Trompsberg. Flip uses fewer paddocks that are much larger, resulting in slower rotation times. A portion of Flip's farm was burnt accidentally in May of 1995. None of the areas sampled had been grazed for at least 6 months prior to a given sampling event. For clarity these sites are collectively referred to as the Trompsberg sites, but where relevant the grazing and fire histories are given.

Figure 2.2 15-month post burn sward of *Themeda* in the Trompsberg area (semi arid).

Hluhluwe Umfolozi Park

Hluhluwe-Umfolozi Park (HUP) is one of the oldest reserves in South Africa, situated in the northern part of KwaZulu Natal. Initially established as two separate reserves over 100 years ago, Hluhluwe and Umfolozi Game Reserves were joined in the late 1980's, with the joined total area of the park extending over about 900 km^2 (Brooks and Mac Donald, 1983). HUP supports a wide range of indigenous fauna and flora, representative of a functioning savanna ecosystem.

The climate of HUP is tropical and frost free with a long growing season (Table 2.1). Rainfall is usual higher in the northern section (Hluhluwe) 985mm, decreasing towards the south (Umfolozi), about 600mm. Most of the rain falls in the mid summer months with dry periods from June-August (Brooks and Mac Donald, 1983). Climatic analysis shows periodic fluctuations in rainfall, producing wet and dry phases of between four and ten years in length (Balfour and Howison, 2001). Work conducted for this thesis was restricted to the Hluhluwe section of the park. Hluhluwe is characterised by a hilly landscape, ranging in altitude from about 750m to about 70m.

Three study areas, with different climatic conditions within Hluhluwe, were used for investigations. The initial intention was to choose two sites within the park representing extremes of the rainfall gradient (dry and wet). The initial "dry" site was on the Corridor road (referred to as the Corridor site or Hluhluwe "dry"). However, this site had to be abandoned after the first set of experiments since the local community unexpectedly harvested the grass in the area for thatch. A second "dry" site was therefore selected for the remaining experiments, referred to as the Nqumeni site. The "wet" site was situated to the far north of the park in the Magangeni area, and is referred to as the Magangeni site (or Hluhluwe "wet"), Figure 2.3.

Where relevant in the text and results sites are referred to individually. For general discussions, or experiments where only one site was used (commonly Magangeni), the area is referred to as Hluhluwe (tropical, wet/dry cycles, variable rainfall and periodic drought).

All sites were subject to natural utilisation by indigenous animals. However sites were specifically chosen in areas where animal densities were low in an attempt to mitigate the effects of heavy grazing. The primary consumers of *Themeda* in HUP are buffalo, Figure 2.4, which occurred in low densities around the sites chosen.

Unlike the semi arid study area (Trompsberg) fire is an integral part of the management strategy in HUP. Fire frequency is dependent on fuel load. During wet cycles a given area is generally burnt biannually although annual burns may occur. Burning is less frequent in drier years. Each of the areas chosen had burning frequencies staggered on either side of the road. For example at Magangeni the western side of the road had been burnt in 1995 whereas the eastern side had been burnt in 1996.

Figure 2.3 Characteristic tall form of *Themeda* (15 month post burn) occurring at Magangeni in HUP (variable, wet/dry rainfall cycles interspersed with drought).

Figure 2.4 African buffalo in HUP, the primary consumers of *Themeda.*

Ukulinga

Ukulinga is a research farm, 8 km's to the south east of Pietermaritzburg, run by the University of Natal, Pietermaritzburg. Work was conducted on the "plateau" of the research farm (Figure 2.5). This area is described as moderately mesic, with predictable summer rainfall, moderate seasonal fluctuations in temperature and occasional winter frost, Table 2.1. This area is usually burnt biannually. The last burn prior to the commencement of this study (1996) was in July 1995. Half the area was burnt again in September of 1996 and the other half was burnt in August of 1997. In the year prior to 1995 there was moderate grazing by cattle on the plateau but during the study grazers were absent from the area.

Figure 2.5 One-year post burn sward of *Themeda* on the plateau at Ukulinga research farm, near Pietermaritzburg, (moderately mesic).

Kamberg Nature Reserve

Kamberg is situated in the foothills of Ukhahlamba Drakensberg Park (Figure 2.6). This montane area is mesic, with high predictable summer rainfall with a low coefficient of variation in rainfall. Seasonal fluctuations in temperature are marked; winters are very cold associated with frost and sometimes snow. Different blocks in the area are burnt at different frequencies. For the purposes of this study, the main areas used for the study are biannually burnt. Two blocks were used, the first, called the "camp" site was burnt in April 1995 and August 1997, the second block, called the "wattle" site was bunt in August 1996. A third block called Stillerust, which is burnt annually, was incorporated into some demographic studies.

The reserve supports low densities of indigenous wildlife, the most common grazers being black wildebeest. However these were in low densities and grazing impacts were considered to be negligible at the sites chosen.

Figure 2.6 Early year post burn sward of *Themeda* in Kamberg Nature Reserve in the Drakensberg, (mesic predictable rainfall, very cold winters).

Table 2.1 Climatic data, based on long term statistics, for the four study sites used in the investigations.

	Trompsberg Fauresmith (29° 46'S; 25° 19'E)	Nqumeni Mpila (28°18’S; 31°51’E	Corridor	Magangeni	Ukulinga PMB (29° 36'S; 30° 26'E)	Kamberg Cedara (29°32’S; 30°17’E
Location (lat, long)	$30^0$03’ $25^0$78	28° 12’ 21” 31° 57’ 07”	$28^0$13’24’’ $31^0$00’15’	28° 04’ 32” 32° 07’ 20”	$29^0$40’ $30^0$24’	$29^0$37’ $29^0$70’
Elevation (m)	1433	300	220	150	762	1525
Mean annual rainfall, mm.yr^{-1}	419 (1913-2002)	690	650	900	844	1049 (1953-2002)
CV rainfall	30-35%	25-30%	25-30%	25-30%	20-25%	<20%
Mean max temp	24.2	27.4	**35	**35	25.5	22.4
Mean min temp	8.6	16.8	**13	**13	11.4	9.9
Mean temp.	16.4	22.1	unavailable	unavailable	18.5	16.2
Temp range	15.6	10.6	unavailable	unavailable	14.2	12.5
Days Min temp. <5°C	118	0	0	0	67	75
Days,0°C	45	0	unavailable	unavailable	13	9
Recorded period	1961-1990	1981-1990			1961-1990	1961-1990

* Rainfall data comes directly from each site but temperature data comes from the closest South African Weather Bureau station recording temperature, as indicated below the site names.

** Greyling and Huntley, 1984

3 Characteristic traits and phenotypic plasticity among the study populations of *Themeda*

3.1 Introduction

Themeda plants from different localities vary in their appearance (Woodland, 1964; Ndawula-Senyimba, 1972; Groves, 1975, Downing and Groves, 1985). Distinctive traits are often retained in plants cloned from field populations or germinated from seed and grown under controlled conditions, indicating that differences reflect genetic divergence and not just phenotypic plasticity (Theunissen, 1992; Groves, 1975, Downing and Groves, 1985). Further evidence for the divergence is the variation in the chromosome number among populations (Brown and Emery, 1957; Gluckman, 1951; Woodland 1961; Birari, 1981; Liebenberg, 1986; Fossey and Liebenberg, 1987; Spies and Gibbs Russel, 1988b; Liebenberg, 1990; Fossey and Liebenberg, 1992; Liebenberg, *et al.*, 1993). This is consistent with a general pattern in which grasses are known to have greater genetic differentiation among populations compared to other species (Godt & Hamrick, 1999). Patterns of high divergence in the grasses have been attributed to the high percentage of selfers within the grasses relative to other species.

The breeding systems of *Themeda* display “considerable versatility” (Evans & Knox, 1969) in that the proportion of sexual versus apomictic embryo development differs among populations and chromosome race. For example, Evans and Knox (1969) reported that some diploid races were entirely sexual whereas some tetraploids were almost wholly apomictic but most had both to varying degrees. Since the distribution of genetic diversity is strongly associated with the breeding system of a plants (Godt & Hamrick, 1999) differences in genetic diversity can be expected among populations of *Themeda* with differing combinations of sexual to asexual breeding systems. Asexual breeding systems may assist in preserving a winning combination of genes/characteristics under certain conditions whereas genetic flexibility associated with sexual genotypes may be more advantageous in other conditions. Variation in the breeding systems among populations of *Themeda* is likely to have an effect on the divergence and gene flow among populations.

The purpose of this chapter is to explore divergence and determine and describe *key characteristics* distinguishing the field populations of *Themeda* chosen for investigation. The approach was to focus on differences in gross morphology (architecture) and growth characteristics, rather then cytology and floral biology, that are easiest to measure (as recommended by Tcacenco and Lance (1992)) and are the most practical variables for managers to use when assessing variation in the field. Differences in such characteristics may also have important ecological implications in terms of plant response. Variables used to define characteristics were kept as simple as possible for rapid field assessments using traits that would reflect the ecological characteristics of the respective forms rather than their taxonomic distinction.

The extent to which distinctive morphological traits and growth characteristics of field populations are genetically fixed, rather then environmentally controlled was also assessed. This was done by growing both plants collected from field populations and plants germinated from seed collected from the study sites under controlled conditions. These results may also provide an indication of whether there are differences in the degree of plasticity among the populations.

3.2 Methods

3.2.1 Characteristics of natural field populations of *Themeda*

3.2.1.1 Morphological characteristics

At each site listed in Table 3.1, 25 tussocks were randomly selected for sampling. In the field, maximum height of flowering tillers (held erect) and maximum height of vegetative canopy were measured with a tape measure. One flowering and one vegetative tiller were then harvested from each tussock at ground level and taken back to laboratory for assessment. The number of visible nodes, aerial tillers and branches (elongating aerial tillers) per tiller were counted and the maximum height of aerial tillers initiation was recorded (Figure 3.1& Figure 3.2). In flowering tillers stem diameter was determined at the lowest node from which flowers were initiated and uppermost visible node in the case of vegetative tillers (Figure 3.1& Figure 3.2). Tillers were cut at these points and the diameter across the cut was measured with callipers. Seed production per flowering tiller was determined by counting the number of spikelets on the flowering head, (Figure 3.1).

Data from the one and two year post burn sites were combined for analyses performed in this chapter. Data on seed production is analysed in more detail in chapter 4.

Table 3.1 Populations for which morphological characteristics of *Themeda* were assessed. Populations burnt < 14 months prior to assessment are referred to as one year post burn sites whereas those burnt more then 14 months prior to assessment are referred to as two year post burn sites.

Site	Last burn	Collection date	Post burn age at collection
Magangeni (moist tropical, no frost)	7/96	2/97	7 months
	7/95	2/97	19 months
Corridor (dry tropical, no frost)	7/96	2/97	7 months
	7/95	2/97	19 months
Trompsberg (semi-arid, severe frost)			
	5/95	2/97	21 months
Ukulinga (mesic moderate frost)	9/96	11/97	14 months
	7/95	11/97	28 months
Kamberg (wet, severe frost)	8/96	2/97	6 months
	4/95	2/97	24 months

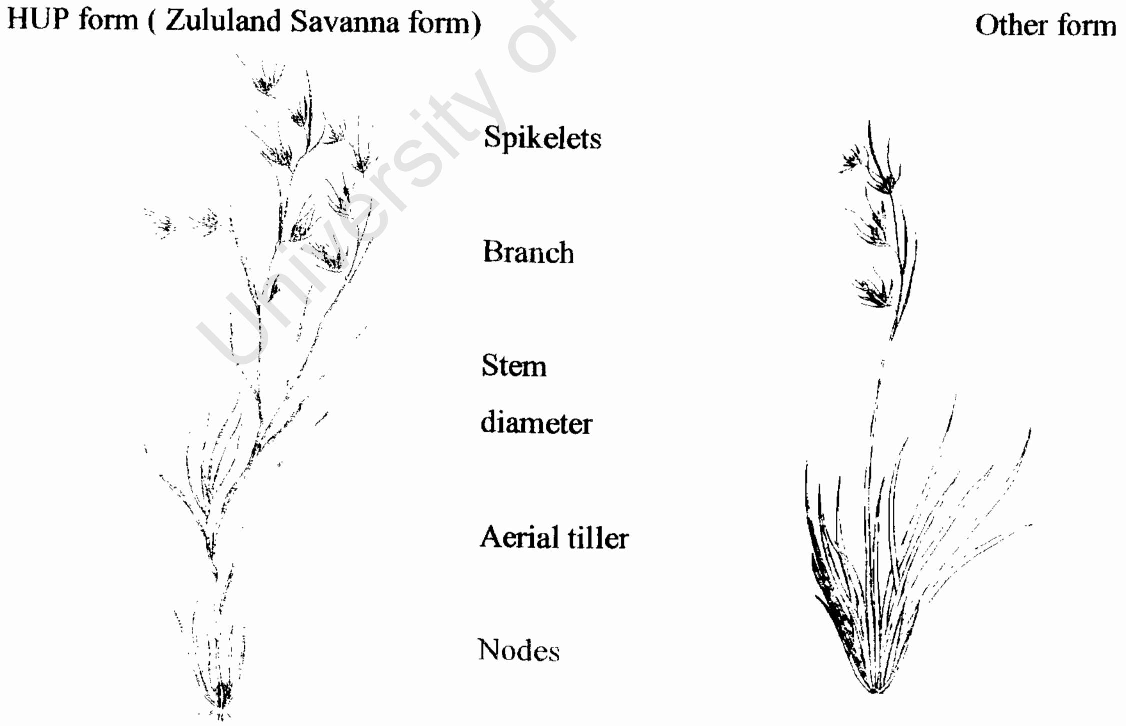

Figure 3.1 Diagrammatic representation of morphological characteristics measured on flowering tillers collected from one and two-year post burn field populations of *Themeda* at the sites listed in Table 3.1. (Note HUP form is the Zululand Savanna form)

Figure 3.2 Diagrammatic representation of morphological characteristics measured on vegetative tillers collected from one and two-year post burn field populations of *Themeda* at the sites listed in Table 3.1

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From this initial study it became clear that vegetative tillers could be further subdivided into more informative functional categories, the abundance and extent of which varied among populations. The following categories were identified and are illustrated in Figure 3.3.

Basal: the classic vegetative tiller where stems are condensed and secondary tiller development occurs laterally.

Elongated tillers: Tillers in which the stem starts to extend vertically.

These could be further divided:

Elongated vegetative tillers: the stem is elongated slightly with just one or two nodes visible and the majority of phytomers condensed around the apical node which is only elevated several centimetres above the soil surface. Scott and Rabie (1956) also reported on the ability of vegetative tillers to elongate.

Immature reproductive tillers: stem and apical bud extend, revealing more nodes and greater internodal distances with regular and well separated phytomers compared to elongated vegetative tillers. It should be noted that for the above-described morphological study the “vegetative” tillers used in Magangeni and Corridor sections were subsequently classified as immature elongating reproductive tillers. However, dissection of the apical region is the only way to tell with certainty whether a tiller is reproductive or vegetative, therefore tillers thought to be immature reproductive tillers had to be combined with the elongated vegetative tiller category in these investigations.

Aerial tillers: initiated from the axial/nodes of phytomers on elongating stems of parent tillers (elongated vegetative, immature reproductive and mature flowering tillers). A separate study (not reported here), shows that the position of aerial tillers varies considerably among the ecotypes.). Mean maximum height of aerial tiller initiation was as follows: 96.9 cm in Magangeni; 25.4 cm in Ukulinga, 11 cm in Kamberg and 9.6 cm in Trompsberg populations. Aerial tillers also had the ability to elongate, in turn producing tillers referred to here as *secondary* or even *tertiary aerial* tillers. These were mainly seen in Magangeni populations where it was not uncommon for elongating aerial tillers to flower.

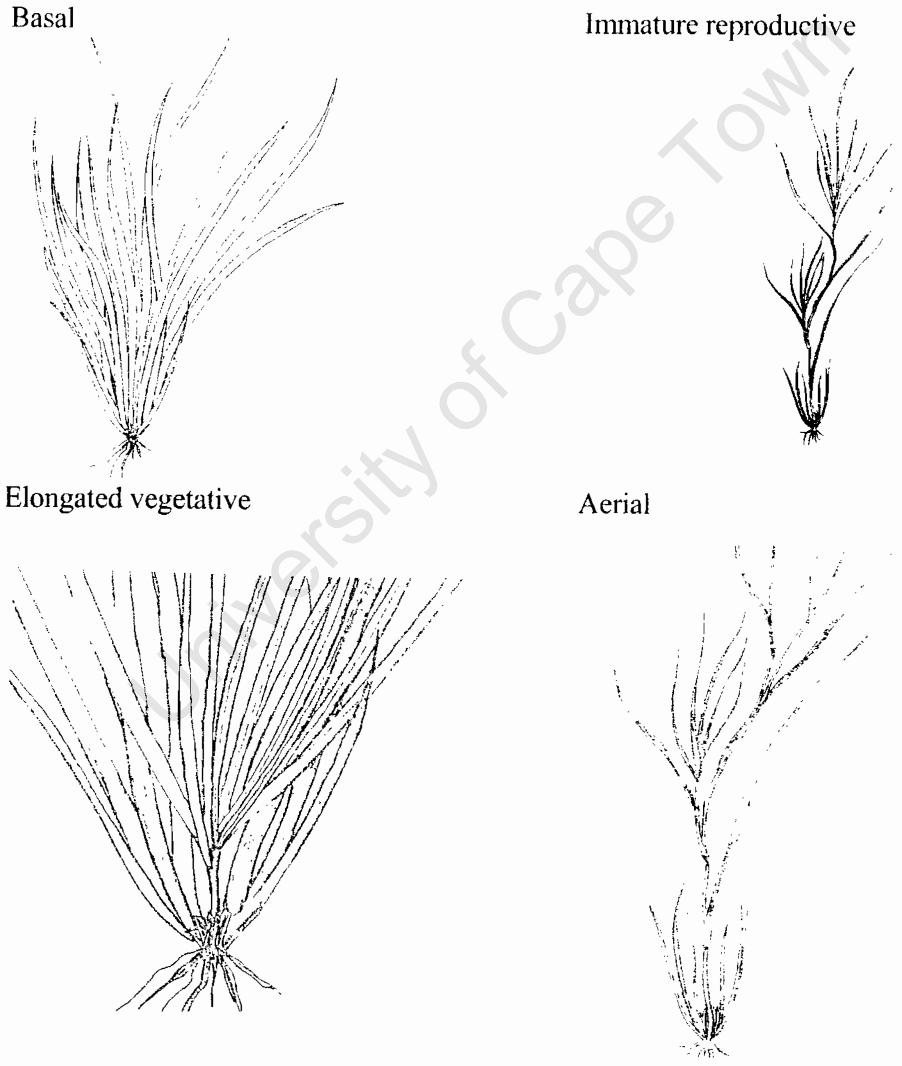


Figure 3.3 Diagrammatic representation of the functional categories of tillers identified after the initial study was conducted.

3.2.1.2 Growth characteristics

Studies on morphological characteristics revealed that the proportion of the different functional tiller types and the time to anthesis might be important traits distinguishing populations and influencing their appearance. Eight-month-old post burn stands of *Themeda* were used (see Table 3.2) to investigate differences in proportions of various functional tiller types among the study populations. The rationale for using recently burnt sites was two fold. Firstly, differences that may be attributed to inherent tiller development characteristics are more clearly detectable. Secondly, light conditions among the sites, which may affect tiller development, were more consistent among sites compared to older stands.

Table 3.2 Populations used to investigate growth characteristics (tiller proportion and biomass per unit area).

Site	Last burn/graze	Age of stand harvested
Nqumeni (dry tropical, no frost)	8/97	8 months
Magangeni (moist tropical, no frost)	8/97	8 months
Trompsberg (semi-arid, severe frost)	High density grazing 9/97	7 months
Ukulinga (mesic, moderate frost)	6/97	10 months
Kamberg (wet, severe frost)	8/97	8 months

Note that the Nqumeni site (dry, tropical, no frost) is equivalent to the Corridor population, which for reasons described in chapter 2, could not be used for further investigation.

At each site listed in Table 3.2, the above ground material from ten randomly selected tussocks was harvested in May 1998 (towards the end of the growing season). Clear transparencies were used to trace the basal area after harvesting. These were later traced onto black paper, cut out and fed through a licor leaf area meter to determine area per tussock in cm^2. Harvested material was divided into the following categories: basal tillers, elongating tillers (immature flowering + elongated vegetative), reproductively mature tillers, aerial tillers (from reproductive tillers and elongating tillers). The number of tillers per category was counted. Dry weights of each category as well as dead litter biomass per unit area were determined after drying plants at 75°C for 48 hours. These data are analysed in more detail in chapter 4.

Statistical analyses

Statistical analyses were performed in order to: a) determine if there are significant differences among populations and b) identify important variables that distinguish the populations from each other. Three discriminant function analyses (DFA) were used for this purpose: firstly, morphological data (combining one and two year post burn ages) were analysed. The second DFA used the data on growth characteristics. The third DFA then incorporated a combination of morphological and growth data, where variables identified as important in discriminating groups in the two preceding analyses were assessed.

Three recommendations when performing DFA's are that: there is no co-linearity (resulting from highly correlated variables); that there are five replicates per group (population) per variable and that the variables used are common/measurable in all groups (i.e. no zero frequencies for any groups) (Statistica 5.1). A Correlation matrix was therefore produced for traits that were measurable in all populations. Where traits were highly correlated, only one trait was selected for the analysis.

3.2.2 Plants grown under controlled conditions

Two sources of material were used to determine whether characteristics of field populations of *Themeda* are maintained under controlled growing conditions in a greenhouse: plants cloned from field-collected tussocks and plants grown from seed collected from study populations.

Clonally propagated plants

Plants were collected from Magangeni, Trompsberg, Ukulinga and Kamberg populations in July 1996 (dormant season) for propagation. The above ground material was cut approximately 4-5cm from the base leaving only stubble from which new growth would occur. The plants were transported in plastic bags to the University of Cape Town. All soil was washed off the roots. Individual samples (roughly 4x4cm) were placed into pots (40cm long, with a 15.5cm diameter). There were 60 pots per ecotype. Pots were made of PVC piping. Squares of 90% shade cloth were glued on as bases with Tangit PVC weld. The soil media was a sand/perlite mix of 4:1.5. Plants were grown under controlled greenhouse conditions at the University of Cape Town.

The plants were used in a 2-phase experiment equating to two growing seasons. During the first phase (one growing season) plants were given equal amounts of water and light whereas the effect of light and water treatments on productivity were tested in the second phase/season of growth (see chapter 5 for details on treatment). In the first season of the experiment plants were watered three times a week; twice with (400ml) de-ionised water and once with (400ml) 1/4 strength Rorrison nutrient solution (Band, and Hendry, 1993). After seven months the amount of water was reduced to mimic the onset of the dry season during which plants become dormant but nutrient solution applications continued. Occasionally salts would build up due to the application of nutrients. When this happened nutrient applications were substituted with deionised water. Pots were moved every 5 weeks to control for positional effects.

Plants grown from seed
Flowering culms were collected in January/February 1997 from Trompsberg and Magangeni populations. These were air dried on wire mesh racks in laboratory in Cape Town. Mature seeds that dropped though the mesh were then collected and de-awned. Dr Ed Granger (University of Natal Petermarizberg) supplied seeds collect from Kamberg Nature Reserve in December/January 96/97. Culms had been collected by hand and then put though a hammer and mill system in order to clean the seed. Unfortunately there was no seed available from the Ukulinga site.

Seeds were stored in glass containers in the laboratory. On commencement of the experiment, seeds were dusted with APRON to avoid fungal infections and then germinated in plastic petri dishes on three layers of Whatman filter paper in a controlled germination chamber with a 12/12 day night, 25°C /15°C cycle. Filter paper was moistened when necessary with distilled water. After three weeks viable seedlings were transplanted into pots (40cm long with a 15.5cm diameter), containing acid washed sand. Plastic beads were places around the seedlings on the surface of the sand to avoid desiccation. For the first two weeks pots were also covered with clear cling wrap plastic to keep the top layer of sand from drying out. For the first three weeks seedlings received 200ml de-ionised water per day. Thereafter 400 ml of 1/8 strength Rorrison solution was applied three times per week for one month, after which the strength of the solution was increased to ¼ strength. The experiment took place under controlled greenhouse conditions where the temperature was maintained at 25^{0}C/15^{0}C cycle. Pots were moved into randomised position every two weeks to control for positional effects. Plants were harvested 5 and a half months after germination.

3.2.2.1 Morphological characteristics

Clonally propagated plants

Morphological traits were measured at the end of the second phase of the experiment. The maximum height of the flowering culms, and the length and number of nodes of one randomly selected flowering tiller per pot were determined where possible. The number of aerial tillers per reproductive tiller was calculated at the final harvest by dividing the total number of aerial tillers occurring on reproductive tillers for a given pot, by the number of flowering tillers of that pot.

Seedlings

The number of nodes and aerial tillers on elongating and flowering tillers were recorded.

3.2.2.2 Growth characteristics

Clonally propagated plants

After the first season of growth (10 months) the number of tillers in the following categories was counted: vegetative (where basal and elongating tillers were combined), aerial, and flowering tillers in each pot (n=60 per ecotype). The length and breadth of each plant was measured with a ruler as a crude measure of the area of the plant. Of the 60 replicates for each site 35 were randomly selected and the above ground material harvested. Dry mass for each of the above mentioned categories as well as dead litter biomass was determined after oven drying samples in brown paper bags at 75°C for 48 hours.

At the end of the second growing season, live plants were harvested, tillers were separated into the following categories: basal, extending, aerial and flowering. The number of tillers in each category was counted. Dry mass for each of the above mentioned categories as well as dead litter, root and stubble (junction between root and tillers) biomass was determined after oven drying samples in brown paper bags at 75°C for 48 hours.

Seedlings

For each plant the number of basal, extending, flowering, and aerial tillers were recorded. The dry weights of these categories as well as root, stubble and dead litter were recorded after drying plants at 75°C for 48 hours.

Statistical analyses

High mortality in the second growth season in clones resulted in poor replication for analysing the morphological characteristics in some populations. Statistical analyses could therefore not be conducted. Results are presented as box and whisker pots.

Results from investigations of growth characteristics of clones measured after the first growing season were analysed in the same way as those for field populations, using discriminant function analysis to determine if populations could be separated using these characteristics after ten months of growth under controlled conditions.

3.2.3 Phenotypic plasticity

3.2.3.1 Morphological characteristics

Where possible, data collected from seedlings and clones are compared to those of field populations to determine if traits of field populations are maintained under controlled conditions and to assess whether the traits found by DFA's to be important in discriminating among groups were evident in plants grown under controlled conditions. Poor replication in cloned plants again prevented statistical analysis. Data are however graphically compared using means, mean standard error and mean standard deviations. It is generally assumed that if one group's mean falls out side of another groups mean standard error, the means are significantly different (Murray, 1961).

3.2.3.2 Growth characteristics

Traits used in discriminant function analysis for growth characteristics of field populations were used to compare differences between field populations and plants grown under controlled greenhouse conditions. As with morphological characteristics, comparison was though graphic representation of means, mean standard error and mean standard deviation.

3.3 Results

3.3.1 Characteristics of field populations

3.3.1.1 Morphological characteristics

Data from investigations of morphological characteristics of field populations of *Themeda* are presented in Figure 3.4 and Figure 3.5. Magangeni and Corridor plants are taller, have bigger stem diameters and have significantly more nodes and aerial tillers on flowering tillers then the other ecotypes. Aerial tillers are virtually absent in Trompsberg populations. The position of aerial tillers in Kamberg and Ukulinga plants differs to that in Magangeni and Corridor populations in that they were generally found on the lower nodes and seldom exceeded the height of the vegetative canopy of basal tillers. Aerial tillers in Magangeni and Corridor plants, however, were found at regular intervals on the upper nodes of elongating stems, contributing to increasing the height of the canopy. As reported earlier, the mean maximum height of aerial tiller initiation is greatest in Magangeni specimens (96.7cm) followed by Ukulinga (25.4), Kamberg, (11cm) and lowest in Trompsberg (9.6cm). “Branching” is a distinctive feature of Corridor and Magangeni populations. Seed production per reproductive tiller was greatest in Magangeni followed by the Corridor and Trompsberg ecotypes. Seed production in Ukulinga and Kamberg ecotypes is relatively low. The variation among Magangeni plants was generally high compared to other ecotypes and lowest among Trompsberg plants.

Differences in the characteristics of vegetative tillers (Figure 3.5) among field populations are mostly a function of the fact that the tillers collected for morphological assessment consisted of several functional categories of tillers, which varied in their proportions among sites. These functional types included immature flowering, basal or elongated vegetative tillers. Vegetative tillers used for Magangeni ecotypes were generally thought to be immature flowering tillers and therefore not truly vegetative. The vegetative tillers used for Kamberg and Trompsberg were only those in the basal tiller category, while there were a combination of basal and elongated vegetative tillers found in the Ukulinga populations. An assessment of each individual category of these functional tiller types would have been more useful for morphological comparison. Data suggests (see figure 3.5d) that the proportion of tillers in different categories vary among ecotypes, reflecting differences in growth and development traits among populations.

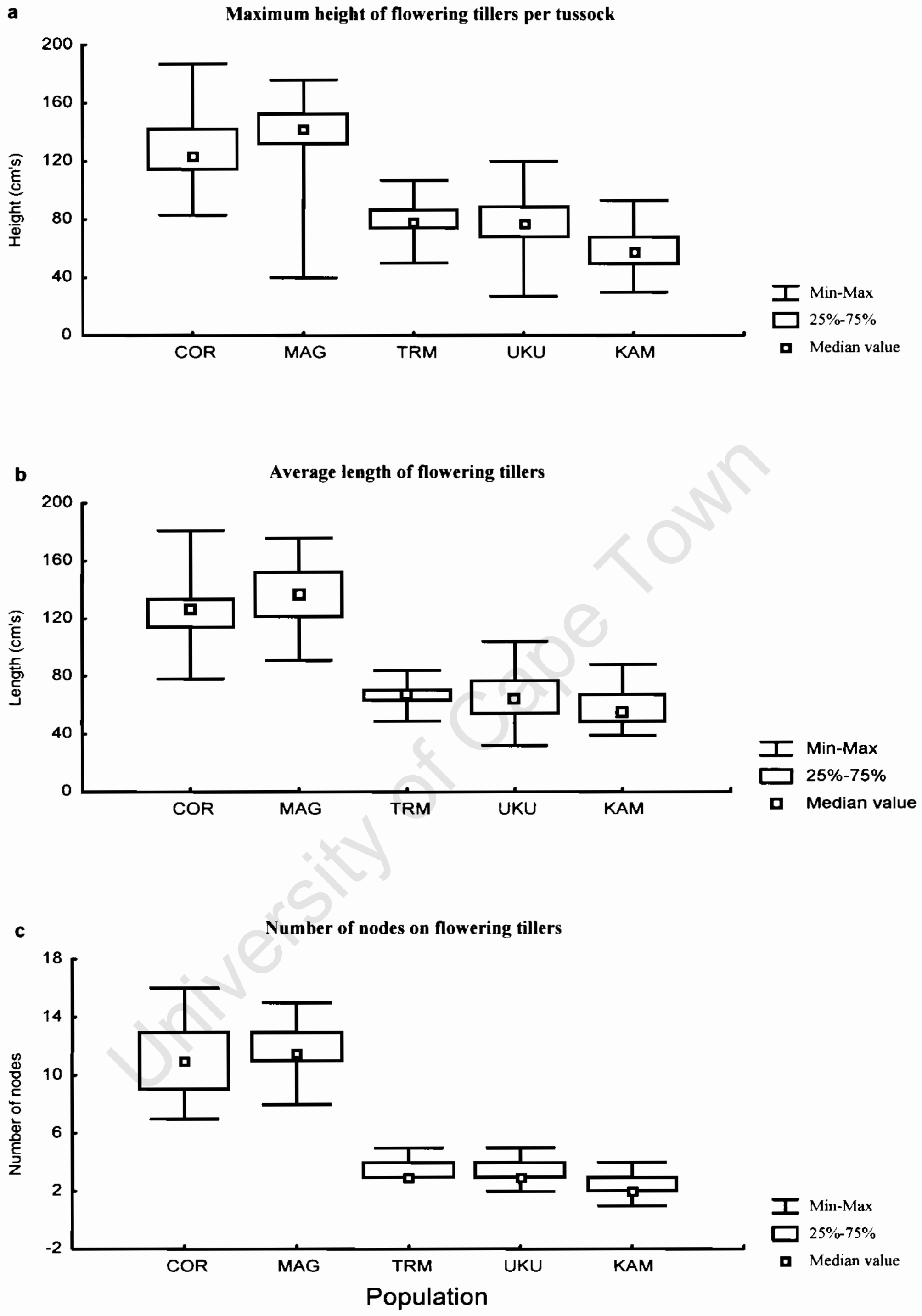
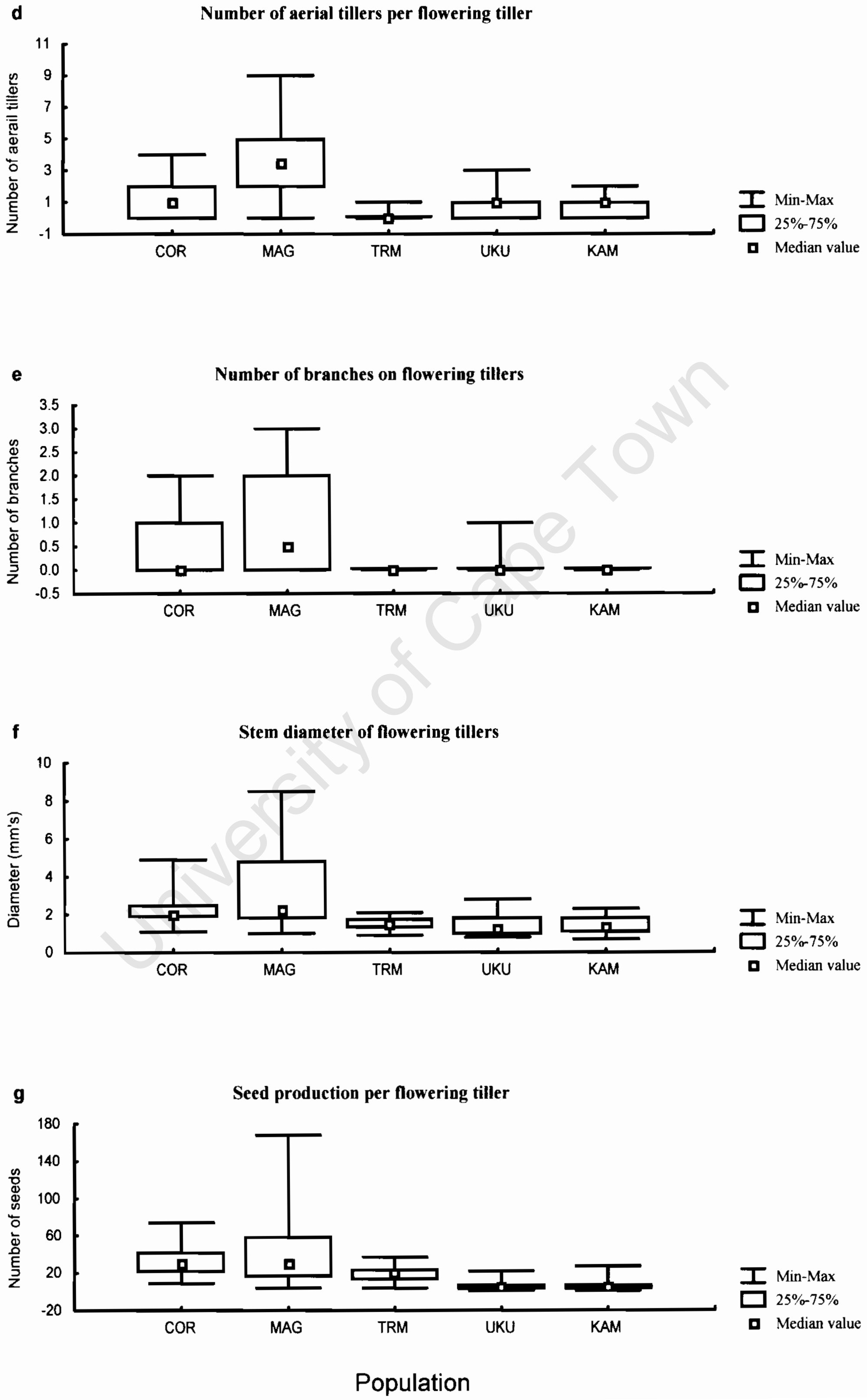


Figure 3.4 Box and whisker plots (median, range and quartiles) for data collected on the morphological characteristics of reproductive tillers collected from field populations of *Themeda* listed in Table 3.1. N=50 for Corridor, Magangeni, Ukulinga and Kamberg. N=25 for Trompsberg. COR = Corridor (dry tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

Figure 4 Cont.



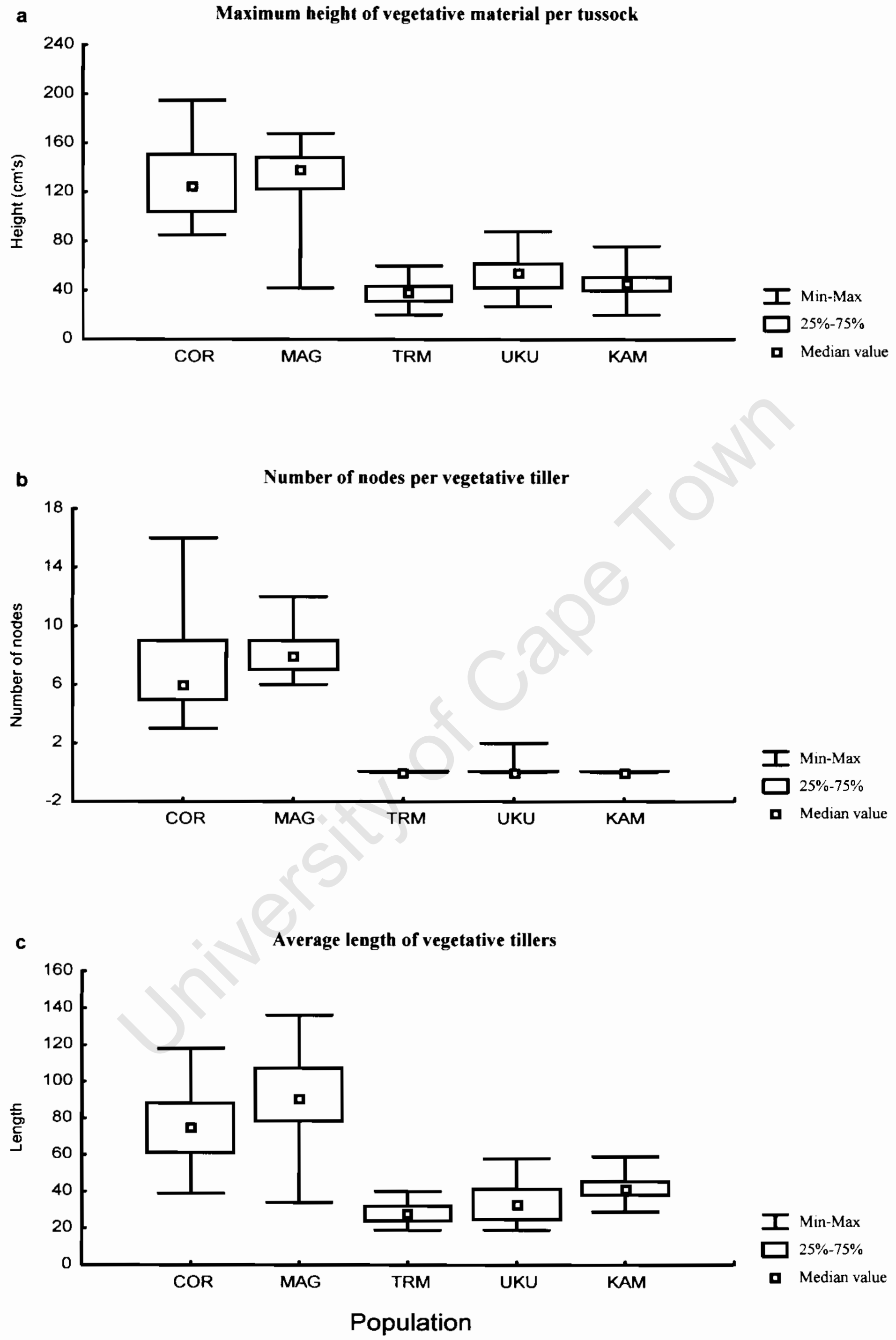
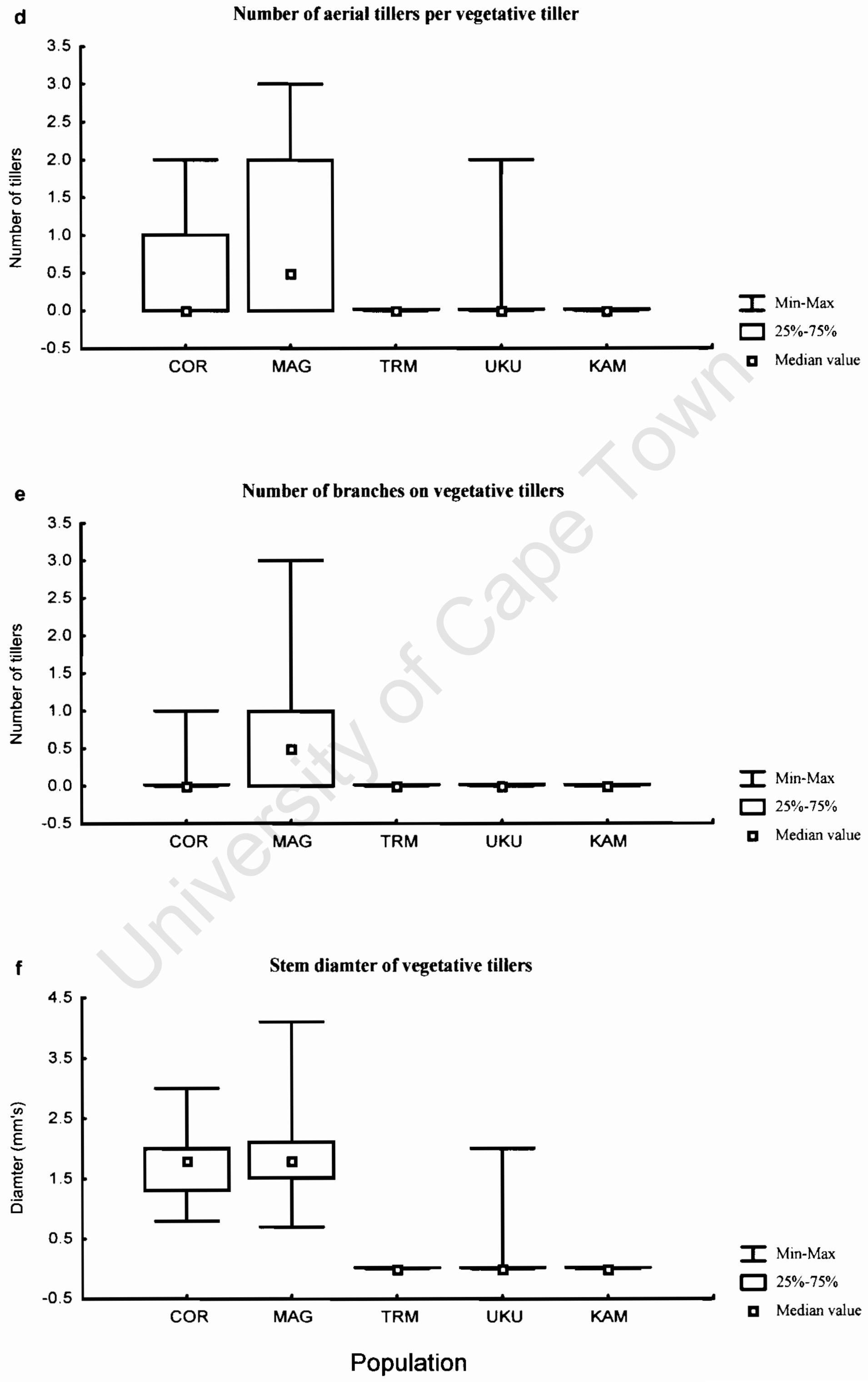


Figure 3.5a-f Box and whisker plots (median, range and quartiles) of data collected on morphological characteristics of vegetative tillers collected from the field populations of *Themeda* listed in table 1. N=50 for Corridor, Magangeni, Ukulinga and Kamberg. N=25 for Trompsberg **COR** = Corridor (dry tropical, no frost); **MAG** = Magangeni (wet tropical, no frost); **TRM** = Trompsberg (semi-arid, high frost); **UKU** = Ukulinga (mesic, moderate frost); **KAM** = Kamberg (high rainfall, high frost).

Figure 3.5 Cont.



Data from one and two year post burn ages were combined for analysis of morphological traits of field populations of *Themeda*. Traits chosen for discriminant function analysis need to be common to all groups and coliniarity needs to be avoided. Branching of flowering and vegetative tillers was only prolific in the Corridor and Magangeni populations and entirely absent from Kamberg and Trompsberg populations (Figure 3.4e and Figure 3.5e), hence were not included in the analysis. Remaining characters common to all groups were tested for colinearity, Table 3.3.

Discriminant function analysis requires five replicates per group therefore only five variables could be included in the analysis since the highest replication shared by all groups was twenty-five. The number of nodes on flowering tillers was strongly correlated with the maximum height of flowering tillers and average height of flowering tillers hence maximum and average height of flowering tillers were not included in the DFA's in order to avoid colinearity. The remaining five variables were used in the DFA. Results of the DFA are presented in Table 3.4.

Table 3.3 Correlation matrix of morphological traits measurable in field populations of *Themeda* (one and two year post burn ages combined) (N=225).

	FH	VG	FL	DF	ND	SD	AT
FH	1.00	.93	.81	.61	.85	.63	.53
VG		1.00	.84	.61	.91	.60	.54
FL			1.00	.66	.91	.71	.58
DF				1.00	.62	.81	.69
ND					1.00	.64	.53
SD						1.00	.59
AT							1.00

FH = maximum height of flowering tillers, VG = maximum canopy height of vegetative material, FL = average length of reproductive tillers; DF = Diameter of flowering tillers; ND = Number of visible nodes on flowering tillers; SD = Seed production per flowering tiller; AT = Number of aerial tillers on flowering tillers.

All variables were included in the model, none were removed. Based on the F- to remove values, the number of nodes on flowering tillers contributes the most to discriminating populations, followed by seed production per flowering tiller; aerial tiller production on flowering tillers, and the maximum height at which vegetative material is found. The diameter of flowering tillers also contributed significantly to discriminating among populations but this contribution is redundant considering the high F-to remove values of the other variables.

Table 3.4 DFA summary, Wilks' Lambda: .0278 approx. F (20,72)=69.77 p<0.000.

	Wilks' Lambda	Partial Lambda	F-remove (4.22)	p-level
ND	.0740	.3756	89.77	0.000
SD	.0429	.6488	29.24	.0000
AT	.0382	.7284	20.13	.0000
VG	.0377	.7374	19.23	.0000
DF	.0303	.9173	4.87	.0009

ND = Number of visible nodes on flowering tillers; AT = Number of aerial tillers on flowering tillers; SD = Seed production per flowering tiller; VG = Maximum height of canopy of vegetative material; DF = Diameter of flowering tillers.

The percentage of plants correctly classified was relatively high for all sites (Table 3.5). The Trompsberg ecotype was classified most accurately followed by Ukulinga, Magangeni, Corridor and lastly Kamberg ecotypes. Mis-classification of Corridor samples were into the Magangeni populations and visa versa. Mis-classifications of Ukulinga samples were into the Kamberg populations and *visa versa*. The only mis-classification of Trompsberg samples was into the Ukulinga population.

Table 3.5 Classification matrix from DFA where rows are observed classifications and columns predicted classifications.

	Percent Correct	COR p=.2222	MAG p=.2222	TRM p=.1111	UKU p=.2222	KAM p=.2222
COR	76.0	38	12	0	0	0
MAG	82.0	9	41	0	0	0
TRM	96.0	0	0	24	1	0
UKU	82.0	0	0	1	41	8
KAM	68.0	0	0	0	16	34
Total	79.1	47	53	25	58	42

COR =: Corridor (dry tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi arid, severe frost); UKU = Ukulinga (mesic moderate frost); KAM = Kamberg (Wet severe frost).

To determine the significance with which the roots contribute to discriminating populations, a Chi-square test was performed; results are shown in Table 3.6.

All roots contributed significantly to separating the populations. However, according to the Eigen-values, roots one and two account for the majority of the separation hence from here on only results for root 1 and 2 will be presented. Figure 3.6 provides a visual representation of the separation of populations by roots 1&2.

Table 3.6 Chi-square tests with successive roots removed

Root	Eigen-value	Canonical R	Wilks' Lambda	Chi-Sqr.	df	p-level
1	12.93	.964	.0278	784.6	20	0.000
2	1.07	.719	.3874	207.7	12	0.000
3	.184	.394	.8018	48.38	6	.0000
4	.054	.225	.9492	11.42	2	.0033

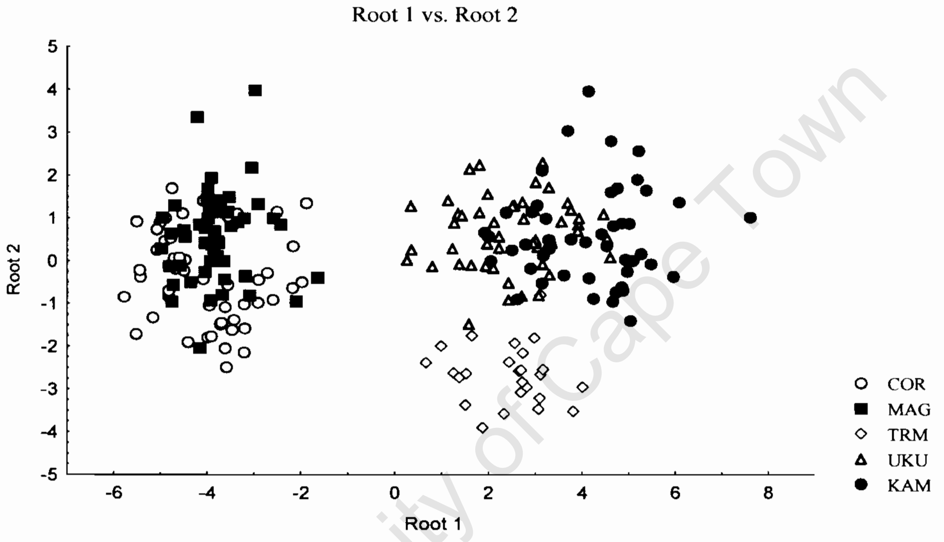


Figure 3.6 Scatter plot of z scores for morphological data from field populations of *Themeda* (one and two-year post-burn ages combined) showing the separation of populations by root one and two. COR = Corridor (dry, tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost);UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

Standardised coefficients provide an indication of how much a variable contributes to the discriminatory power of the root. Standardised coefficients show that the number of nodes on flowering tillers and the maximum height of vegetative material per tussock are the most important variables in root 1 whereas the seeds produced and the number of aerial tillers on flowering tillers are most important in root 2.

Table 3.7 Standardised Coefficients for Canonical Variables

	Root 1	Root 2
ND	-.9088	-.0875
AT	.2930	.5743
SD	-.1690	-1.112
VG	-.3590	.4874
DF	.1240	.4993
Eigenval	12.93	1.07
Cum.Prop	.9082	.9833

ND = Number of visible nodes on flowering tillers; AT = Number of aerial tillers on flowering tillers; SD = Seed production per flowering tiller; VG = Maximum height of canopy of vegetative material; DF = Diameter of flowering tillers.

3.3.1.2 Growth characteristics of field populations

There are differences in the growth and development characteristics, in terms of the proportion of tillers produced per tiller category, in eight month post burn stands of *Themeda* for the five populations tested (Figure 3.7).

The occurrence of flowering tillers in the Nqumeni, Magangeni and Trompsberg populations made them distinct from the Kamberg and Ukulinga populations. The Trompsberg population had both flowering and basal tillers. Extending tillers in Nqumeni and Magangeni populations were thought to be immature flowering tillers (pers.obs) whereas those from Ukulinga were considered to be elongated vegetative tillers. These had elongated slightly, having very thin stems that only extend about 1 – 3 nodes, with the apex elevated only a few cm's above the soil surface and phytomers condensed around the apical bud. The high number of elongated (vegetative) tillers at Ukulinga is most likely a response to higher levels of light competition due to the older post burn age of this population. Kamberg was distinct in only having basal tillers.

Nqumeni and Magangeni populations were distinct from other populations in having aerial tillers. However despite the high density of aerial tillers they contributed relatively little to the biomass per unit area. The most notable result regarding biomass proportions is the relatively high accumulation of dead litter biomass in Ukulinga populations. This may be a consequence of higher levels of light competition due to the older post burn age of this population demonstrating the necessity for plants to elevate vegetative tillers as was observed.

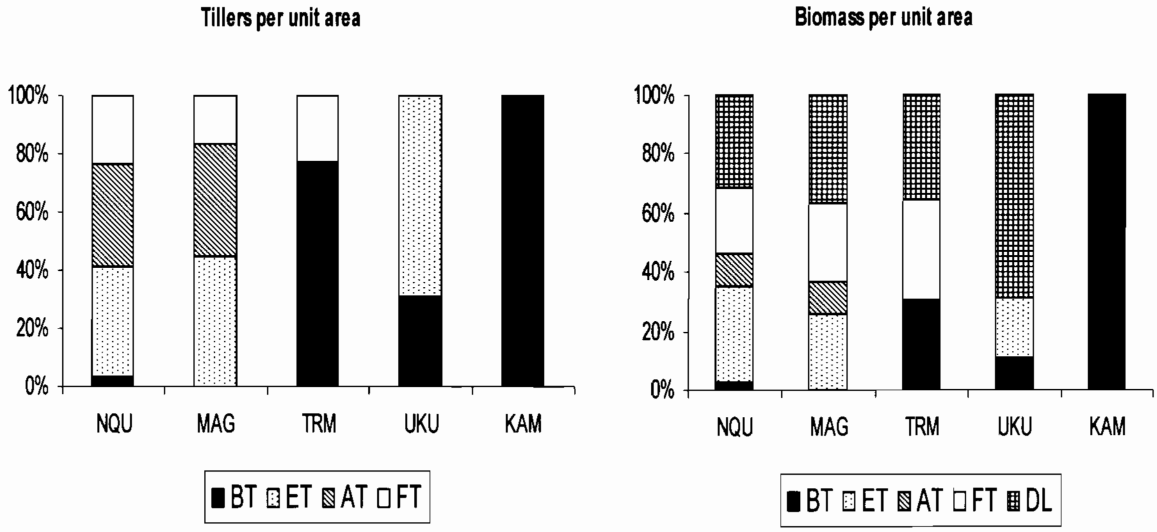


Figure 3.7 Proportional distribution of tillers and biomass per unit area for different functional tiller types in eight-month post burn field populations of *Themeda.* BT = basal tillers; ET = elongating tillers; AT = aerial tillers, FT = flowering tillers; DL = dead litter. NQU =Nqumeni (dry tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

The replication for assessing growth characteristics of 8-month post burn field populations of *Themeda* was ten per population thus only allowing for two variables to be assessed in the discriminant function analysis. Since not all tiller categories were common to all populations, only total tiller production per unit area and total biomass production per unit area was legitimate for inclusion in DFA. These data are presented in Figure 3.8

There was a poor correlation between tillers per unit area and mass per unit area (0.2799), therefore these variables meet the recommendation for limiting colinearity for discriminant function analysis. This lack of pattern is most likely a function of the differences found in the proportions of different functional tiller types among populations.

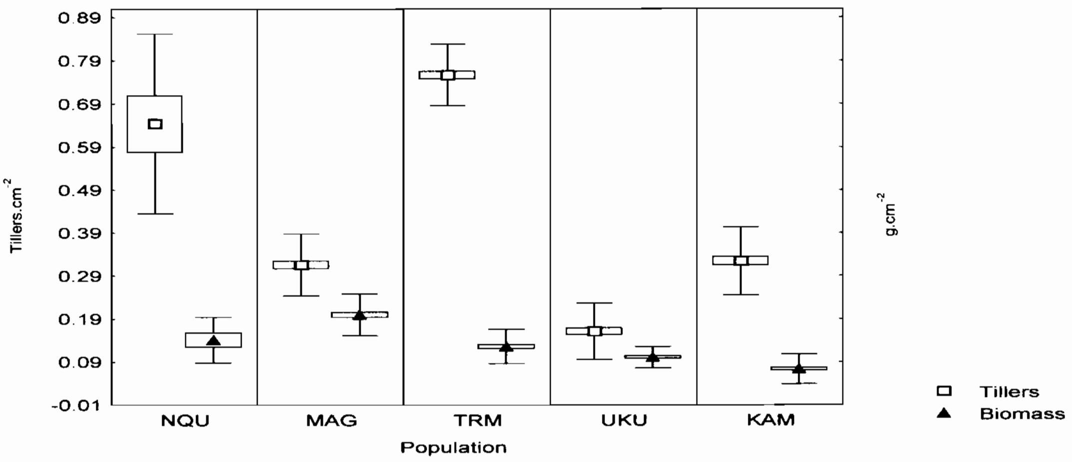


Figure 3.8 Means, mean standard error (box) and mean standard deviation (whisker) for total number and total biomass of tillers per unit area (cm^2) for each of the populations investigated. NQU= Nqumeni (dry, tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost);UKU = Ukulinga (mesic, moderate frost). KAM = Kamberg (high rainfall, high frost). **Note:** Scale for g/cm^2 is the same as for Tillers /cm^2

Both variables (total number of tiller per unit area & total biomass per unit area) were included in the stepwise analysis. The F-remove values (Table 3.8) show that tillers per unit area contribute more to discriminating populations then total biomass per unit area.

Table 3.8 Discriminant function analysis summary, Wilks' Lambda: .0704, approx. F (8,88)=30.47 p< .0000.

	Wilks'Lambda	Partial Lambda	F-remove (4,44)	p-level
TL	.4676	.1505	62.10	.0000
MS	.1830	.3844	17.62	.0000

TL = Total number of tillers per unit area. MS = Total biomass per unit area

According to the classification matrix (Table 3.9) Magangeni was distinct. Nqumeni, Ukulinga and Kamberg populations were classified reasonably accurately. Trompsberg was the least distinct, with mis-classifications mainly into the Nqumeni population. Likewise Nqumeni mis-classifications were mainly into the Trompsberg population.

Table 3.9 Classification Matrix (rows: observed classifications; columns: predicted).

	Percent Correct	NQU p=.2000	MAG p=.2000	TRM p=.2000	UKU P=.2000	KAM p=.2000
NQU	70.00	7	0	2	0	1
MAG	100.0	0	10	0	0	0
TRM	60.00	4	0	6	0	0
UKU	80.00	0	2	0	8	0
KAM	80.00	1	1	0	0	8
Total	78.00	12	13	8	8	9

NQU =: Nqumeni (equivalent to the Corridor site, dry tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi arid, severe frost); UKU = Ukulinga (mesic moderate frost); KAM = Kamberg (Wet severe frost).

Both roots one and two are significant in separating populations but most of the discrimination occurs in root one as seen by the relatively high eigen-value compared to root 2 (Table 3.10). Figure 3.9 provides a visual indication of the separation of populations by roots 1&2.

Table 3.10 Chi-square tests with successive roots removed

Root	Eigen- value	Canonical R	Wilks'Lambda	Chi-Sqr.	df	p-level
1	5.647	.9217	.0704	120.7	8	.0000
2	1.138	.7296	.4677	34.58	3	.0000

Analysis of the distance between groups showed that Trompsberg and Nqumeni populations were not significantly different (0.09). All other combinations of populations were however highly significantly different.

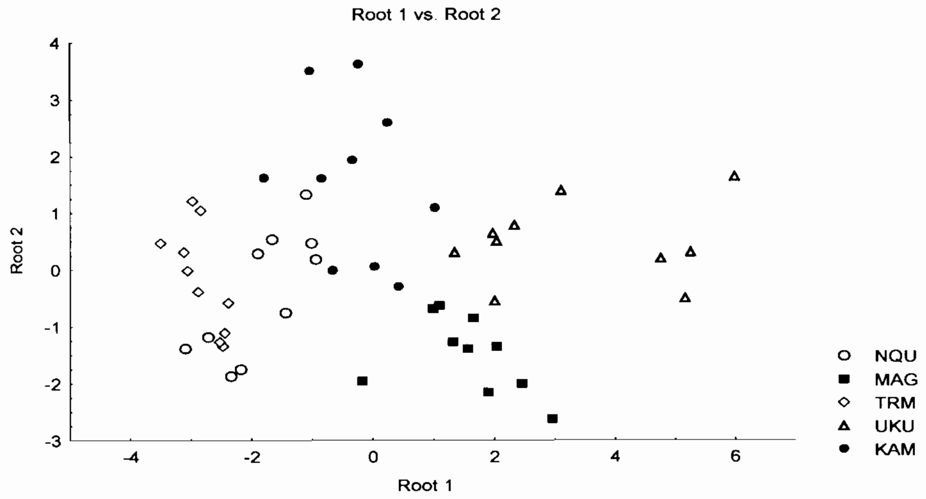


Figure 3.9 Scatter plot of Z-scores for data on growth characteristics of eight month post burn field populations of *Themeda* (tillers and biomass per unit area) representing the separation of populations by roots 1&2. NQU = Nqumeni (dry, tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost);UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

Results obtained indicate that the number of tillers per unit area is the more important variable contributing to the discriminant function in root 1 whereas total biomass per unit area is important in root 2, Table 3.11.

Table 3.11 Standardised coefficients for canonical variables

	Root 1	Root 2
TL	1.1581	-.01064
MS	.5935	-.9946
Eigenval	5.6469	1.1383
Cum.Prop	.83224	1.0000

TL = Total number of tillers per unit area. TM = Total biomass per unit area

3.3.1.3 Morphological characteristics combined with growth characteristics

Data from morphological and growth characteristics of field populations of *Themeda* were combined for analysis. Only two variables could be used for discriminant function analysis because there were only 10 replicates per group for growth characteristics. The number of nodes on flowering tillers and tiller number per unit area (cm^2) were therefore chosen since these were found to be the most important variables discriminating groups in the preceding DFA's. Results from the DFA are presented in Table 3.12. Both variables were included in the stepwise analysis. The F-remove values (Table 3.12) show that number of nodes on flowering tillers contributed more to the discriminant function then tillers per unit area.

Table 3.12 Discriminant function analysis summary: Wilks' Lambda: .0099, approx. F (8,88)=99.44, p<0.0000.

	Wilks' Lambda	Partial Lambda	F-remove (4,44)	p-level
ND	.1830	.0542	191.96	.0000
TL	.0526	.1885	47.35	.0000

ND = Number of visible nodes on flowering tillers; TL = Tillers per unit area.

Classifications of all populations were very accurate (Table 3.13). The Trompsberg population was distinct. Mis-classifications of Magangeni samples were into the Nqumeni/Corridor population and *vice versa*. Mis-classifications between Ukulinga and Kamberg populations occurred.

Table 3.13 Classification matrix (rows: observed classifications columns: predicted classifications)

Site	Percent Correct	COR/NQU	MAG	TRM	UKU	KAM
		p=.2000	p=.2000	p=.2000	p=.2000	p=.2000
COR/NQU	80.0	8	2	0	0	0
MAG1	90.0	1	9	0	0	0
TRM	100.0	0	0	10	0	0
UKU	90.0	0	0	0	9	1
KAM	90.0	0	0	0	1	9
Total	90.0	9	11	10	10	10

COR/NQU =: Corridor/Nqumeni (dry tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi arid, severe frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (Wet, severe frost).

Both root one and root 2 were significant in separating populations but Eigen-values show that the majority of separation occurs in root 1 (Table 3.14).

Table 3.14 Chi-Square tests with successive roots removed

Root	Eigen- value	Canonical R	Wilks' Lambda	Chi-Sqr.	df	p-level
1	19.3462	.9751	.0099	209.9	8	.0000
2	3.9543	.8934	.2019	72.81	3	.0000

The distance among all groups was highly significantly different, Figure 3.10.

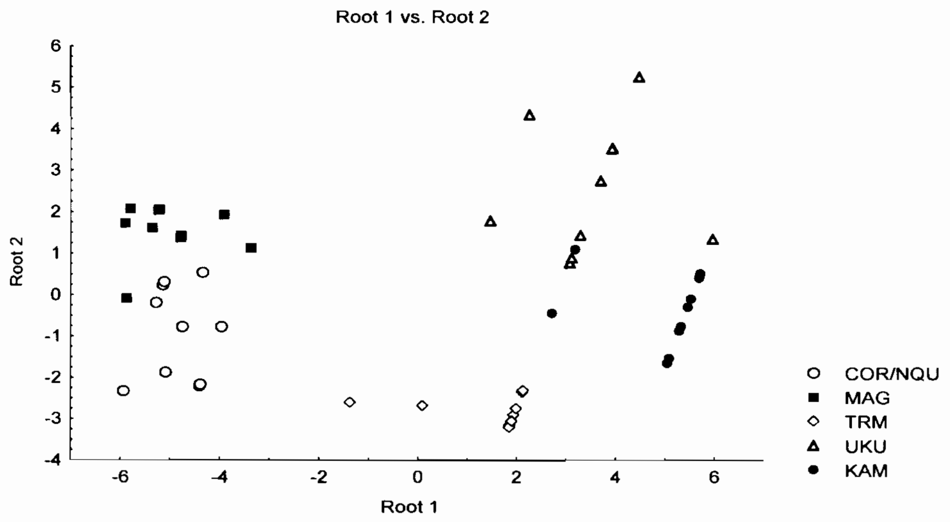


Figure 3.10 Scatter plot of Z-Score obtained when morphological and growth characteristics from field populations of *Themeda* are combined. COR/NQU = Corridor/Nqumeni (dry, tropical, no frost); MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost);UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

Standardised coefficients indicate that number of nodes per flowering tiller is the most important variable separating populations in root 1 whereas tillers per unit area is more important in root 2 Table 3.15.

Table 3.15 Standardised coefficients for canonical variables

	Root 1	Root 2
ND	-.9901	.1831
TD	-.2975	-.962
Eigenval	19.35	3.9543
Cum.Prop	.8303	1.0000

ND = Nodes per flowering tiller; TD = tiller density per unit area

3.3.2 Plants grown under controlled conditions

3.3.2.1 Morphological characteristics

Clonally propagated plants

Data from morphological assessment of cloned plants from study populations, grown under greenhouse conditions are presented in Figure 3.11. Flowering tillers of Trompsberg and Magangeni plants were generally longer then those in Ukulinga and Kamberg plants. Magangeni plants had more nodes and aerial tillers on flowering tillers compared to other populations. However aerial tillers were apparent in all the ecotypes tested.

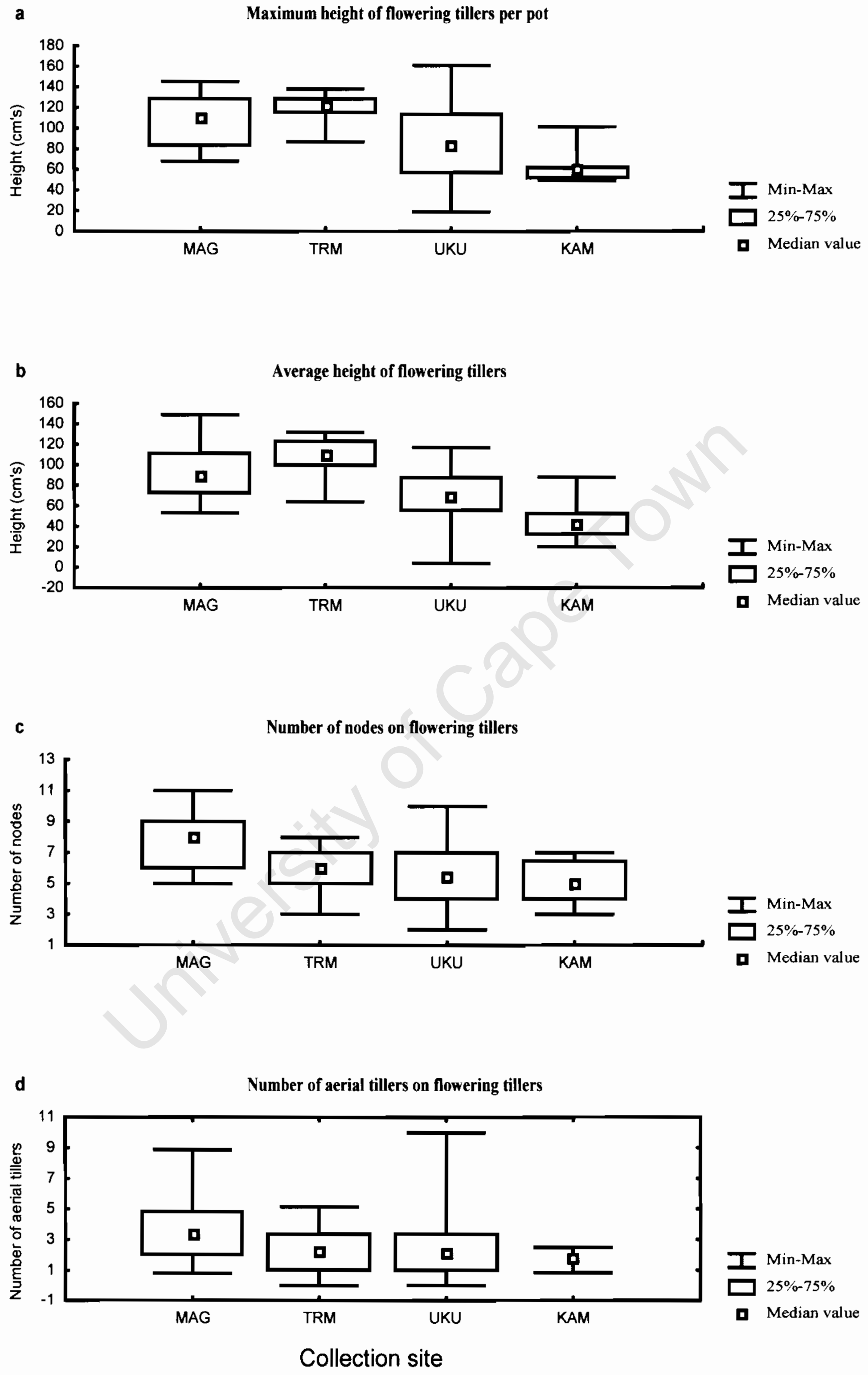


Figure 3.11a-d Morphological characteristics of plants grown under controlled conditions after two seasons growth. N=24 for Magangeni, N=30 for Trompsberg, N=10 for Ukulinga N=4 for Kamberg. MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

Seedlings

Due to the young age at which seedlings were harvested (five and a half months), comparison of morphological traits with other data sets, which assessed traits at one and two year stages, was limited. However, Table 3.16 provides an indication of some of these characteristics of the three populations tested. After five and a half months only plants from seeds germinated from Magangeni populations had flowering tillers. The relatively large number of nodes on these tillers and the more prolific initiation of aerial tillers for these plants are consistent with field observations. Trompsberg plants had elongating tillers; these were thought to be immature flowering tillers.

Table 3.16 Mean number of nodes and aerial tillers on extending and reproductive tillers for the three populations tested.

SITE	NDE	NDR	AT
MAG	3.1 (N=9)	5.3 (N=3)	.78 (N=9)
TRM	1.8 (N=5)		.11 (N=9)
KAM			0.0 (N=9)

NDE = number of visible nodes on elongating tillers; NDR = number of nodes on flowering tillers; AT = Aerial tillers on flowering or elongating tillers.

Replication of the morphological characteristics of clonally propagated plants was poor for Ukulinga and Kamberg populations due to high mortality of these populations in the second season of growth. Discriminant function analysis could therefore not be performed on these data. Likewise, the seedlings were too young to provide a full set of data for analysis.

3.3.2.2 Growth characteristics

Growth data from clonally propagated plants harvested at 10 months are presented in Figure 3.12. Unfortunately elongating and basal tillers were not separated at this harvest. Magangeni plants had vegetative (basal + elongating), flowering and aerial tillers, whereas other plants only had vegetative tillers (basal + elongating). The distribution of biomass in Magangeni plants is different to all the other populations in that there is a high allocation to flowering tillers (Figure 3.12). As with field populations, despite high aerial tiller densities, their contribution to biomass is relatively low. Magangeni populations have proportionately less dead litter after 10 months, indicating lower senescence. This is possibly due to lower levels of light competition within individuals resulting from the tall morphology and the elevation of tillers into aerial positions of this ecotype. There are no evident differences in biomass proportions among Trompsberg, Ukulinga and Kamberg populations. However this may be misleading since no distinction was made between basal and extending tillers.

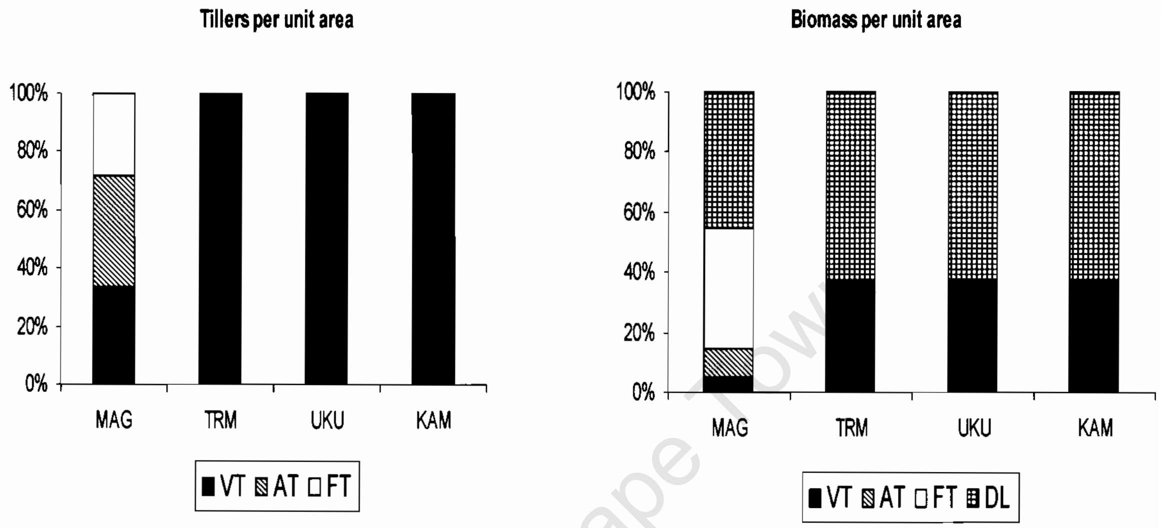


Figure 3.12 Proportional distribution of tillers (N=60) and biomass (N=35) per unit area for different functional tiller types in clones after 10 months of growth under controlled greenhouse conditions. VT = Vegetative tillers (basal tillers + elongating tillers); AT = aerial tillers, FT = flowering tillers; DL = dead litter. MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost)

Data from the second season harvest is more detailed than the first harvest in that tiller categories are separated (Figure 3.13). All tiller categories were present in all ecotypes, contrary to field observations. There are however differences in the proportions of tiller types and biomass distribution among ecotypes. Magangeni plants have significantly more aerial tillers then other ecotypes. Kamberg had the most basal tillers, consistent with field observations. Ukulinga plants accumulated the greatest amount of dead litter and Magangeni plants the least, consistent with results from field studies.

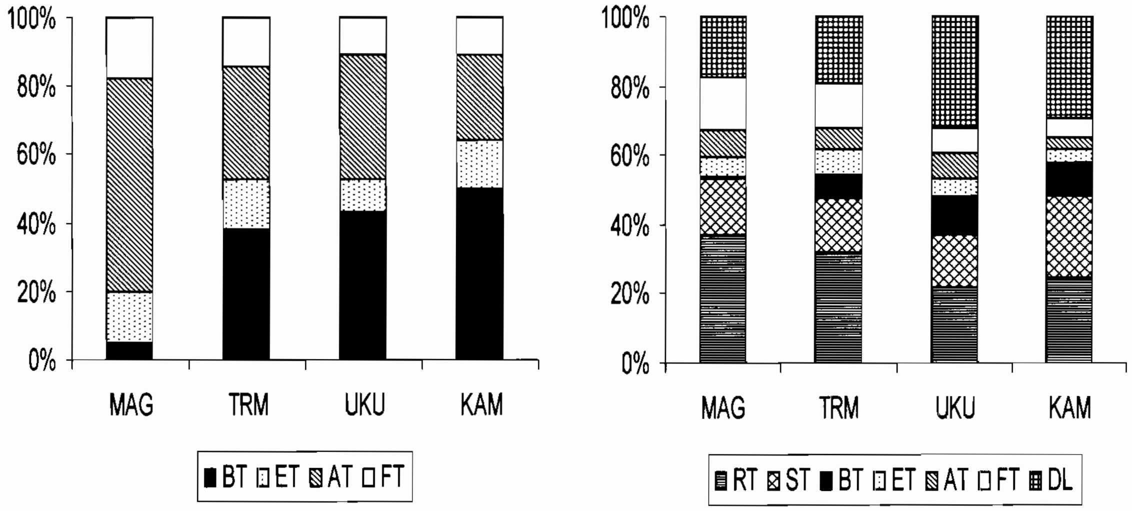


Figure 3.13 Proportional tiller and biomass distribution of different functional tiller types at the end of the second season of growth for plants grown under controlled conditions N=24 for Magangeni, N=30 for Trompsberg, N=10 for Ukulinga N=4 for Kamberg. BT = Basal tillers; ET = elongating tillers; AT = aerial tillers; FT = flowering tillers; DL = dead litter. RT = roots; ST = stubble (junction between roots and tillers). MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

A Discriminant function analysis was performed on growth data collected at ten months from clones grown under controlled conditions using tiller number and mass. Both variables were included in the stepwise analysis, Table 3.17. The F-remove values show that total biomass per unit area contributes more to discriminating populations than tillers per unit area. This is contrary to results from field studies, where tiller density contributed more to discriminating populations.

Table 3.17 Discriminant function analysis summary: Wilks' Lambda: .29 approx. F (6,28)=39.71 p<0.0000

	Wilks' Lambda	Partial Lambda	F-remove (3,14)	p-level
TL	.3480	.8332	9.27	.0000
MS	.9156	.3167	99.97	0.000

TL= tiller number; MS=Mass

Classifications were not as accurate as those for field populations (Table 3.18). Magangeni was the most distinct, and Ukulinga the least. Mis-classifications of Magangeni plants only occurred into the Trompsberg group whereas Trompsberg was mis-classified into the Magangeni and Kamberg groups. Most mis-classifications of Ukulinga and Kamberg plants occurred between each other.

Table 3.18 Classification matrix (rows: observed classifications; columns: predicted classifications)

	Percent	MAG	TRM	UKU	KAM
	Correct	p=.2500	p=.2500	p=.2500	p=.2500
MAG	77.78	28	8	0	0
TRM	63.89	7	23	0	6
UKU	33.33	0	1	12	23
KAM	58.33	0	2	13	21
Total	58.33	35	34	25	50

Both roots are highly significant in contributing to the discrimination among groups (Table 3.19).

Table 3.19 Chi-square tests with successive roots removed

Root	Eigen-value	Canonicl R	Wilks' Lambda	Chi-Sqr.	df	p-level
1	2.1608	.8268	.2899	173.32	6	0.000
2	.0911	.2889	.9165	12.20	2	.0022

Figure 3.16 provides a schematic view of how the roots separate populations. Distances among all groups were highly significant except between Ukulinga and Kamberg where distances were just significant (0.0419).

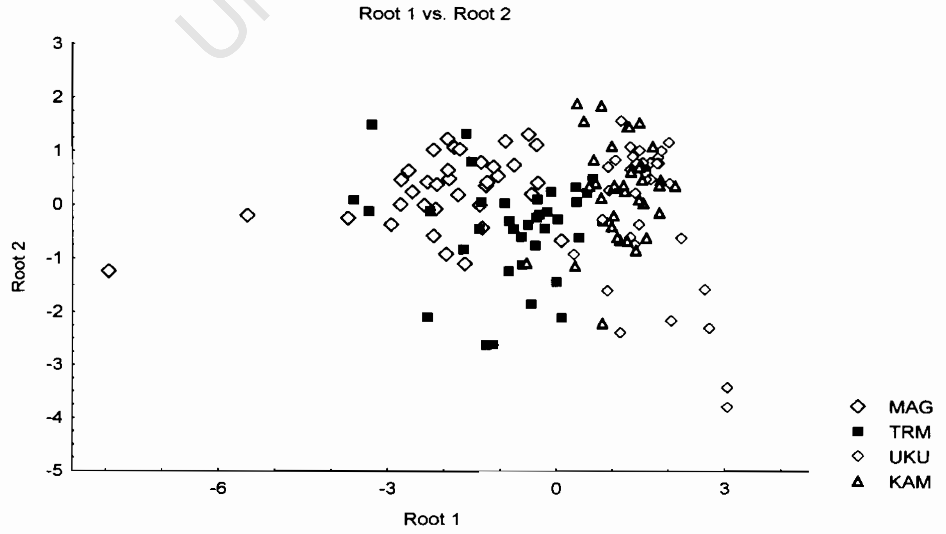


Figure 3.14 Figure 15 Scatter plot of Z-scores obtained from data on growth characteristics of clones after ten months of growth under controlled conditions.

Biomass per unit area was most important in root one whereas tiller densities per unit area were more important in separating groups in root 2 (Table 3.20).

Table 3.20 Standardised coefficients for canonical variables

	Root 1	Root 2
TL	.4053	-1.01
TM	-1.088	.0253
Eigenval	2.161	.0911
Cum.Prop	.9596	1.000

TL = Total number of tillers per unit area. TM = Total biomass per unit area

Seedlings

Growth data for five and a half-month-old seedlings are presented in Figure 3.16. Magangeni plants had elongating and reproductively mature tillers 5 and a half-months after germination. Trompsberg plants also had elongating tillers. These were considered to be immature reproductive tillers. Kamberg plants were distinct in only having basal tillers. Magangeni and Trompsberg plants had initiated aerial tillers. Magangeni plants produced more aerial tillers per extending/reproductive tiller than Trompsberg plants. Notable is the fact that Magangeni plants produce proportionately more root material than other populations. This may be related to the morphology of the plant where the roots have to support a taller more robust plant compared to other populations. Magangeni plants also had lower dead litter biomass per unit area, consistent with observations in clones grown under controlled conditions.

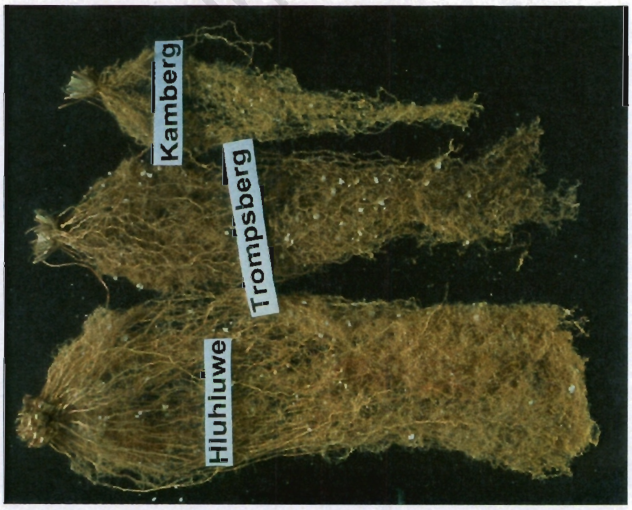


Figure 3.15 Roots from five and a half month old seedlings grown under controlled conditions. From top: Kamberg, Trompsberg, Hluhluwe. **/--------/ =10 cm**

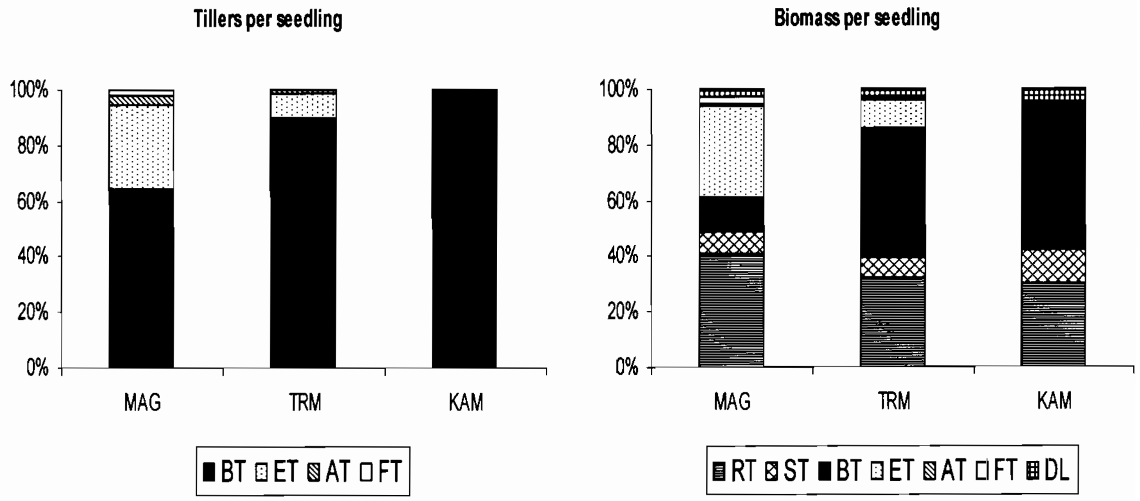


Figure 3.16 Proportional tiller and biomass production of different functional tiller types of 5 and a half-month-old plants grown from seed under controlled greenhouse conditions. BT = Basal tillers; ET = elongating tillers; AT = aerial tillers; FT = flowering tillers; DL = dead litter. RT = roots; ST = stubble (junction between roots and tillers). MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); KAM = Kamberg (high rainfall, high frost).

3.3.3 Phenotypic plasticity

3.3.3.1 Morphological characteristics

A comparison of three traits common to data sets from field and clonally grown plants are presented in Figure 3.19. Number of replicates in field populations were: N=50 for Magangeni, Ukulinga and Kamberg. N=25 for Trompsberg. Number of replicates for plants grown under controlled conditions were: N=24 for Magangeni, N=30 for Trompsberg, N=10 for Ukulinga, N=4 for Kamberg.

Maximum flowering height in Magangeni plants was reduced when grown under controlled conditions whereas it increased in Trompsberg and Ukulinga populations. The increase in flowering height in Trompsberg plants was such that it equated to that of clones of the Magangeni ecotype, but was still lower then values recorded for field populations of Magangeni.

The number of nodes found on flowering tillers was less in Magangeni plants grown under controlled conditions compared to the field population. All other ecotypes showed an increase in the number of nodes on flowering tillers when grown under controlled conditions. This was particularly evident in Trompsberg clones. However, values were still significantly lower then those of Magangeni clones.

The number of aerial tillers produced per flowering tiller was similar in field populations and plants grown under controlled conditions for the Magangeni ecotype. In all other populations tested there was a significant increase in the number of aerial tillers produced on flowering tillers when grown under controlled greenhouse conditions. However, these values were still significantly lower then those for field plants and clones of the Magangeni ecotype.

Based on standard error and standard deviation values (Figure 3.19), variation of plants grown under controlled conditions equated to, or was slightly lower than that in field populations for the Magangeni ecotype. All other populations, however generally showed an increase in the extent of variation within traits when grown under controlled conditions. This higher degree of variation may however be a consequence of different responses within an ecotype to the treatments applied in the second season.

Figure 3.17 Clonally propagated plants grown under controlled conditions for10 months. From the left: Kamberg, Ukulinga, Hluhluwe, Trompsberg

Figure 3.18 Clonally propagated plants grown under controlled conditions for 2 seasons, (cut at 10 months, medium water treatment). From left: Hluhluwe, Ukulinga, Kamberg, Trompsberg

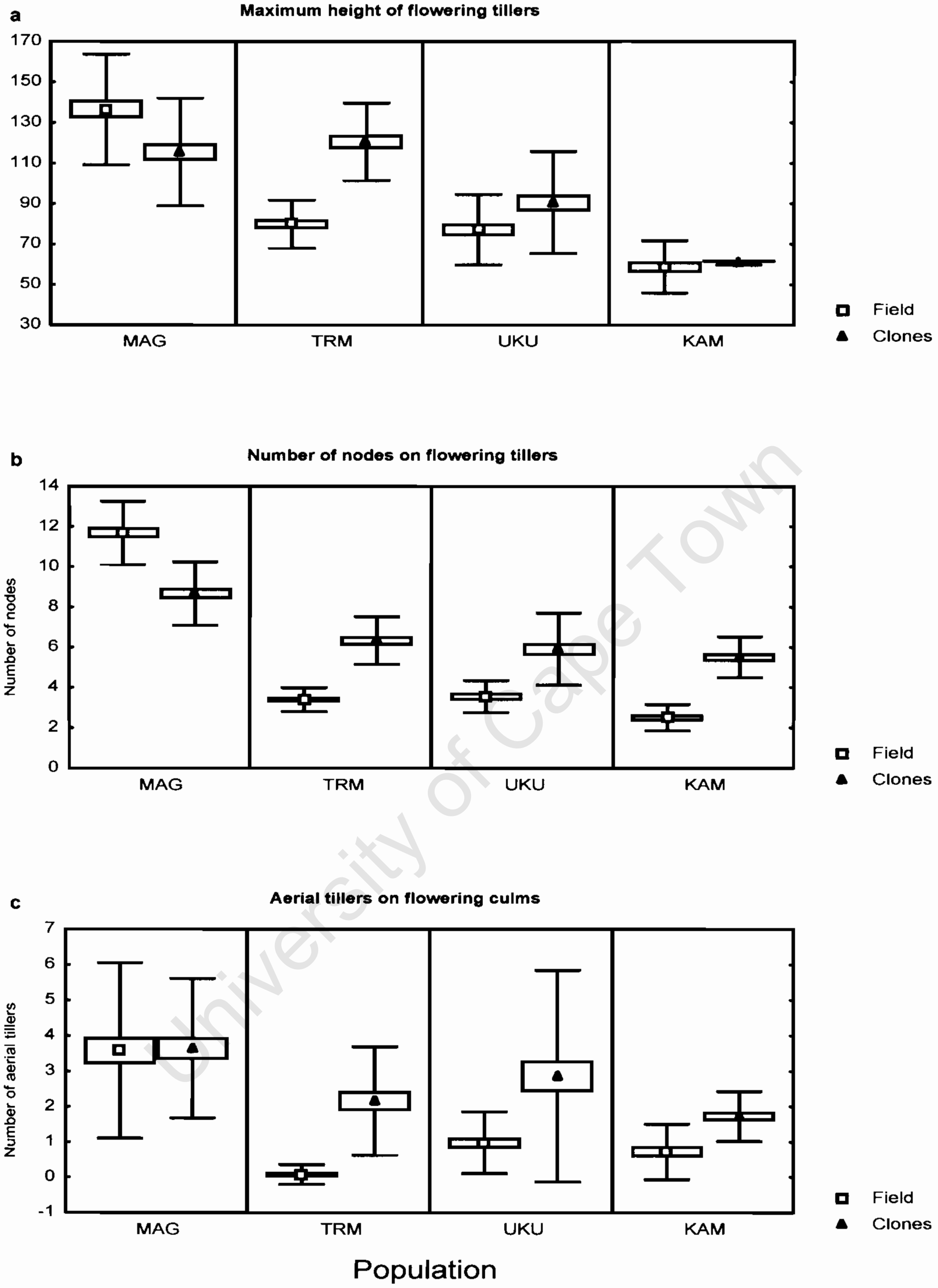


Figure 3.19a-c Comparison of means, standard error and standard deviation of morphological characteristics between field populations and clones grown under controlled conditions among the four populations tested. MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost).

3.3.3.2 Growth characteristics

Data on the total tiller density per unit area and the total biomass per unit area for field populations and plants grown under controlled conditions are compared in Figure 3.20. Note that the method used to determine basal area differed between the two data sets. Basal area was traced in field populations, whereas length x breadth was calculated to obtain areas in clonal plants. Values of biomass per unit area were much greater in clonal plants, hence these were halved when graphed.

Tiller density was greater in all populations when grown under controlled conditions, Figure 3.20. There was a difference in the pattern of tiller density among populations between field and controlled conditions. Most notably, the Ukulinga population, which has the lowest tiller density in field populations, had the second highest tiller density compared to other ecotypes when grown under controlled conditions. This pattern was not correlated to biomass. All populations showed an increase in biomass per unit area when grown under controlled conditions. The pattern of biomass per unit area among populations was however similar between field and clonal plants with Magangeni plants having the highest values followed by Trompsberg.

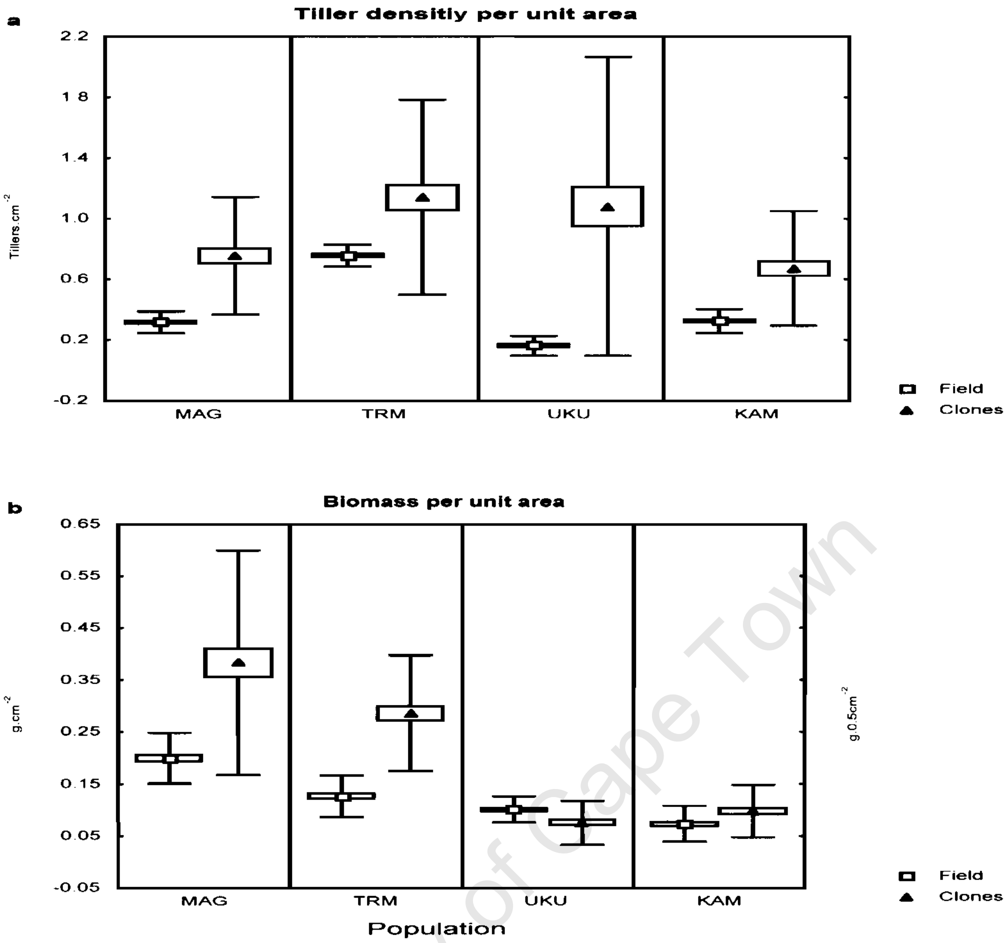


Figure 3.20 Comparison of a) tiller density (N=10 & N=60 for field and greenhouse study respectively) and b) biomass per unit area (N=10 & N=30 for field and greenhouse study respectively) between field populations and plants grown under controlled greenhouse conditions. MAG = Magangeni (wet tropical, no frost); TRM = Trompsberg (semi-arid, high frost); UKU = Ukulinga (mesic, moderate frost); KAM = Kamberg (high rainfall, high frost). Note the biomass for clonal plants was much greater then that of field samples, therefore for ease of fitting both results onto a single scale the value for biomass in clonal plants was halved.

3.4 Discussion

Natural populations of *Themeda* from different localities (reflecting different climatic conditions) do vary in their appearance. Variation is a function of both morphological characteristics, phenological development, relative proportions of different functional tiller types, biomass distribution and tiller density.

Discriminant function analysis identified the extent of apex elevation in terms of the number of nodes extended, followed by seed production, aerial tiller production and the height of the canopy of vegetative material as important traits separating populations. These results accord with those found by Theunissen (1992) who, using a PCA and cluster analysis, found characters with strong factor loadings included culm length, mean internode length and number of internodes for this species.

Magangeni and Corridor/Nqumeni populations have the most distinct morphologies; tall, with robust culms and large numbers of aerial tillers although these are fewer in Nqumeni/corridor populations. Aerial tillers are produced all the way up the stems resulting in a high vegetative canopy giving plants a leafy, shrubby appearance. Ndawula-Senyimba (1972) describes a similar form, in which *Themeda* culms continue growing for several seasons, producing new seasonal growth on small branches growing from the axial of phytomers on old flowering stems. The lower numbers of aerial tillers in Nqumeni/Corridor populations is most likely a function of the lower moisture availability in these sites. This is consistent with Ndawula-Senyimba (1972) who observated that prolific aerial tillering in these tall forms is not a feature of dry areas.

In Australia Groves et al. (1982) also described forms similar to the Magangeni population from the Nowra and Deniliquin in Australia. Notably all these populations are typified by tropical, frost-free conditions with warm summers and mild winters. These conditions are conducive to selecting for plants with an increased ability to elongate tillers and elevate the vegetative canopy.

The production of aerial tillers is often considered indicative of under-utilised veld that is becoming moribund. In Magangeni and Nqumeni/Corridor populations stem elongation of "basal" tillers starts soon after tillers are initiated. The high incidence of aerial tillers in these populations may therefore be considered as the equivalent of "lateral" tiller development but on a vertical plan/scale. This may reduce mortality of tillers resulting from self-shading. Early stem elongation and initiation of aerial tillers (often prior to flowering) in young (eight month) post burn sites where light competition is not yet intense also indicates that these are not produced in response to low light conditions. In these populations, therefore, aerial tillering is not necessarily an indication that veld needs burning or grazing to maintain productivity, but rather an inherent strategy conferring a competitive advantage with respect to light competition. The relatively low proportion of dead litter biomass in field and greenhouse studies on Magangeni provides support that self shading is limited and does not reduce productivity in this ecotype to the extent that it does in other ecotypes (see chapter 5).

Trompsberg, Ukulinga and Kamberg populations were similar in terms of their vegetative appearance. In the field, aerial tillers produced were usually on the lowest nodes, and did not increase the vegetative height of the canopies much. All these populations experience cold winter with frost. Groves et al. (1982) found forms from Tantangara and other sites in the Snowy Mountains in Australia (high frost occurrence, 1500m mild summer) that were also relatively short (0.5m). These patterns indicate that the occurrence of frost limits the extent to which vegetative material may be elevated and height at which aerial tillers are produced. In high rainfall areas it can therefore be expected that productivity will be limited by self-shading, as seen in Ukulinga populations that accumulate higher proportions of dead litter (chapter 5).

Magangeni, Corridor/Nqumeni (variable rainfall, periodic drought) and Trompsberg (semi arid) populations are similar in terms of their reproductive output having high seed production from robust flowering tillers. Ukulinga and Kamberg (mesic) populations on the other hand had lax flowering tillers, with low seed production. This accords with the hypothesis that reproductive output would be greater in more arid areas or areas which experience periodic droughts and unpredictable rainfall.

The initiation of reproductive tillers and the time to anthesis is faster in Magangeni, Nqumeni and Trompsberg plants compared to Ukulinga and Kamberg plants. This again accords with the hypothesis that populations from arid or drought prone environments maximise their reproductive output when conditions are favourable. Opperman and Roberts (1978), working on *Themeda* plants growing under natural conditions in the field from the Central Orange Free state, found that *Themeda* and other species had the ability to flower twice a year (early and late summer) provided soil moisture conditions are favourable. Groves (1975) also found differences in the number of days to anthesis and the range of days over which flowering occurred among population of *Themeda* from different localities when grown from seed under controlled conditions.

Phenotypic plasticity or genetic divergence?

Theunissen (1992) successfully separated 5 ecotypes of *Themeda,* in plants grown from seed under controlled conditions for 14 months, using morphological, epidermal and chemical characteristics of plants from various populations concluding that differences in morphology and chemical composition are genetically based. Downing and Groves (1985) noted differences in plants germinated from seed from four populations (Ukulinga, Hluhluwe, Frankenwald, Sehlabathebe) indicating that certain traits are a function of genetic divergence and not environmentally controlled. Results presented in this thesis provide further evidence that there has been genetic divergence among *Themeda* populations. Differences in phenological development were generally maintained under controlled conditions, with rapid initiation and growth of reproductive tillers in Magangeni and Trompsberg plants. Most morphological characteristics showed some degree of plasticity, and there were differences in the degree of plasticity exhibited among populations. Despite this plasticity, traits identified as important in separating field populations remained distinct and were still useful in discriminating among populations.

The Trompsberg populations showed the greatest shift (towards the Magangeni morphology) when grown under controlled conditions. Trompsberg is typified by very low rainfall and a high incidence of winter frost. In the absence of these constraints, this population has the genetic ability to exploit optimum conditions. Kamberg and to a lesser extent Ukulinga, also have winter frost. However these populations did not increase their reproductive output in the absence of frost or under optimum water conditions. This provides evidence to support the hypothesis that populations from high rainfall areas rely inherently on vegetative propagation for maintaining populations whereas Trompsberg and Magangeni populations exploit optimum moisture conditions to maximise reproductive output to ensure the populations' survival during dry periods. Further evidence for this is provided in chapter 5.

In the absence of frost, aerial tiller production increased in Kamberg, Ukulinga and Trompsberg ecotypes but only in the second season of growth. Aerial tiller initiation in Kamberg and Ukulinga took place later than Magangeni and Trompsberg ecotypes most likely in response to low light levels. The occurrence of aerial tillers in seedlings of Trompsberg plants puts it closer to Magangeni phenology, initiating tillers prior to intense light competition.

In summary:
1) Morphology and growth characteristics differ among field populations of *Themeda*, depending on locality. The extent of apex elevation, phenological development and proportions of different functional tiller types are of primary importance in separating populations.

2) Plants propagated under greenhouse conditions show a certain degree of plasticity. Trompsberg and Ukulinga plants had the most plastic response whereas Magangeni and Kamberg plants showed the least plastic response. There was, however, clear evidence for genetic divergence among populations, indicating adaptations to local climatic conditions.

3) Trompsberg and Magangeni plants have an inherent ability to initiate reproductive tillers within a shorter period of time compared to Ukulinga and Kamberg plants. This is consistent with the hypothesis that these populations optimise reproductive output under optimal moisture conditions.

4) The presence of frost limits the productivity, extent of apex elevation and the degree of aerial versus lateral tiller development in the field populations from Trompsberg, Ukulinga and Kamberg populations.

5) Water may limit the productivity and phenological development of Trompsberg plants.

4 Allocation patterns in *Themeda*

4.1 Introduction

The way in which a plant allocates its resources provides an indication of the life history traits or ecological strategy that the plant has evolved, and the selection pressures producing such a strategy (Wright and Westoby, 2001). Chapter 3 describes clear morphological and phenological differences, variation in number of, and biomass partitioning to, different tiller types in populations of *Themeda* of different origins. Other studies have shown that the forage quality, palatability, phenol and lignin content of *Themeda* vary depending on locality and ecotype (Theron and Booysen, 1966; Ollermann, 1959, in Viljoen and Roberts, 1968; Viljoen and Roberts, 1968; Ndawula-Senyimba, 1972; Theunissen, 1995a). These differences may reflect either inherent genetic divergence in the chemical composition associated with different life history strategies and plant traits, or differences in conditions at a locality.

One of the main objectives of this thesis was to determine whether the observed variation among *Themeda* populations was indicative of divergent life history strategies (LHS). Chapter 1 outlines various schemes proposed for predicting plant strategies and functional types based on the conditions associated with a given area. The approach in this thesis is novel in that an attempt was made to develop sets of key traits associated with different climatic conditions, particularly rainfall, for a single species that could be used to predict general rangeland attributes in regions across climatic gradients. Specifically, this chapter attempts to elucidate whether observed variation among *Themeda* populations is a function of inherent differences in allocation patterns that confer a selective advantage under the different environmental conditions. The hypotheses tested are: in regions with high and predictable rainfall, LHSs are a function of self-regulating processes (density-dependence), with allocation patterns reflecting selective advantages in situations of high competition for light and space. It is expected that propagation in these stable mesic areas is primarily vegetative, associated with a low allocation to seed production. In areas with low and/or unpredictable rainfall the hypothesis is that LHSs are primarily related to limited or variable moisture availability. Here, allocation patterns that confer some advantage for acquiring resources opportunistically in times of moisture availability, with propagation primarily through sexual reproduction and associated with high seed production are expected.

Growth analyses of the way in which a plant allocates its resources can be used to investigate LHSs (Poorter, 1990). The approach taken in this investigation is to determine relative patterns of allocation to seed, flower, and vegetative tiller production, in terms of numbers and dry mass allocation under natural field conditions of four populations of *Themeda* occurring over a rainfall gradient. Thereafter, a glasshouse experiment was done using plants propagated from seed and grown under controlled conditions to determine whether differences observed in the field had an inherent genetic basis. These plants were used for growth analyses and the determination of inherent leaf traits. It is useful to briefly introduce some of the theory regarding growth analyses.

Growth analyses

Growth analyses are valuable for discerning and understanding plant strategies, as these provide insight into plant function as dependent on its genotype and environment (Grime, 1979; Poorter, 1990). There are a number of parameters used in growth rate analysis, the primary components of which include inherent relative growth rate (RGR), specific leaf area (SLA), leaf weight ratio (LWA) and leaf area ratio (LAR) (Poorter, 1990; Lambers, *et al.* 1998; Wright and Westoby, 2000). These factors are in turn affected by the chemical (phenolics/secondary compounds) and structural composition (e.g. lignin content, cellulose) of the leaves, nitrogen use efficiency and leaf thickness (Poorter, 1990; Niemann, *et al.*,1992; Lambers, *et al,* 1998). Inter-specific variation in RGR is most commonly accounted for by variations in SLA, whereas the relationship between RGR and NAR is less clear and will not be addressed in this thesis (see Poorter, 1990; Wright and Westoby, 2000).

Relative growth rate

The relative growth rate (RGR) of a species is measured in terms of mg.g^{-1}.day^{-1} and differs greatly among species (Poorter, 1990, Lambers and Poorter, 1992; Wright and Westoby, 2001). Determining the RGR of seedlings germinated and grown under favourable controlled conditions is considered a useful method for determining the "potential ability of species to take advantage of favourable growth opportunities; that is, of a species' growth strategy" (Wright and Westoby, 2001). Differences in potential RGR among species are considered to be habitat related (Poorter, 1990). Commonly, species from favourable environments have an inherently higher RGR compared to species from less favourable environments (Grime and Hunt, 1975; Lambers and Poorter, 1992; Lambers, *et al.*, 1998). To understand the ecological significance of variation in inherent growth rate, an understanding of the physiological traits associated with RGR is required. There is a large amount of literature on this topic (e.g. Poorter, 1990; Lambers, *et al.*, 1998) but discussion of this will be limited to the points that are of relevance to the studies presented in this thesis.

Specific leaf area (SLA)

Specific leaf area (SLA) is the leaf area per unit leaf dry mass as measured in $m^2.kg^{-1}$. SLA is considered to be one of the most important parameters explaining variation in inherent RGR (Poorter, 1990; Wright and Westoby, 2000) and a critical measure of the allocation strategy of a plant (Wright and Westoby, 1999).

Generally, SLA is positively correlated with RGR, and lower SLA values are associated with lower RGR (Poorter, 1990; Atkin, *et al.*, 1996; Wright and Westoby, 2000; Wright and Westoby, 2001). It has been proposed that lower SLA values are associated with plants from nutrient-poor or dry areas (see Cunningham, *et al.*, 1999).

Plant attributes associated with high SLA values include: thinner leaves, higher leaf water content, higher nitrogen concentrations and lower leaf life span (Lambers, *et al.*, 1998). Plants with lower SLA values tend to be associated with: thicker leaves, greater structural strength associated with higher amounts of lignin and starch, containing more sclerenchymatic cells (characterized by thick-walled cells), cell wall components per unit leaf area, and an accumulation of secondary compounds like phenols and tannins, all of which may be associated with longer leaf life spans (Waring, *et al.*, 1986; Dijkstra, 1990).

The ecological significance of variation in leaf life span and its implications for plant ecophysiology, growth and ecosystem resource cycling is well recognized (Reich, *et al.*, 1992, Craine, *et al.*, 1999). Relative growth rates (RGR) and leaf area ratio (LAR) of seedlings decreased with increasing leaf life span in certain tree species (Reich, *et al.*, 1992). Negative correlations have been demonstrated between SLA and increasing leaf life span (Reich, *et al.*, 1992). This is though to be an adaptation to minimize tissue loss in nutrient-poor environments (Ryser and Urbas, 2000). However a study on 32 garden-grown grass species revealed that leaf life span was negatively associated with SLA as well as disturbance rate, leading the authors to conclude that although longer leaf life spans are an important means of reducing nutrient losses, it is only a selective advantage in low-disturbance, low-defoliation regimes (Ryser and Urbas, 2000).

Leaf weight ratio (LWR)

Leaf weight ratio (LWR) is the fraction of total plant biomass allocated to leaves, measured in $g.g^{-1}$. In adverse environments, physiological integrity of organs over a longer time is important, therefore lower LWRs (and/or SLAs) will be more prevalent (Poorter, 1990).

Leaf area ratio (LAR)

The leaf area ratio (LAR) is the amount of leaf area per unit total plant weight, measured in $m^2.kg^{-1}$ and is calculated as follows:

LAR = SLA x LWR

There is often a strong positive correlation between RGR and LAR (Poorter, 1990; Reich, *et al.*, 1992). Low LAR values are considered by some to be an adaptation to frost or chilling (small cell sizes and lower water content) (Poorter, 1990).

4.2 Methodology

4.2.1 Field studies

In November 1997, the sites listed in Table 4.1 were sampled in order to determine tiller densities and biomass partitioning in a given unit of area for *Themeda*. By sampling one- and two-year post-burn sites it was possible to capture early differences in tiller proportions (vegetative versus reproductive) and biomass partitioning among plant parts and to see if and how these patterns changed with a second season of growth. It was also important to determine whether some populations accumulated more litter then others. Unfortunately there were no recently burnt sites that could be assessed in the semi-arid population (Trompsberg).

Twenty plots (0.15 x 0.15 m = 225 cm^2) were randomly selected by walking at least five transects at each site and using the densest patch of *Themeda* occurring closest to every 1-metre interval. If the *Themeda* on the transect was not dense enough to fill the plot or was not monospecific, the plot was left unselected. All the material occurring in the plot was harvested at ground level.

Harvested material was counted according to the following categories:
Flowering culms; basal tillers; aerial tillers (combined from reproductive and extending tillers); and extending tillers. The dry mass of each category was recorded after oven drying samples in brown paper bags at 75°C for 48 hours.

Table 4.1 Sites and post-burn age of sites used to determine tiller densities and biomass allocation per unit area after one and two seasons of growth in swards of *Themeda*.

Site	Post-burn age at collection (months)
Magangeni (tropical, periodic drought)	5
	30
Trompsberg (semi-arid, severe frost)	
	15
Ukulinga (moderately mesic, frost)	2.5
	28
Kamberg (mesic, severe frost)	2.5
	15

* Note: different age sites represent adjacent sites of differing post burn age collected at the same time, not the same stand collected at different ages.

Seed production

Reproductive tillers that were harvested for morphological studies (n = 25), as described in Chapter 3, from the sites listed in Table 4.2 were used to determine seed production. The number of seeds per tiller was determined by counting the number of spikelets on the flowering head as an indication of seed production. Data were analysed in more detail here and unlike in Chapter 3, post-burn age of the stands was taken into account.

Table 4.2 Seed production on individually harvested reproductive tillers was determined at the following sites.

Site	Post-burn age at collection (months)
Magangeni (tropical, variable rainfall)	7
	19
Trompsberg (semi-arid, severe frost)	Unavailable
	21
Ukulinga (moderately mesic, frost)	14
	28
Kamberg (mesic, severe frost)	6
	24

4.2.2 Glasshouse experiment

Plants from the seedling experiment described in Chapter 3 were used to determine phenological development (tiller production), biomass allocation and inherent RGR, SLA, LWR and LAR values when grown under controlled conditions. Source populations were Magangeni (tropical, frost free, wet/dry cycles), Trompsberg (semi-arid, frost prone) and Kamberg (mesic, frost prone). These plants were also used to determine digestibility, water content and phenolic content of leaf material.

At five and a half months after germination, the number of basal, extending (immature reproductive), flowering and aerial tillers were counted. Plants were then cut 5 mm above the soil surface and the material was divided into basal, extending, flowering and aerial tillers, and dead leaves. The total number of live leaves for each of these groups was counted. The number of dead leaves for each whole plant was also recorded. Leaves from the different tiller types were initially kept separate. The sheaths were removed from all the live leaves. Total leaf area was recorded for each category (without sheaths). Wet mass of all the plant parts except roots and stubs was recorded. Plant material was oven dried at 90°C for 24 hours and dry mass was recorded. These data were used to determined specific leaf area (SLA), leaf weight ratio (LWR), leaf area ratio (LAR).

RGR was calculated by determining the combined mass of 30 seedlings for each population tested, and then determining the mean weight by dividing the total by 30 (individual seedling mass was too small to be measured accurately on a four-point balance). The natural log of the seedling mass was subtracted from the natural log of the total mass and divided by $T_1 - T_2$ (154 – 30 days) and multiplied by 1 000 to get $mg.g^{-1}.day^{-1}$.

Water content

Values for water content were obtained by dividing the mass of the basal tiller leaves (excluding sheaths) by the number of basal tiller leaves, to get a value for individual leaf weight for both wet and dry mass. Individual dry leaf mass was then subtracted from individual wet leaf mass to obtain a value for water content in grams.

Cellulase digestion

Leaf material of the various tiller types was combined for each individual and ground in a Wiley mill, 40 mesh. Duplicate samples of 0.02 g were used in a cellulase digestion procedure as described by Zacharias (1986). The digestion was run against standards obtained from the Range and Forage Department, University of Natal Pietermaritzburg.

Total phenols

The modified Prussian blue assay for total phenols (Price and Butler, 1992) was used to determine the phenolic content of the leaf material. Again, the material used in this assay was that of the combined ground leaf material. Results are presented in gallic acid equivalents (GAE).

4.2.3 Seed mass

Seed mass was determined by weighing 100 randomly selected seeds from the seed stocks described in Chapter 3. At a later stage, limited seed from the Ukulinga site became available and these were incorporated into the analysis.

Analysis

All data were analysed using one-way analysis of variance (ANOVA) (Statistica package 97). Data were tested for homogeneity of variance using Bartlet's test. If variances were significantly different (meaning data does not fit the assumption for a one-way ANOVA), data were log-transformed and re-tested. Here data were accepted for ANOVA at the 0.01 significance level.

4.3 Results

4.3.1 Field studies

Tiller production

In the first season of growth, total tiller production was significantly different among all sites for which there was data, being most prolific in swards of *Themeda* from the most mesic site, Kamberg, and least prolific in the tropical, variable rainfall site, Magangeni (Table 4.3). There was a decline in tiller production in Kamberg and Ukulinga (moderately mesic) in the second season, but total tiller number was still greater compared to Magangeni and Trompsberg (semi-arid). Conversely, tiller production at Magangeni increased in the second season of growth. Tiller production at the semi-arid site (Trompsberg) was similar to that of the Magangeni site (variable rainfall) in the second season of growth.

Basal tillering followed the same pattern as for total tiller production in Kamberg and Ukulinga. Basal tillering in the most mesic site (Kamberg) was comparable to that in the semi-arid populations (Trompsberg) in the second season of growth. No basal tillers were found in the Hluhluwe populations (Table 4.3).

No aerial tillers were found at the Kamberg site. Aerial tiller production was significantly higher in the second season of growth compared to the first season at all sites where they were found. There was no significant difference in the production of aerial tillers between the older post-burn sites of Magangeni and Ukulinga (Table 4.3). However, the position of these tillers differed considerably in that they were found at greater heights and more evenly spaced out in the Magangeni populations compared to other populations (pers. obs.).

No extending tillers were found in either of the Kamberg sites or at Trompsberg. The number of extending tillers was significantly greater in the second season of growth at Ukulinga compared to Magangeni. It should be noted that the extending tillers from Ukulinga were thought to be vegetative tillers extending slightly (only up to about 4 cm above the soil surface) so as to improve light acquisition, whereas those in the Hluhluwe populations were though to be immature reproductive tillers (Table 4.3).

No flowering tillers were found in the mesic site (Kamberg) and were more abundant in the variable rainfall site (Magangeni), compared to the moderately mesic site (Ukulinga) in the early part of the first growing season. Flowering tillers were significantly more prolific in the second year of growth in all sites sampled, being most prolific at Kamberg. The number of flowering tillers at Magangeni and Trompsberg were comparable in the second season of growth. Ukulinga had the fewest (Table 4.3).

Table 4.3 Means and standard deviations (in brackets) of tiller production per 225 cm^2 (0.15 x 0.15m), comparing young and old post-burn stands of *Themeda* among four study populations investigated, and results from one-way ANOVA and LSD tests. Populations with different letters denote significant differences. Data were log transformed where necessary.

Site	Trompsberg	Magangeni	Magangeni	Ukulinga	Ukulinga	Kamberg	Kamberg
Post burn age	15 months	5 months	30 months	2.5 months	28 months	2.3 months	15 months
Total tillers F=64.7 Df= 6, 130 ***	53.8 (19.3) **b**	22.1 (6.2) **a**	52.2 (18.9) **b**	97.9 (24.9) **c**	83.5 (28.8) **c, e**	137.1 (33.7) **d**	72.9 (19.6) **e**
Basal tiller F=73.5 Df=4, 92 ***	38.6 (16.3) **d**	0.0	0.0	93.4 (24.5) **a**	23.9 (7.1) **b**	137.1 (33.7) **c**	38.3 (18.0) **d**
Aerial tiller F=98.4 Df=4, 92 ***	0.2 (0.5) **a**	3.2 (3.8) **a**	30.0 (14.4) **b**	2.1 (1.4) **a**	33.5 (15.1) **b**	0.0	0.0
Ext. tiller F=13.2 Df=2, 57 ***	0.0	10.7 (5.4) **a**	7.1 (5.7) **a**	0.0	18.6 (9.8) **b**	0.0	0.0
Rep. Tiller F=47.1 Df= 5, 111 ***	14.9 (9.0) **b**	8.3 (3.7) **a**	15.1 (5.9) **b**	2.5 (1.4) **c**	7.6 (6.0) **a**	0.0	34.7 (13.2) **d**

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Biomass production

Results on biomass allocation, comparing one and two seasons' worth of growth are given in Table 4.4 and Figure 4.1. Data was log-transformed for analyses. Total biomass production and biomass partitioning for all the categories sampled were significantly different among populations.

The Magangeni sites (tropical, frost free, variable rainfall) had the highest total biomass per unit area in both the first and second season of growth. In the second season of growth, the semi-arid frost-prone site (Trompsberg) had the lowest biomass, whereas the mesic site, Kamberg, had the lowest biomass in the first season. Biomass per unit area increased significantly within two seasons of growth in swards of *Themeda* for all the sites investigated.

The biomass of reproductive tillers per unit area increased in all sites in the second season except at Ukulinga (moderately mesic). This increase was most significant at the tropical, variable rainfall site (Magangeni) (Figure 4.1). The biomass of dead material also increased in the second season; this was most evident in the mesic sites, Kamberg and Ukulinga (Figure 4.1). The semi-arid site (Trompsberg) had the lowest biomass of dead material per unit area but this made a proportionally high contribution to total biomass.

Although the actual biomass of dead material accumulated in the older Magangeni site was relatively high, its proportional contribution to total biomass was low compared to the mesic sites (Ukulinga and Kamberg) where dead litter formed the greatest contribution to total biomass. At Magangeni, reproductive tillers contributed the most to total biomass.

Table 4.4 Mean and standard deviations for biomass in g.m^{-2} for young and old post-burn sites in four study populations of *Themeda* and results from one-way ANOVA and LSD tests. Populations with different letters denote significant differences. Data were log transformed where necessary.

Site	Trompsberg	Magangeni	Magangeni	Ukulinga	Ukulinga	Kamberg	Kamberg
Post burn age	15 months	5 months	30 months	2.5 months	28 months	2.3 months	15 months
Total biomass F=123, Df=6, 130 ***	741 (326) **f**	1594 (584) **a**	3138 (1025) **b**	409 (138) **c**	1876 (429) **a**	275 (93) **d**	1235 (403) **e**
Basal tiller biomass F=13.5, Df=4, 92 ***	162 (96) **b**	0	0	333 (122) **a**	156 (59) **b**	275 (93) **a**	172 (81) **b**
Aerial tiller biomass F=62.8 Df=4, 92 ***	0.6 (1.5) **a**	18 (21) **a**	224 (108) **b**	7 (4.6) **a**	248 (124) **b**	0	0
Ext. tiller biomass F=4.44 Df=2, 57 **	0	271 (79) **a**	198 (110) **b**	0	171 (134) **b**	0	0
Rep. Tiller biomass F=109 Df=5, 111 ***	143 (93) **c**	784 (312) **a**	1796 (724) **b**	26 (16.48) **c**	125 (108) **c**	0	463 (190) **d**
Dead litter biomass F=152 Df=5, 111 ***	435 (188) **f**	521 (260) **a, e, f**	940 (428) **b**	43 (21) **c**	1175 (284) **d**	0	600 (232) **e**

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$;

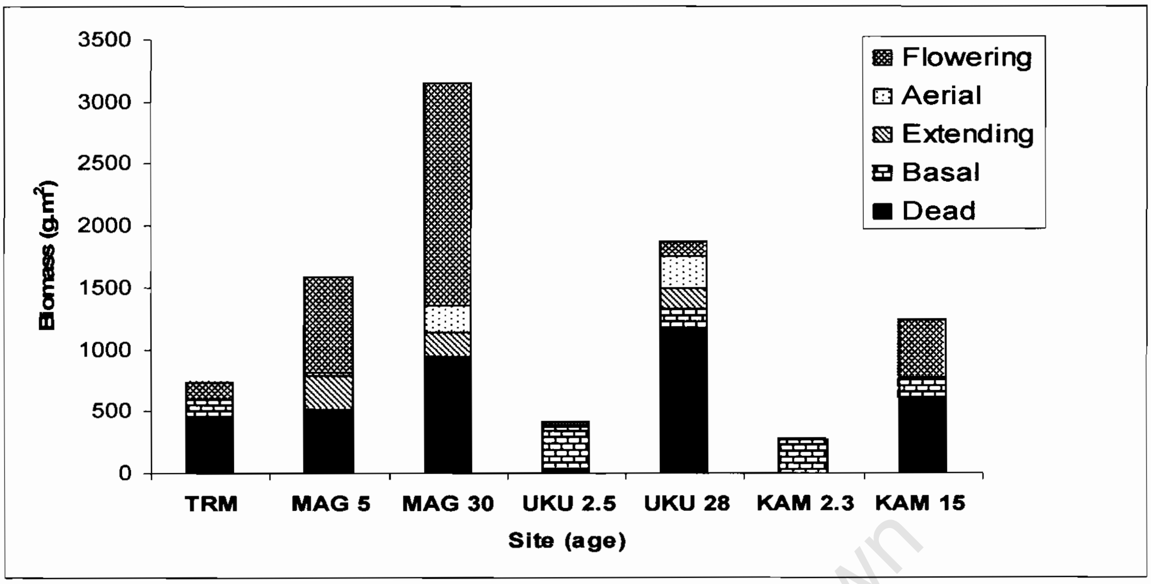


Figure 4.1 Total biomass (g.m^{-2}) and partitioning of biomass for four populations of *Themeda*, comparing one- and two-year post-burn swards.

Seed production

Data were log-transformed. In the semi-arid sites and sites which experienced periodic drought (Trompsberg, Magangeni), seed production was significantly higher compared to that in the mesic sites (Kamberg and Ukulinga) (Figure 4.2). Seed production was higher in tillers from the second season of growth at all sites except Ukulinga.

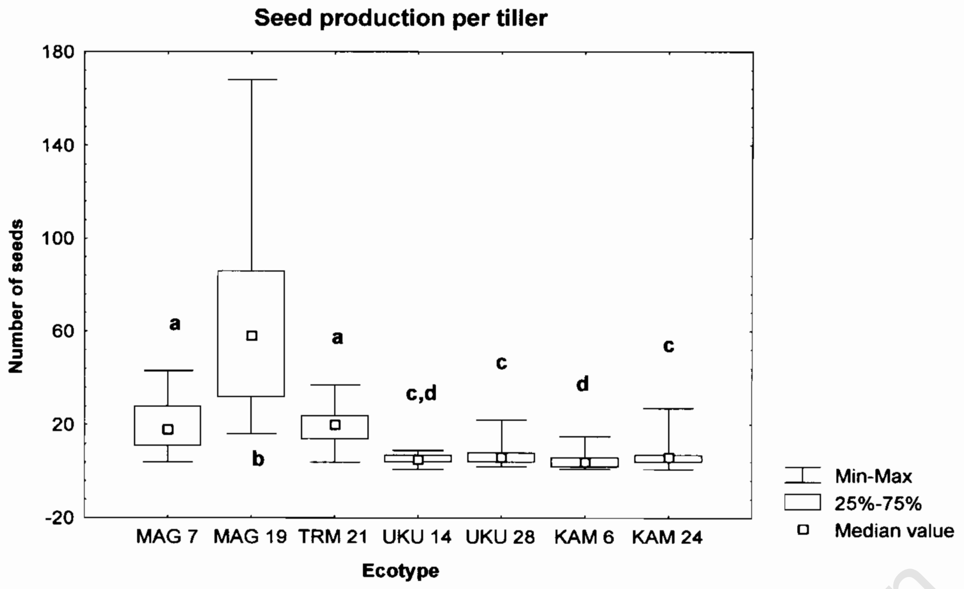


Figure 4.2 Seed production per reproductive tiller harvested from two post-burn ages of *Themeda* stands. Differences among populations were statistically significant (ANOVA on log transformed data, $P < 0.01$, F=79.5, df=6,132) Populations with different letters denote significant differences ($P < 0.05$) after LSD tests.

Seed mass

Ukulinga seeds were significantly heavier than those at all other sites, followed by the Trompsberg seeds, which were significantly heavier than the Kamberg and Hluhluwe seeds, Figure 4.3.

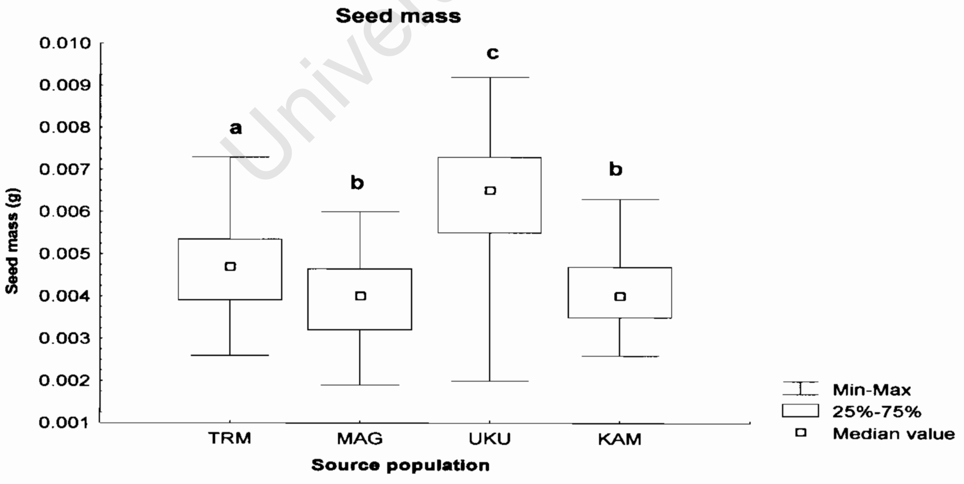


Figure 4.3 Median, range and minimum, maximum seed mass (actual data) for four populations of *Themeda*. Differences among populations were statistically significant (ANOVA on log transformed data, $P < 0.01$; F=69.6; df=3, 395). Populations with different letters denote significant differences ($P < 0.05$) after LSD test.

4.3.2 Glasshouse experiment

Tiller production

There was no significant difference in the total number of tillers or number of basal tillers produced among the three ecotypes grown in glasshouse conditions from seed (Table 4.5). This was inconsistent with field data as well as data from clonally propagated plants (see Chapter 5). However the pattern of proportional allocation to the types of tillers produced differed, with the Hluhluwe and Trompsberg plants showing an opportunistic early allocation to reproductive structures. No aerial or extending tillers were produced in the Kamberg plants, which was consistent with results from field studies. Extending tillers produced by Hluhluwe and Trompsberg plants were thought to be immature reproductive tillers, with the Hluhluwe plants producing more. The Hluhluwe plants also produced slightly more aerial tillers than the Trompsberg plants (Table 4.5).

The Hluhluwe (Magangeni) plants were the only ones to have produced mature flowering tillers at five and a half months (Table 4.5). This rapid phenological development is consistent with results obtained from field studies.

Table 4.5 Mean tiller production and (standard deviation) per seedling where $n = 9$ and results from one-way ANOVA and LSD test. Populations with different letters denote significant differences.

Site	Trompsberg	Magangeni	Kamberg
Total NS	17.44 (11.8)	18.67 (5.46)	20.89 (8.09)
Basal tillers NS	16.22 (12.34)	11.89 (4.2)	20.89 (8.09)
Aerial tillers	0.11 (.33)	0.78 (1.72)	0
Extending tillers F= 21.8 Df= 1, 16 ***	1.11 (1.45) a	5.56 (2.46) b	0
Flowering tillers	0	0.44 (.73)	0

NS = not significant, $^{***}p < 0.001$.

Biomass production

Actual biomass production for seedlings

The total biomass production differed significantly among the three ecotypes investigated (Table 4.6). The Hluhluwe plants produced the most biomass, followed by Trompsberg, with Kamberg the least, consistent with field observations. The same pattern was evident in total above-ground biomass. The high above ground biomass in Hluhluwe plants could be attributed to a significantly higher value for extending tiller biomass. The Hluhluwe plants also accumulated significantly more dead leaf biomass per seedling than the Trompsberg and Kamberg plants. The mass of roots was significantly different among all ecotypes, heaviest in Hluhluwe plants with Kamberg plants producing the lowest root biomass.

Table 4.6 Mean biomass production (g) per seedling ($n = 9$) and results from ANOVA and LSD tests performed on log-transformed data. Populations with different letters denote significant differences.

Site	Trompsberg	Hluhluwe	Kamberg
Total mass (g) F=32.1 Df=2, 24, ***	7.06 (4.22) a	17.05 (5.4) b	2.67 (1.31) c
Total above ground F= 22.1 Df=2, 24 ***	4.55 (2.69) a	10.20 (4.01) b	1.91 (1.11) c
Root F= 38.9 Df=2, 24 ***	2.51 (1.57) a	6.88 (3.08) b	0.76 (0.25) c
Stubble F=13.5 Df=2, 24 ***	0.60 (0.43) a	1.34 (0.47) a	0.30 (0.10) b
Basal tiller mass NS	3.23 (2.05) a	2.18 (0.99) a, b	1.5 (1.03) b
Aerial tiller mass NS	0.02 (0.05)	0.08 (0.18)	0
Extending tiller mass F=18.5 Df=1, 12 **	0.58 (0.81) a	5.56 (2.51) b	0
Flowering tiller mass	0	0.60 (.93)	0
Dead litter mass F=5.1 Df= 2, 24 *	0.13 (.09) a	0.45 (0.30) b	0.15 (0.06) a

NS = not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Proportional distribution of biomass for seedlings

The three ecotypes partitioned biomass differently within five months of growth (Figure 4.4). Including extending tillers as reproductive structures (immature flowering tillers), the Hluhluwe (tropical, variable rainfall) plants had a much larger proportion of biomass in reproductive structures compared to vegetative material, consistent with field observations. The Trompsberg (semi-arid) plants also partitioned biomass to reproductive structures but to a lesser extent. The Kamberg (mesic) plants produced the most vegetative biomass proportionally. The proportion of plant biomass attributed to dead material was highest in the Kamberg plants, followed by the Trompsberg plants, and lowest in the Hluhluwe plants, consistent with results obtained from field populations.

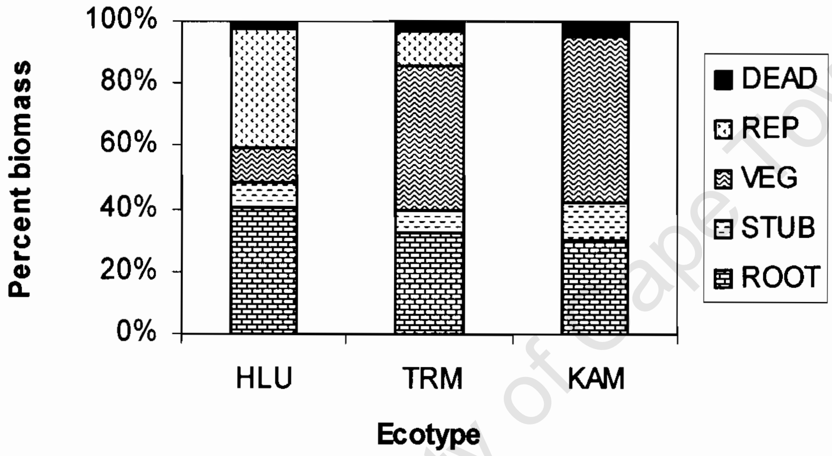


Figure 4.4 Partitioning of biomass in *Themeda* plants from three localities grown under controlled conditions, (n = 9 for each ecotype). HLU = Hluhluwe; TRM = Trompsberg; KAM = Kamberg; STUB = stubble; DEAD = dead leaves; VEG = vegetative material; REP = reproductive tillers.

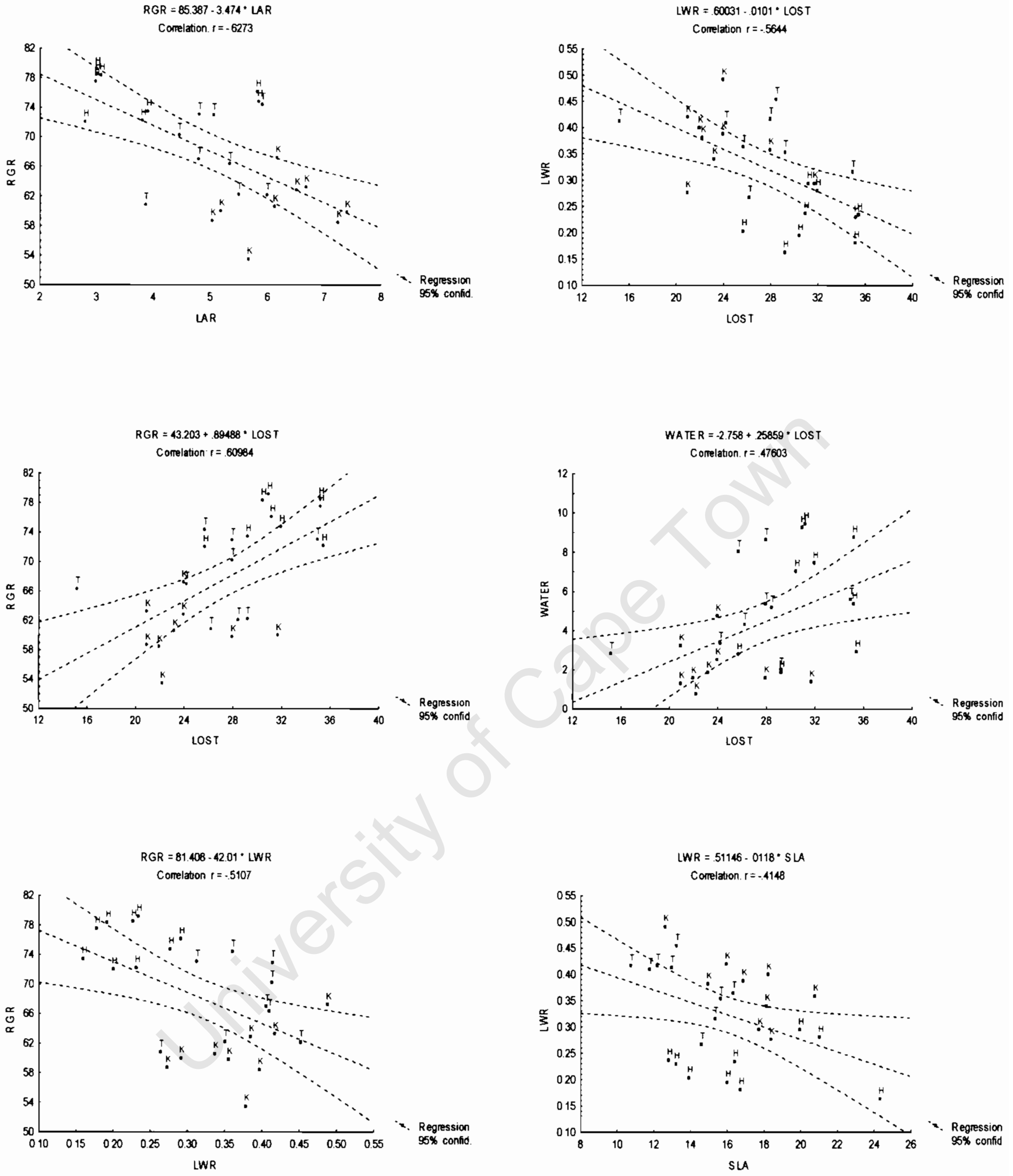
Growth analysis

Means and results of ANOVA and LSD tests are presented in Table 4.7. Relative growth rates were significantly different among the populations. The Hluhluwe plants had the highest RGR followed by Trompsberg, and then Kamberg (Table 4.7). Allocation patterns showed that LWR was significantly higher in the ecotypes with lower RGRs (Kamberg and Trompsberg). SLA was significantly lower in the Trompsberg plants. There was no pattern relating SLA to RGR among the populations. LAR was significantly different among all ecotypes (Table 4.7), being lowest in the Hluhluwe plants and highest in the Kamberg plants, indicating a negative correlation with RGR. The Trompsberg plants had the highest phenolic content, which was significantly greater than that in the Kamberg plants (Table 4.7). Less material was lost in digestion in the Kamberg and Trompsberg plants compared to the Hluhluwe plants. Water content was significantly higher in the Hluhluwe plants compared to the Kamberg plants.

Table 4.7 Means of parameters measured in seedlings and results from ANOVA tests(Df=2, 24 for all tests). Populations with different letters denote significant differences ($P < 0.05$) after LSD tests. WC = water content.

	RGR ($mg.g^{-1}.d^{-1}$) F=32.1 ***	LWR ($g.g^{-1}$) F=21.3 ***	SLA ($m^2.kg^{-1}$) F=4.43 *	LAR ($m^2.kg^{-1}$) F=13.9 ***	Phenolic content ($mg.g^{-1}$ DW) F=3.98 *	Digestion (% lost) F=8.01 **	WC. Leaf[1] (g) F=6.1 **
HLU	75.65 a	0.22 a	17.2 a	3.82 a	46.26 a, b	31.8 a	6.05 a
TRM	67.53 b	0.39 b	13.5 b	5.14 b	53.75 a	26.7 b	4.35 a, b
KAM	60.33 c	0.37 b	17.1 a	6.24 c	41.32 b	24.1 b	2.05 b

Some of these results were surprising in the light of the common trends reported in other studies, notably, the lack of correlation between SLA and RGR, and the lack of common trends in trade-offs among the populations. This was further explored by looking at correlations



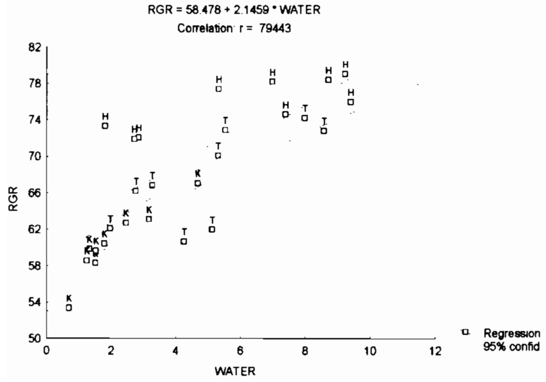


Figure 4.5 **Correlations between various plant traits for seedlings grown under controlled conditions (*n* = 27). H = Hluhluwe, T = Trompsberg, K = Kamberg. Units:** RGR ($mg.g^{-1}.d^{-1}$), LWR ($g.g^{-1}$); SLA ($m^2.kg^{-1}$); LAR ($m^2 .kg^{-1}$) WC. $Leaf^{-1}$ (g), Digestion (% lost)

4.4 Discussion

Phenological development, biomass production and distribution, and reproductive output differed among the populations of *Themeda* studied, both in the field and under controlled conditions. The results indicated that the Hluhluwe (tropical, periodic droughts), and to a lesser extent Trompsberg (semi arid) ecotypes had more rapid growth, earlier apex elevation and greater allocation to reproductive structures than the Kamberg (mesic) ecotypes under optimum conditions, concurring with results presented in chapter 3. Groves (1975) and Downing and Groves (1985) also noted differences in morphology, tiller production, biomass partitioning and time to anthesis among plants from various source populations (Ukulinga, Hluhluwe, Frankenwald, Sehlabathebe) grown from seed under controlled conditions. These authors attempted to relate differences among populations to physiological adaptations to temperature, but concluded there was little evidence for this. Reappraisal of data from Downing and Groves's (1985) revealed that apex elevation and flowering in plants grown under controlled conditions was significantly earlier in plants from more arid areas which concur with results presented here. Genotypic variation in phenological development and relative allocation to vegetative and reproductive output has also been reported in *Panicum maximum* Jacq. (Usberti *et al.*, 2002), however, studies of this comparative nature are lacking (Tainton, 1981).

Early differences in resource partitioning and phenological development observed in the seedling experiment were consistent with field observations which provided confirmation that these differences manifest in the natural environment. Tiller production was generally not well correlated to total biomass production. For example, Magangeni (tropical, variable rainfall, periodic droughts) plants had lower tiller production than the Kamberg and Ukulinga (mesic) plants but produced far greater biomass per unit area. Both the mesic populations (Kamberg and Ukulinga), showed a higher allocation to vegetative material compared to reproductive structures, and ultimately density-dependent processes became evident, associated with declining tiller production and a high load of dead leaf matter.

Ukulinga plants could not be included in the seedling experiment presented in this thesis because of lack of seeds at the commencement of the experiment. However, results from Downing and Groves (1985) showed that plants from seed originating from Ukulinga, when grown under controlled conditions, had high vegetative tiller production and flowered later then other populations. Results correspond to those presented here for field populations tested. The high production of vegetative tillers in these mesic populations early in the season is likely to confer a competitive advantage, in terms of space and light acquisition, in the competitive environments typical of these areas.

The patterns observed indicating differences in life history strategies are particularly evident within the first season of growth where populations from semi-arid sites, or areas where rainfall was variable, interspersed with drought, exhibited rapid phenological development under favourable conditions to maximize reproductive output within a short space of time. Differences in the timing and rate of apex elevation among ecotypes of *Themeda* have been noted before (Booysen, Tainton and Scott 1963, Tainton and Booysen, 1965; Rethman, 1971, Tainton, 1981, Downing and Groves, 1985) and may have important management implications. Opperman and Roberts (1978) stress the importance of understanding phenological development of rangeland plants, particularly shoot apex elevation, since damaging the shoot apex though fire, grazing or drought may have a detrimental effect on productivity and reproductive output.

Results from the growth analyses reflect differences in phenological development and allocation strategies among the populations. Specific leaf area, LAR and LWR are considered important predictors of growth rate. Higher values generally correlate with higher RGR (Poorter, 1990). Slower growth rates are generally associated with lower SLA values (Lambers, *et al.*, 1998). SLA, however, was not a good predictor of RGR for the three forms of *Themeda* studied. The Hluhluwe form had the highest RGR, and Kamberg the lowest RGR, but the SLA values for these forms were similar, and higher than those for Trompsberg. The fact that no overall patterns relating SLA, LWR and LAR to RGR were found suggests that ecotypes partition their resources differently. This is partly accounted for in the differential allocation to vegetative and reproductive structures, and the lack of correlation between tiller production and biomass. Appraisal of Downing and Groves's (1985) data showed that there was a poor correlation between tiller production and biomass, consistent with results presented here. Sugiyama (1995) found a negative correlation between RGR and tiller production in genotypes of a perennial grass species where those producing fewer tillers had larger tillers and higher RGR, whereas more smaller tillers were produced in genotypes with lower RGR, also consistent with results presented here.

Inherent variability in the leaf properties among ecotypes may, in part, also account for some of the pattern or the lack thereof in the relationships among growth parameters. Phenolic content, digestibility, and water content, which differed among ecotypes, are factors that affect SLA, LWR and LAR and would lead to ecological implications relating to palatability, leaf longevity and litter accumulation. Lower SLA values are associated with an increase in the amount of chemical components in cells (Van Arendonk and Poorter, 1994). Van Arendonk and Poorter (1994) stress the importance of the components of SLA, rather than SLA itself, in determining the success of species in stressful environments. The low SLA values for the Trompsberg plants may be attributed to the high phenolic content and relatively low digestibility of these plants. Theunissen (1995a) also found differences in the phenolic content in several ecotypes of *Themeda* grown under controlled conditions. The low digestibility in the Trompsberg form further indicates an investment in cell wall components like lignin and (hemi)cellulose, commonly associated with lower SLA values (Van Arendonk and Poorter, 1994). These traits may result in lower palatability and longer leaf life spans (Waring, *et al.*, 1985; Dijkstra, 1990; Lambers, *et al.*, 1998), consistent with the theory that plants in resource (nutrients and water)-limited environments tend to minimize tissue loss (Van Arendonk and Poorter, 1994; Lambers, *et al.*, 1998).

Higher RGR's were associated positively with water content and digestibility. This explains the results from the Kamberg plants, which had the lowest RGR, water content and the least material lost in digestion, indicating that these plants contain more structural tissue than the Hluhluwe and Trompsberg plants. After reviewing the literature, Lambers, *et al.* (1998) concluded that low potential RGR does not confer an ecological advantage and they offer an alternative explanation, suggesting that the components linked to RGR are the traits targeted by natural selection and not RGR itself. These include the traits that protect the tissue as described above. The difference between Kamberg and Trompsberg populations which have both invested in protecting leaf tissue is that they use different traits to achieve this. Kamberg has a lower phenolic content compared to Trompsberg plants but more structural tissue resulting in lower digestibility and lower water content. Interspecifc studies on grasses have also found low RGR to be associated with higher investments in structural tissue such as lignin, hemicellulose and cellulose (Niemann, *et al.*, 1992; Van Arendonk and Poorter, 1994). This structural investment in Kamberg plants, associated with the lowest phenolic content among ecotypes, may explain the comparable SLA values with the Hluhluwe plants, despite a lower RGR of Kamberg plants.

The low water content in Kamberg plants may be an adaptation to frost (Poorter, 1990), whereas the allocation into leaf structural tissue may result in a lower decomposability of leaf material, accounting for the accumulation of dead leaf material in this form. This may also confer an advantage during cold, frosty winters in protecting the buds. A consequence of the accumulation of dead material is a higher fuel load that would promote fire risk (Bond and van Wilgen, 1996; Bond 1997). Fire is necessary to maintain the productivity and presence of *Themeda* in mesic grasslands (Everson 1994). These plants may therefore be designed to burn, thereby reducing the risk of being replaced by other species more tolerant to shading (see Bond 1997).

The pattern in the Hluhluwe plants was opposite to that in Kamberg, by having the highest RGR, highest water content and the most easily digested material, possibly resulting in higher decomposability of leaf material, and accounting for the proportionately low accumulation of dead leaf material despite the high RGR. The proportionately low amount of dead leaf material may also be a function of the relatively lower vegetative tiller output in these plants. Recognized advantages of high RGR are: occupation of space (acquisition of resources) and maximized reproductive output (Lambers, *et al.*, 1998). The phenological development and associated high growth rates in the Hluhluwe populations can therefore be assumed to be an adaptation to maximizing reproductive output within a short time in periods when water is not limiting. These plants produced the greatest number of seeds but had the lowest seed mass.

The low LAR values for Hluhluwe are attributed to low leaf mass ratios (LMR) in these plants, where allocation to reproductive structures, such as the culm, accounts for more biomass than leaf material. Other studies on monocotyledons have also shown that LMR does not necessarily correlate well with RGR for these species (Lambers, *et al.*, 1998). These culms also serve to support aerial tillers and act as a morphological deterrent to grazers.

Conclusion

Data obtained from field and greenhouse experiments support the hypothesis that populations of *Themeda* from different rainfall conditions have developed different LHSs. These differences are reflected in the RGRs, phenological development, allocation patterns, leaf traits and reproductive output of study populations. In low, unpredictable rainfall regions, populations have evolved a strategy in which growth and the development of reproductive structures is rapid under optimal moisture conditions with a high allocation to sexual reproduction (r-selection). Propagation through seed is therefore likely to be an important process contributing to population persistence in these areas where mortality due to periodic droughts is high (see O'Connor and Bredenkamp, 1997). This strategy is consistent with the suggestion by Lambers, *et al.* (1998) (see Chapter 1) that fast-growing species are more common in unpredictable environments where disturbance occurs. Populations from high and predictable rainfall conditions (Kamberg and Ukulinga) rely more on vegetative propagation for maintaining population structure (K-selected). The slower inherent relative growth rate of the Kamberg plants was consistent with the suggestion that slow-growing, longer-lived species are more common in predictable environments (Lambers, *et al.* 1998). But instead of a low incidence of disturbance, disturbance (fire) has a positive effect in maintaining *Themeda* populations, since without frequent burning, *Themeda* disappears and is replaced by other species more tolerant of shading. Differences in leaf traits and their relation to growth parameters presented interesting relations. A more specific investigation into the ecological significance of these characteristics and their relationships would be well worth while.

The ecological implications of the different strategies in terms of productivity and demography of the *Themeda* populations are further investigated in Chapters 5 and 6 respectively.

5 Variation in the production characteristics of *Themeda*

5.1 Introduction

Understanding what controls plant production is central to effective management and decision making in rangelands (Archer and Smeins, 1993). Two dominant paradigms exist pertaining to determinants of productivity. The first is that animal numbers/ carrying capacities and fire could be used as tools to control and maintain plant productivity in rangelands by keeping the plant community within a favourable successional state according to the objectives of the manager (Tainton and Mentis, 1980). This is based on the assumption that density-dependent processes within plant communities, such as competition for light and space, are factors that strongly influence productivity (Knapp and Seastedt, 1986). Fire increases productivity by removing standing dead litter material that accumulates from the growth of the previous year (Towne and Owensby, 1984; Knapp and Seastedt, 1986). For example, regular fires (biannual) and/or grazing are necessary for maintaining the productivity of key species in the montane grasslands of the Natal Drakensberg and temperate grasslands of Australia, and, if absent, palatable grasses are replaced by other species (Everson, *et al.*, 1985; Everson *et al.*, 1988; Lunt and Morgan, 2002). Groves (1974) reported high post-fire productivity in temperate *Themeda* grasslands, which declined considerably after two years, indicating density-dependent processes were important. Furthermore McDoughall (1989) predicted that *Themeda* tussocks in temperate grasslands of Australia would die if they remained unburnt for too long a period.

The alternative paradigm stems from several studies which show that variability in plant productivity and other plant responses such as tiller development, flowering and seed set are primarily a function of fluctuations in moisture availability (Opperman and Roberts, 1978; Danckwerts *et. al.*, 1984; O'Connor, 1985; Snyman and Fouché, 1993; Milchunas, *et al.*, 1994; Lunt and Morgan, 2002) rather then density-dependent processes or biomass removal through grazing or fire. Studies in the tall-grass prairies of America have also shown that above-ground net primary production (ANPP) varies substantially from year to year (Risser, *et al.*, 1981; Towne and Owensby, 1984, Knapp, *et al.*, 1998) and that these fluctuations can be correlated to annual fluctuations in moisture availability as well as factors such as solar radiation, temperature and potential evapo-transpiration (Risser, *et al.*, 1981; Knapp, *et al.*, 1998).

Neither of these paradigms is incorrect, but may be applicable to different systems or different periods in the same system. In South Africa, it is becoming increasingly important to manage our grasslands sustainably, to yield maximum benefit (dependent on objectives), with minimum degradation. The challenge therefore is to define more clearly, yet simply, what processes are important in the various grassland systems, since this has drastic implications for the options available to managers and how one goes about managing the veld.

Results from Chapter 4 indicate that density-dependent processes may be strong in mesic areas, whereas growth in populations from semi-arid or variable rainfall climates is opportunistic depending on moisture availability. In this chapter, the processes controlling productivity and the extent to which populations have adapted to these processes are explored. The following hypotheses are tested. Variations in plant productivity in arid areas or regions with unpredictable rainfall result primarily from fluctuations in rainfall and moisture availability. In these systems the primary limitation on productivity would be moisture availability. In mesic areas, however, where rainfall is predictable, fluctuations in plant productivity would be a function of density-dependent factors such as competition for space and light, carry-over effects and biomass removal (through fire and grazing). Here the primary limitation on productivity would be access to light, where, if there is no biomass removal, plants eventually self-shade themselves, resulting in reduced productivity. In regions that experience wet and dry cycles with periodic droughts, the causes and control of fluctuations in productivity are expected to vary, depending on whether it is a wet or dry cycle. During wet cycles, density-dependent factors (self-shading) will be more important in influencing productivity, whereas rainfall will account for fluctuations in productivity in dry years or during droughts and in the transition periods between such cycles. This was investigated by tracking productivity of field populations of *Themeda* occurring over a rainfall gradient during one growing season.

To determine whether differences in the determinants of plant productivity among populations have resulted in the genetic divergence of plant response to moisture availability and density-dependent effects, light, water and biomass removal (cutting) treatments were applied to clonally propagated plants collected from the four study populations of *Themeda*. Their response to these treatments was determined. Differences in the patterns of response of the clonally propagated plants under the same treatments would reflect genetic divergence among the source field populations studied and provide an indication as to what the important selection pressures are in populations from different climatic templates.

5.2 Methods

5.2.1 Field studies of productivity

Treatments

The aim of this experiment was to investigate the effect of self-shading on grass productivity in field populations of *Themeda.* Assuming that self-shading is a function of the previous year's dead standing biomass (see Knapp and Seastedt, 1986), we predicted that the initial biomass (B_t) of the season would have a greater influence on productivity in mesic areas, whereas rainfall would influence *Themeda* productivity more in semi-arid or drought-prone areas.

Five sites across a rainfall gradient were chosen for the study: Nqumeni (semi-arid, wet/dry cycle); Magangeni (wet and dry cycles with periodic droughts), Trompsberg (semi-arid, unpredictable rainfall), Ukulinga, (moderately mesic, predictable rainfall), Kamberg (mesic, predictable rainfall). All sites were burnt approximately one year prior to the start of the experiment. The experiment commenced in the dormant season (July) of 1997. At each site, five 5 x 1-m long permanent transects were established and marked out with iron stakes. Each transect was divided into five 1 x 1-m plots giving a total of 25 1 x 1-m plots at each site.

Biomass was not measured directly, but rather by means of a disc pasture meter, which measures the settling height of the disc (in cm) on the vegetation, providing an indication of biomass (Bransby and Tainton, 1977). It was not necessary to calibrate settling height to biomass since it was the relationship between initial biomass and current year's productivity that was important, not the actual biomass. In order to obtain a data range that could be used to determine the relationship between starting biomass and current productivity for each site, five manipulations, with five replicates per manipulation, were applied to the 1 x 1-m plots. Swards were cut to 100 (no cut), 75, 50, 25 and 15% of the initial height of the stand of *Themeda*. Treatments were randomly assigned to 1 x 1-m plots. The transect positions and the treatments within each transect were mapped for each site. Biomass was estimated (cm) using a pasture disc meter. Measurements were recorded at one point within each 1 x 1-m plot. The centre of the disc measurement was then marked with small steel pins. Measurements were repeated on the exact points of the initial measurements (after removing the pins) at four and 10 months after initial biomass manipulations, for all sites expect Kamberg, where data at 10 months could not be collected due to the disappearance of the poles marking the transects. For the second set of measurements, a metal detector was used to locate the pins at the Ukulinga, Nqumeni and Magangeni sites. Grazers were excluded from the Trompsberg and Ukulinga sites. Few grazers were found in the Kamberg site. The Nqumeni and Magangeni sites were not protected from grazers.

Analysis

To measure negative effects of initial biomass on grass productivity, I followed the approach used by Tillman & Mentis (1990) borrowed from population ecology. Here productivity is expressed as the value $\frac{Bt+1}{Bt}$. A steep slope of $\frac{Bt+1}{Bt}$ plotted against Bt indicates strong negative feed backs of initial biomass on grass productivity. Tilman and Wedin (1990) found that the negative feedbacks to be so strong that grass productivity would cycle in a self regulated or "chaotic" manner due to internal regulation, rather then external factors such as inter annual variation in rainfall. If rainfall variation is a dominant factor driving grass production, the slope should be shallow even constant over Bt (Tilman and Wedin, 1990).

Productivity was estimated as: $\Delta B = \frac{Bt+1}{Bt}$

Where: ΔB is productivity, B_{t+1} is current year's biomass measured as settling height of the disc in cm and B_t is initial biomass, measured as settling height of the disc in cm. Results were graphed as B_t (cm) as the dependent variable and ΔB as the independent variable.

5.2.2 Determinants of plant productivity in clonally propagated plants

Treatments

Plants propagated from field populations of *Themeda* were used to test the effects of shade, initial biomass and moisture availability on plant productivity. The method of collection and propagation of the plants is described in Chapter 3. Plants were grown for one season under uniform conditions prior to the commencement of treatments. Treatments were started in mid August 1997. The following treatments were applied:

1) Watering treatments

Three water treatments were used to simulate a rainfall gradient from semi-arid (500 ml/yr) to mesic (800 ml/yr) to humid (1100 ml/yr).

The amount of water was varied on a monthly basis according to the natural monthly fluctuations from a mesic area, (Ukulinga). Treatments ran for seven months using simulations for the months October to April ("wet season"). Plants were watered three times a week with Rorison nutrient solutions (Band and Hendry, 1993). Nutrient concentrations were adjusted such that all treatments contained the same amount of nutrients, despite differences in water amount. Water treatment and dilutions are summarized in Table 5.1.

The amount of nutrients applied was calculated on the basis of the volume of sand in each pot. The recommendation is 0.4 ml of normal-strength Rorison solution (1 ml stock:1 litre water) per cm^3 of sand. Each pot contained 6895 cm^3 of sand and should therefore have received 2758 ml normal-strength nutrient solution per week. Since the amount of water being applied was the treatment and varied, the ratio of stock solution to be added to water was calculated by dividing the recommended volume of normal-strength nutrient solution by the volume of water for treatment for each month. However, no ratios greater than 10 ml stock per litre of water were allowed. The nutrient solution was applied to the plants using a bucket and scoop method.

Table 5.1 Ratio of stock solution to amount of water for each treatment for each month.

Month	ml water /month (ml nutrient stock per litre)		
	High	Medium	Low
October	84 (7.24)	61 (9.97)	38 (10)
November	108 (5.63)	78 (7.80)	49 (10)
December	184 (3.30)	134 (4.54)	84 (7.24)
January	182 (3.34)	133 (4.57)	83 (7.32)
February	126 (4.83)	91 (6.68)	57 (10)
March	145 (4.19)	105 (5.79)	66 (9.21)
April	91 (6.68)	66 (9.97)	41 (10)
Total for 7-month period	**920**	**668**	**418**

2) The effect of shade and initial biomass on productivity was investigated using the following treatments

a) Cutting plants 5 cm from the base at the beginning of the experiment, coded: no shade, cut (NC).
b) Leaving plants intact with one season's worth of growth, coded: no shade, whole (NW).
c) Cutting plants 5 cm from the base at the beginning of the experiment and shading them with shade cloth sleeves/columns (75% shade cloth) that extended to the maximum canopy height of the relevant population, coded: full shade, cut (FC).
d) Cutting plants 5 cm from the base at the beginning of the experiment and increasing the height of the shade cloth sleeve each week to the same height as the new growth, coded: up-shade, cut (UC).
e) Intact plants with one season's worth of growth and increasing the height of the shade cloth sleeve each week to the same height of the new growth, coded: up-shade, whole (UW).

These treatments were chosen in order to determine whether plants respond in the same way to shading and to initial biomass. A difference, for example, in the response of cut, full-shade plants compared to intact unshaded plants would indicate that the effect of biomass as opposed to just shading is different. It may be expected that biomass may have an additional effect to self-shading, and we would therefore expect productivity to be lower in intact unshaded plants compared to cut, full-shade plants. The treatments were also designed to investigate the impact of both one and two seasons' worth of growth.

Treatments were set up in a factorial design resulting in 15 treatments with four replicates each per populations (total 240 pots). See Table 5.2 for summary of treatment and abbreviations.

Table 5.2 Summary of treatments (and abbreviations) that were applied **after** an initial season of growth with optimum water supply. On commencement of treatments some plants were cut at 5 cm, three shading treatments were applied to these: full shade [shade cloth sleeve (75%) up to the maximum canopy height of the particular populations as determined from field studies]; up-shade [shade cloth sleeve (75%) being moved up to the same height as new growth]; and no shade (plants were left unshaded). Only the up-shade and no-shade treatments were applied to intact plants. Water and shading treatments were maintained for the equivalent of two seasons of growth.

Moisture availability	Shade	Cut/whole	Abbreviation of treatment
High	No shade	Cut	HNC
Medium	No shade	Cut	MNC
Low	No shade	Cut	LNC
High	No shade	Whole	HNW
Medium	No shade	Whole	MNW
Low	No shade	Whole	LNW
High	Full shade	Cut	HFC
Medium	Full shade	Cut	MFC
Low	Full shade	Cut	LFC
High	Up-shade	Cut	HUC
Medium	Up-shade	Cut	MUC
Low	Up-shade	Cut	LUC
High	Up-shade	Whole	HUW
Medium	Up-shade	Whole	MUW
Low	Up-shade	Whole	LUW

Just prior to beginning treatments, the length and breadth of each plant was measured at the base as a measure of the initial size (area) of the plant. Of the 60 replicates for each site, 35 were randomly selected for cutting (C) and the above-ground material harvested. Dry weight for live basal + extending tillers was combined, aerial tillers, flowering tillers and dead litter biomass was determined after oven drying sample in brown paper bags at 75°C for 48 hours. Results on the tiller proportions and biomass distribution are presented in Chapter 3.

Seven months after treatments were started, plant mortality and the number of flowering tillers, elongating tillers, aerial tillers on flowering tillers, aerial tillers on elongating tillers and basal tillers on live plants were counted. All plants were then harvested and material was separated into the following categories: dead litter, stubble (junction between roots and above-ground material), root, flowering tillers, elongating tillers, aerial tillers on flowering tillers and aerial tillers on elongating tillers. Dry weights for each of the categories were determined after oven drying samples in brown paper bags at 75°C for 48 hours. Data from all above-ground biomass categories, except stubble, were combined for subsequent analyses.

Analyses

5.2.2.1 Plant survival

Chi-squared tests were used to determine whether the pattern of plant survival of the four populations was similar or different for each treatment respectively. When analysing water treatments, survival in the low-water treatment was often less than five per population, hence the data for this category was combined with the medium-water treatment for the purposes of analysis. Likewise, survival for the Kamberg population was often too low for data to be incorporated into analyses.

5.2.2.2 Biomass production

Biomass production (B_{t+1}–B_t) was determined by subtracting initial above-ground biomass (B_t) from final above-ground biomass (B_{t+1}) where $B_t = 0$ for cut plants (C) and B_t for intact plants (W) = estimated values. Initial biomass of plants harvested at the start of the experiment (C) and initial plant diameter (known for all plants) were correlated for each population. The equations derived from these correlations and the known values for plant diameter of intact plants (W) were used to obtain the estimates of initial biomass for intact plants (W).

A step-wise regression was used to determine the effect of treatment on biomass production (B_{t+1}–B_t) for all populations combined and for each population separately. Only those plants that survived throughout the experiment were included in the step-wise regression.

An ANOVA was also performed to test the effect of water treatments and population on plant production. Only data from plants subjected to medium- and high-water treatments were included since poor survivorship in the low-water treatment resulted in insufficient replication for inclusion in analysis. Other treatments could also not be included in the analysis due to poor replication. Data were first analysed to test for homogeneity of variance using Bartlet's test. Initial tests showed that data met with the required assumptions for ANOVA so data transformations were not required.

5.2.2.3 Tiller production

Step-wise regression analyses were used to determine the effect of treatments on tiller production for populations combined and for each population individually. Only those plants that survived throughout the experiment were included in the analysis.

ANOVA was also performed to test the effect of water treatments and population on tiller production. Only data from plants subjected to medium- and high-water treatments were included due to poor survivorship in the low-water treatment. Other treatments could not be included in the analysis, due to poor replication. Data were first analysed to test for homogeneity of variance using Bartlet's test. Initial tests showed that data met with the required assumptions for ANOVA so data transformations were not required.

5.2.2.4 Productivity

Productivity was graphed as for that in field populations with (B_t) as the dependant variable and B_{t+1}/B_t as the independent variable. The initial biomass (B_t) used for cut (C) plants was 0 + stubble mass determined in the final harvest, and the estimated biomass determined from correlation equations for intact plants (W) + stubble mass recorded in the final harvest. The stubble mass was included in the initial biomass since one cannot calculate productivity when the initial value = 0. Values used for final biomass (B_{t+1}) were the total above-ground biomass + the mass of the stubble at final harvest.

5.3 Results

5.3.1 Productivity in field populations of *Themeda*

Productivity of field populations of *Themeda* is presented in Figure 5.1. The slope of the curve provides an indication of the extent to which current year's biomass (B_{t+1}) is related to previous year's biomass (B_t): the steeper the slope, the greater the suppression of productivity by initial biomass (B_t). The Ukulinga population had the strongest negative relationship between productivity and initial biomass, followed by the Magangeni, Kamberg and Nqumeni populations respectively. In the Trompsberg site, initial biomass had no apparent effect on productivity.

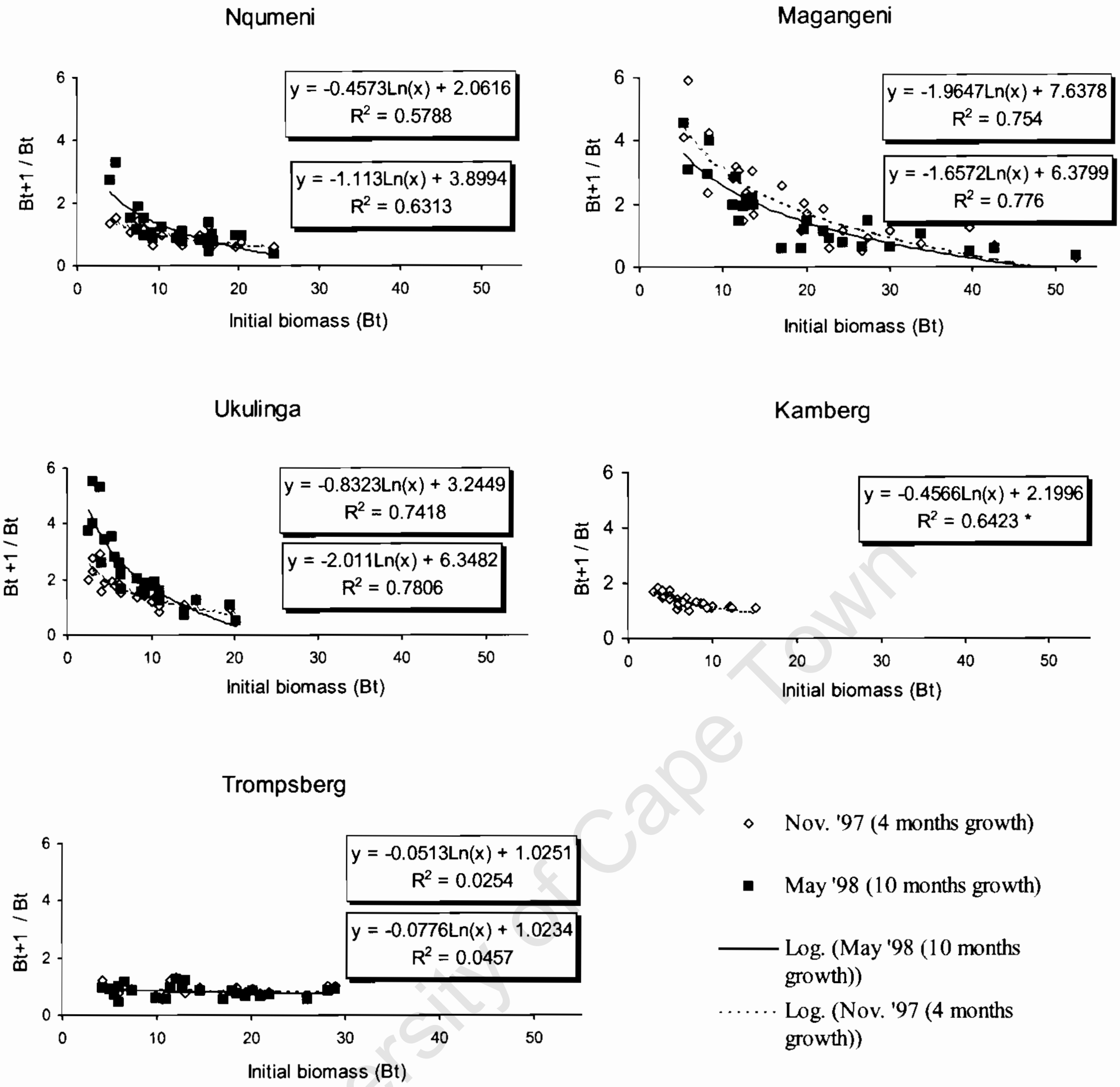


Figure 5.1 Productivity of field populations of *Themeda* as a function of initial biomass and current year's biomass. For each graph the top equation pertains to four months and the bottom equation for 10 months. Note the "log" trend line fitted is according to a logarithmic equation: y=clnx+b.

5.3.2 Response of clonally propagated plants grown under controlled conditions

5.3.2.1 Plant survival

Unfortunately, mortality was high during the experiment, particularly in the low-water treatments and in plants from the Kamberg population (Table 5.3). Low survivorship resulted in difficulties when performing subsequent statistical analyses because of poor replication since the ratio of treatments to replications was not sufficient.

Trompsberg plants were the most resilient for clonal propagation, followed by Magangeni plants. Mortality was greatest in the Kamberg plants. The pattern of survival among treatments was not always the same across populations, with different treatments sometimes favouring different populations. This is explored further by looking at the effects of treatments on specific populations.

Table 5.3 Survival (out of four) for each treatment and population.

Treatment	MAG	TRM	UKU	KAM
HNC	3	4	3	1
MNC	1	3	1	2
LNC	1	2	0	0
HNW	2	3	2	1
MNW	0	3	0	0
LNW	0	0	2	0
HFC	3	4	1	0
MFC	4	4	0	1
LFC	2	1	0	0
HUC	3	4	3	1
MUC	1	3	3	0
LUC	0	1	0	0
HUW	3	1	1	0
MUW	1	2	1	0
LUW	0	0	0	0
Total	24	35	17	6

Chi-squared analysis of survival

Expected values for survival for each population per treatment were calculated by dividing total survivorship (from all populations for a treatment) by total survivorship (for all populations and treatments) and multiplying this value with total survivorship for the given population. For example: total survivorship = 82, total survival for the high-water treatment = 43. Therefore the expected survivorship for Hluhluwe plants would be: 24 x (43/82). Observed survival in the Kamberg plants was often less then 5, hence data from Kamberg was not included in Chi-squared analyses.

Effect of water treatments on survival

Survival data (expected and observed) from the medium- and low-water treatments were combined since survival in the low-water treatment was too low to perform Chi-squared tests on. Populations did not differ significantly in their survival response to water treatments (Table

5.4). All populations showed higher survival in the high-water treatment and lowest survival in the low-water treatment.

Table 5.4 Results of Chi-squared testes on the observed versus expected frequencies of plant survival in relation to water treatments (where data from medium- and low-water treatments were combined) to determine if patterns of plant survival were similar or different among populations and water treatments; df = 1.

Site	Magangeni $X^2 = 0.33$, **NS**			Trompsberg $X^2 = 0.64$, **NS**			Ukulinga $X^2 = 0.54$, **NS**		
	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E
High	14	12.6	0.16	16	18.4	0.30	10	8.9	0.13
Med.+ Low	10	11.4	0.17	19	16.7	0.33	7	8.1	0.15
Sum	24	24.0	0.57	35	35.0	0.69	17	17	0.54

NS = not significant at $p < 0.05$; Obs = observed, Exp = expected.

Effect of shading treatments on survival

There was no significant difference in survival response to shading treatments in any of the populations tested. The pattern of survival in relation to shading treatments was however inconsistent among populations. For example, survival for Hluhluwe plants was highest in the full-shade treatment but the Ukulinga and Trompsberg plants had the lowest survival in this treatment.

Table 5.5 Results from Chi-squared tests on observed versus expected frequencies of plant survival in relation to shading treatments (no shade, full shade and up-shade) to determine if patterns of survival were similar or different among populations and water treatments; df = 1.

Site	Magangeni $X^2 = 2.57$, **NS**			Trompsberg $X^2 = 0.12$, **NS**			Ukulinga $X^2 = 3.35$, **NS**		
	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E
No shade	7	9.95	0.88	15	14.5	0.02	8	7.05	0.13
Full shade	9	5.85	1.7	9	8.54	0.03	1	4.15	2.39
Up shade	8	8.2	0.01	11	11.9	0.08	8	5.81	0.83
Sum	24	24.0	2.6	35	35.0	0.12	17	17.0	3.35

NS = not significant at $p < 0.05$; Obs = observed, Exp = expected.

Effect of cutting treatments on survival

There was no significant difference in the pattern of plant survival with respect to cutting treatments in any of the populations. Survival was better when plants were cut at the start of the treatments compared to when they were left intact in all of the populations.

Table 5.6 Results from Chi-squared tests on observed versus expected frequencies of plant survival in relation to cutting treatments (cut and whole) to determine if patterns of survival were similar or different among populations.

Site	Magangeni $X^2 = 0.04$, **NS**			Trompsberg $X^2 = 0.02$, **NS**			Ukulinga $X^2 = 0.62$, **NS**		
	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E	Obs	Exp	(O-E) **2/E
Cut	18	17.6	0.01	26	25.6	0.01	11	12.4	0.17
Whole	6	6.44	0.03	9	9.39	0.02	6	4.56	0.45
Sum	24	24.0	0.04	35	35.0	0.02	17	17.0	0.62

NS = not significant at $p < 0.05$; Obs = observed, Exp = expected.

In summary, none of the populations differed significantly from the general population's response to water, shading or cutting treatments, although the patterns of deviation from expected values were often inconsistent among populations.

5.3.2.2 Biomass production

In order to obtain estimates for initial biomass of plants that were not cut at the start of the experiment, correlations between the initial biomass of cut plants and the basal diameter of the plants were determined. The associated equation was used to estimate the biomass of intact plants. Correlations are presented in Figure 5.2.

The biomass of plants from Magangeni and Trompsberg was poorly correlated to plant diameter whereas there was a strong correlation between biomass and diameter for the Kamberg and Ukulinga plants.

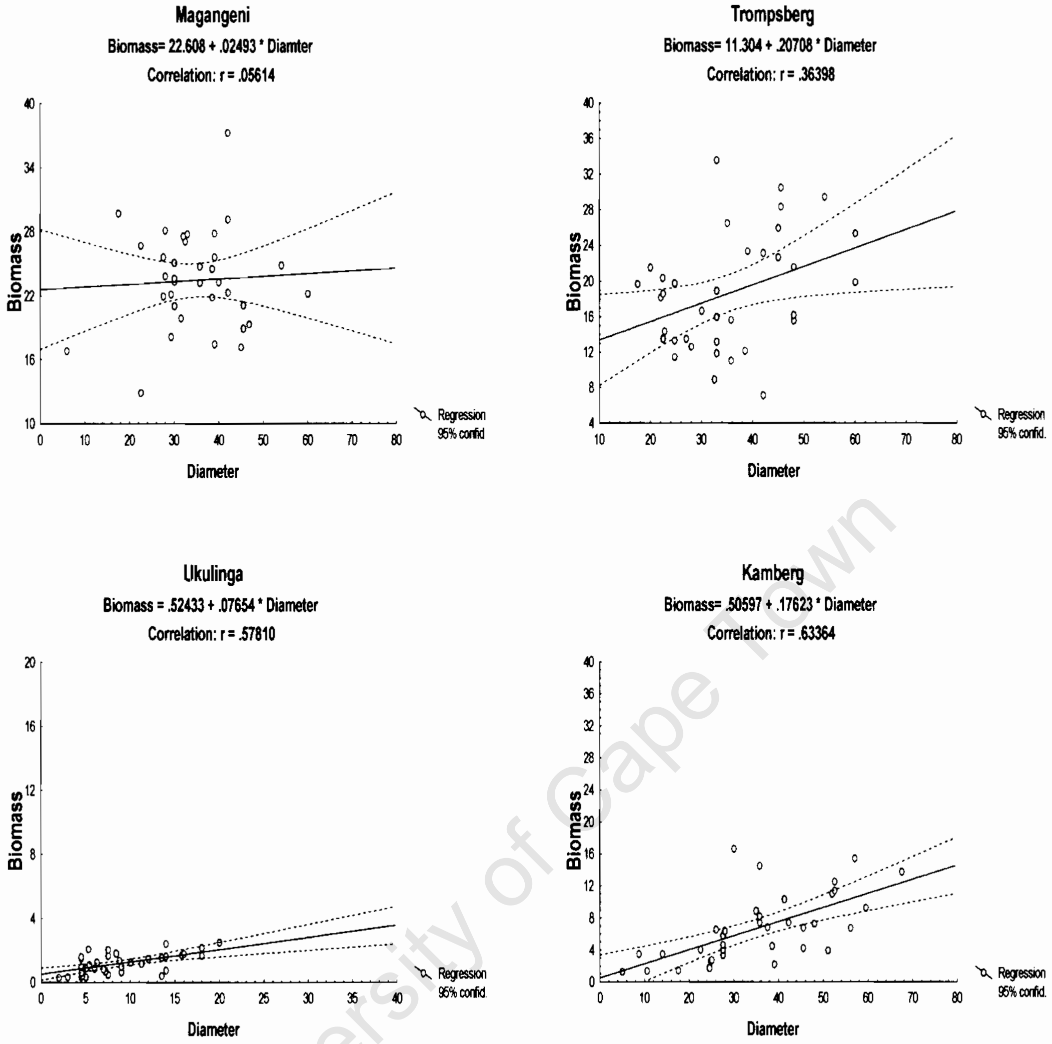


Figure 5.2 Correlations between basal diameter and initial biomass for plants cut at the start of the experiment. Note that the x- and y-axes for Ukulinga are different from the other sites.

Effect of water treatments on biomass production

Biomass production increased with increased water availability for Trompsberg, Magangeni and Kamberg. This effect was most pronounced in the Trompsberg plants, followed by plants originating from Magangeni, Table 5.7 and Figure 5.3.

Table 5.7 Mean biomass production in relation to water regime.

Water regime	Biomass production in grams (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Low	9.52 (3)	3.01 (4)	12.42 (2)	0
Medium	12.83 (7)	13.45 (15)	14.18 (5)	9.63 (3)
High	15.13 (14)	34.70 (16)	13.85 (10)	12.10 (3)
All groups	13.76 (24)	21.97 (35)	13.76 (17)	10.87 (6)

Effect of shade on biomass production

As with survival, the response to shading treatments among populations was inconsistent. Full shade favoured biomass production in the Magangeni plants, whereas no shade favoured biomass production in the Ukulinga plants. Trompsberg plants did well in all treatments, particularly in the up-shade treatment (Table 5.8).

Table 5.8 Biomass production in relation to shade regime

Shade regime	Biomass production in grams (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Full shade	17.35 (9)	16.59 (9)	2.05 (1)	2.17 (1)
Up-shade	10.42 (8)	26.15 (11)	12.69 (8)	23.05 (1)
No shade	12.96 (7)	22.14 (15)	16.30 (8)	9.99 (4)
All groups	13.76 (24)	21.97 (35)	13.76 (17)	10.87 (6)

Effect of cutting on biomass production

Cutting plants resulted in higher production relative to intact plants for the Magangeni, Ukulinga and Kamberg populations. Trompsberg was the exception in that production was higher in intact plants compared to plants that were cut at the start of the treatments, although survival was greater in cut plants (Table 5.9).

Table 5.9 Biomass production in relation to cutting regime

Cutting regime	Biomass production in grams (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Whole	−1.31 (6)	25.19 (9)	12.04 (6)	9.98 (1)
Cut	18.78 (18)	20.86 (26)	14.71 (11)	11.05 (5)
All groups	13.76 (24)	21.97 (35)	13.76 (17)	10.87 (6)

Step-wise regression analysis

A summary of results from the regression analyses of biomass production in relation to treatments is presented in Table 5.10. For the general population's response, the water treatments and the cutting regime were retained in the regression model. Shading treatments and site were removed, indicating that shading treatments did not contribute significantly to explaining variations in biomass production when populations were combined (Table 5.10). Here, water availability was the most significant determining factor for biomass production.

Cutting and increasing moisture availability improved biomass production significantly in clonally propagated plants from Magangeni. Shading was removed from the regression model. The intercept was significantly different from zero, indicating that initial biomass has to be below a certain level and moisture availability above a certain level for plant production to take place (Table 5.10).

Water was the only treatment retained in the regression model to explain variation in biomass production in clonally propagated plants from Trompsberg. Biomass production increased significantly with increased moisture availability, regardless of cutting or shading treatments. The fact that the intercept was negative and significantly different from zero indicates that a minimum amount of water was required in order for plants from Trompsberg to become productive (Table 5.10).

The response of the Ukulinga plants was different from that of the Hluhluwe and Trompsberg plants, in that water was removed from the regression model, indicating that variations in biomass production were not dependent on water availability. Shade and cutting treatments were retained in the final model. Shade regime had a significant effect on plant productivity in clonally propagated plants collected from Ukulinga. Plants in the no-shade treatment had the highest productivity, followed by plants in the up-shade treatment with plants in the full-shade treatment having the lowest productivity (Table 5.8).

There was insufficient data for a regression analysis of biomass production for the Kamberg population.

In summary, populations showed a variable response to treatments in terms of biomass production. Water availability was important in explain biomass production in plants originating from the semi-arid or variable rainfall regions (Trompsberg and Hluhluwe). Initial biomass was also important in explaining variations in biomass for the Hluhluwe plants, whereas shading treatments had the most significant effect on biomass production in plants originating from the stable mesic area (Ukulinga).

Table 5.10 Summary of results from step-wise regression analyses performed to determine which treatments best explain variation in **biomass production** in clonally propagated plants originating from four climatically different populations of *Themeda*, grown under controlled conditions. B= the intercept in the regression equation.

	B	Water	Shading	Cutting	Site	Adjusted R^2	*n*
All sites	–12.1 NS	***	R	NS	R	0.17	82
HLU	–45.2 ***	***	R	***		0.73	24
TRM	–19.3 **	***	R	R		0.54	35
UKU	–10.7 NS	R	**	NS		0.31	16

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, NS = not significant, *n* = sample size, R = removed from regression model.

ANOVA tests

Results from the step-wise regressions indicate that the extent to which water, shade and initial biomass effected biomass production varied among populations of *Themeda*, with those plants originating from semi-arid areas (Trompsberg) most able to take advantage of increased water supply, whereas light availability was more influential in populations from more mesic areas (Kamberg and Ukulinga). An ANOVA was used to test the significance of these differences (Table 5.11 and Figure 5.3). Unfortunately, only the effect of population and water treatments and only for plants occurring in the high- and medium-water treatments could be incorporated into the analysis due to poor replication in other treatments. Remaining data met the assumptions for an ANOVA and no data transformations were required. Biomass production differed significantly among water treatments ($p < 0.05$) and among populations ($p < 0.01$). Furthermore, the interaction between population and water treatment was significant ($p < 0.01$). Production was significantly different in the Trompsberg plants compared to all other sites (Figure 5.3). Furthermore biomass increased significantly with increased water supply in the Trompsberg plants.

Table 5.11 Summary of results for the ANOVA performed to test the effect of water treatments and population on biomass production.

	Df Effect	MS Effect	Df Error	MS Error	F	*p*-level
Site	3	652.8	65	118.1	5.53	0.0019
Water	1	502.8	65	118.1	4.26	0.0431
Interaction	3	565.3	65	118.1	4.79	0.0045

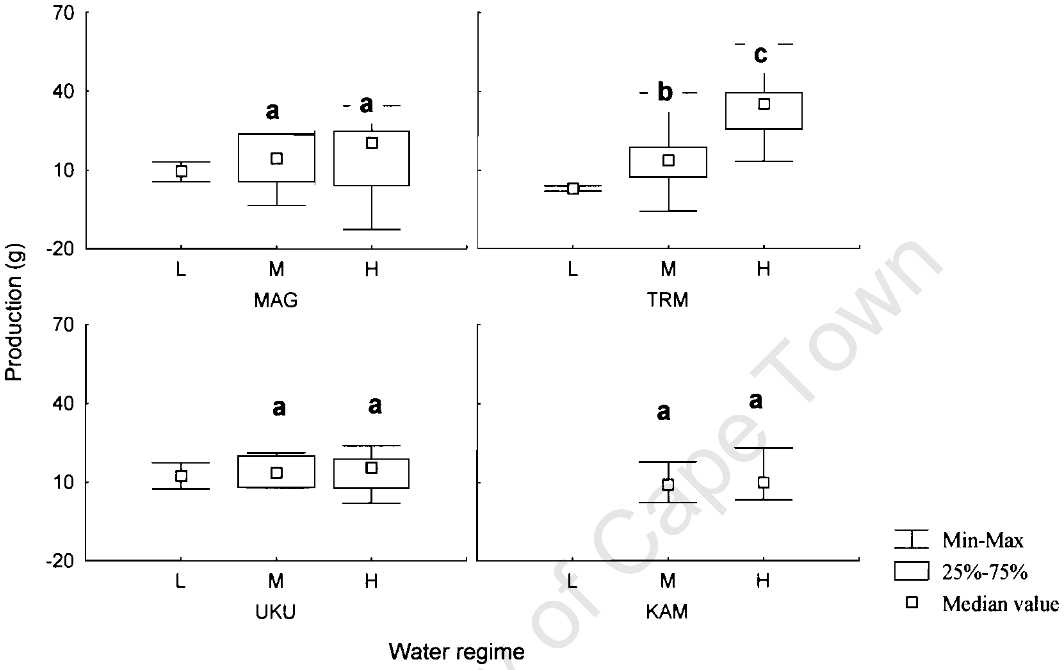


Figure 5.3 Plant production with respect to water regime for the four populations clonally propagated and grown under controlled conditions. MAG = Magangeni, TRM = Trompsberg, UKU = Ukulinga, KAM = Kamberg; L = low, M = medium, H = high water treatments. Letters denote significant differences at $p < 0.01$.

5.3.2.3 Tiller production

Effect of water treatments on tiller production

As with biomass, there was an increase in tiller production with increased water supply in plants from all collection sites. This effect was most pronounced in plants from Trompsberg and is consistent with patterns of biomass production for this population (Table 5.12).

Table 5.12 Mean tiller production in relation to water regime.

Water regime	Tiller production (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Low	38.00 (3)	21.75 (4)	33.00 (2)	0
Medium	47.43 (7)	41.33(15)	41.80 (5)	76.00 (3)
High	61.43 (14)	81.56 (16)	58.80 (10)	102.0 (3)
All groups	54.42 (24)	57.49 (35)	50.77 (17)	89.00 (6)

Effect of shading treatments on tiller production

Tiller production was similar among treatments in the Magangeni and Trompsberg populations. Shading had the most pronounced effect on plants from Ukulinga and Kamberg where shading reduced tiller production (Table 5.13).

Table 5.13 Mean tiller production in relation to shading regime

Shade regime	Tiller production (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Full shade	57.44 (9)	55.33 (9)	13.00 (1)	16.00 (1)
Up-shade	53.88 (8)	61.27 (11)	47.63 (8)	147.0 (1)
No shade	51.14 (7)	56.00 (15)	58.63 (8)	92.75 (4)
All groups	54.42 (24)	57.49 (35)	50.77 (17)	89.00 (6)

Effect of cutting treatments on tiller production

For the Ukulinga, and to a lesser extent, Magangeni plants, tiller production was greater when biomass was removed initially, but greater in intact plants from Trompsberg. Replication in Kamberg plants was too low to draw conclusions (Table 5.14).

Table 5.14 Mean tiller production in relation to cutting regime.

Cutting regime	Tiller production (sample size)			
	Magangeni	Trompsberg	Ukulinga	Kamberg
Whole	50.17 (6)	63.11 (9)	42.17 (6)	110 (1)
Cut	55.83 (18)	55.54 (26)	55.46 (11)	84.80 (5)
All groups	54.42 (24)	57.49 (35)	50.75 (17)	89.00 (6)

Step-wise regression analysis

A summary of results from the regression analyses of tiller production in relation to treatments is presented in Table 5.15. When all populations were combined, site and water treatments were retained in the final model with only water having a significant effect. Shading and cutting treatments were removed.

For the Magangeni population, cutting and water treatments were retained in the final model, but shading treatments were removed. Cutting did not contribute significantly to explaining variations in tiller production. The effect of water treatment on tiller production was not quite significant at $p < 0.05$ (Table 5.15).

For plants originating from the semi-arid site (Trompsberg), only water was retained in the final model and its effect on tiller production was highly significant (Table 5.15).

Shade, water and cutting treatments were retained in the final model for plants propagated from Ukulinga, but only the effect of shading treatments on tiller production were significant, where no shade had a positive effect (Table 5.15).

There was insufficient data for regression analysis of tiller production in the Kamberg population.

In summary, the effects of treatments on tiller production were less pronounced compared to those on biomass production, but the pattern of response was the same. Populations showed a variable response to treatments. Water availability was relatively important in explaining variation in tiller production in plants originating from the semi-arid or variable rainfall regions (Trompsberg and Hluhluwe) whereas shading treatments had the most significant effect on tiller production in plants originating from the stable mesic area (Ukulinga).

Table 5.15 Summary of results from step-wise regression analyses performed to determine which treatments best explained variation in tiller production in clonally propagated plants originating from four climatically different populations of *Themeda*, grown under controlled conditions. B= the intercept in the regression equation.

	B	Water	Shading	Cutting	Site	Adjusted R^2	*n*
all sites	–5.64 NS	***	R	R	NS	0.23	82
HLU	–4.78	NS	R	NS		0.09	24
TRM	–20.4	***	R	R		0.45	35
UKU	–66.9	NS	*	NS		0.35	16

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$, NS = not significant, *n* = sample size, R = removed from regression model.

ANOVA tests

Results from the step-wise regression indicate that the extent to which different treatments affected tiller production varied among populations. An ANOVA was therefore performed to determine the effect of water treatment and population on tiller production. Due to poor replication, other treatments could not be included in the analysis. Again, the low-water treatment was also excluded. The remaining data meet the required assumptions for ANOVA. No data transformations were necessary. Results are presented in Table 5.16 and Figure 5.4.

Biomass production differed significantly. Production was significantly different in the Trompsberg plants compared to all other sites (Figure 5.3). Furthermore, biomass increased significantly with increased water supply in the Trompsberg plants.

Tiller production differed significantly among water treatments ($p < 0.01$) and among populations ($p < 0.05$). The interaction between population and water treatment was not significant (Table 5.16). For all four forms there was an increase in tiller production with an increase in moisture availability, particularly in the Trompsberg plants (Figure 5.4).

Table 5.16 Summary results for the ANOVA performed to test the effect of water treatments and population on tiller production.

	Df Effect	MS Effect	Df Error	MS Error	F	*p*-level
Population	3	2313.9	65	801.27	2.89	0.0422
Water	1	7215.8	65	801.27	9.01	0.0038
Interaction	3	825.2	65	801.27	1.03	0.3853

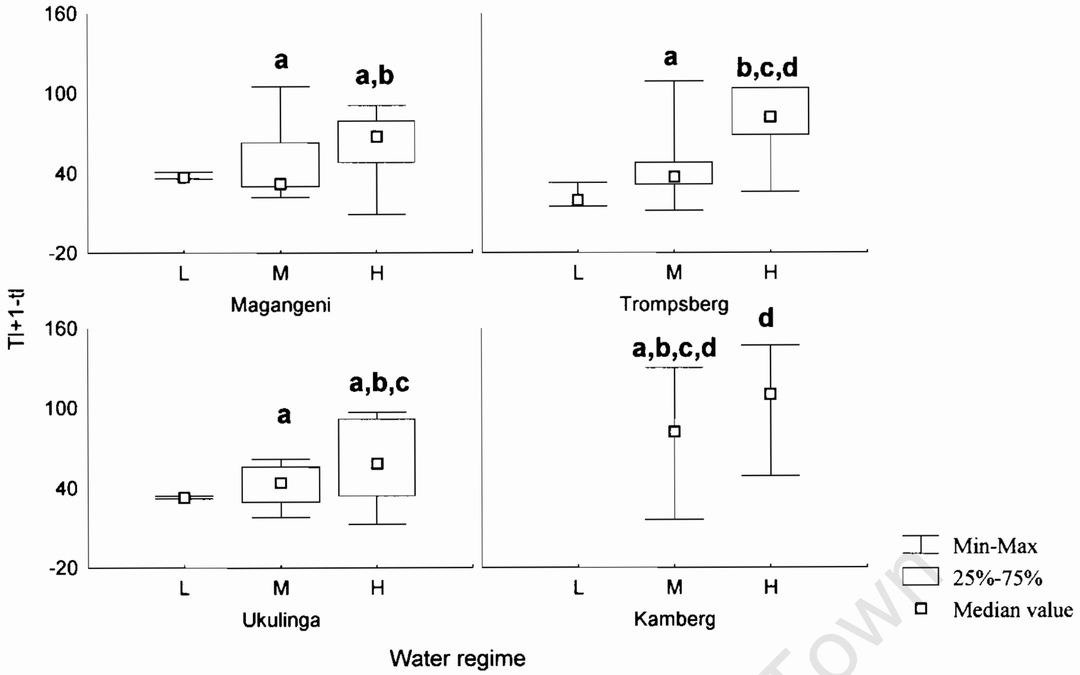


Figure 5.4 Tiller production (T1$_{+1}$–Tl) in relation to water regime for live plants clonally propagated plants for four populations of *Themeda.* L = low, M = medium, H = high water treatments. Letters denote significant differences at $p < 0.01$.

5.3.2.4 Productivity

Productivity was higher in clonally propagated plants compared to field populations. There is a strongly negative effect of initial biomass on productivity of the Ukulinga population, a weaker effect for Magangeni and weaker still for Trompsberg (Figure 5.5). The R^2 value for the productivity curve from plants collected from Trompsberg was very low, indicating that initial biomass had little effect on “current year’s” productivity. These results accord with field observations (figure 5.1), as well as results from analyses on the effect of treatments on tiller and biomass production. The R^2 value for Kamberg was also relatively low, which is contrary to field data, however, this is likely be a function of low survivorship in plants propagated from this population.

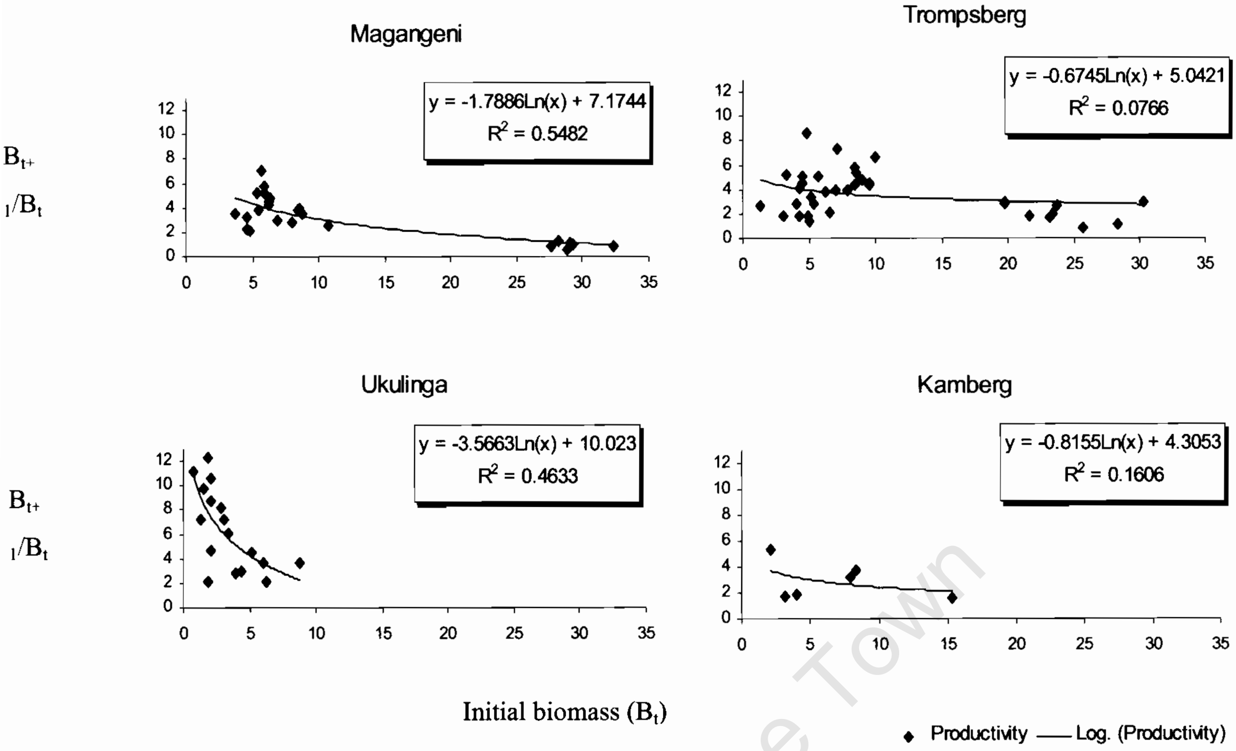


Figure 5.5 Productivity (B_{t+1}/B_t) of clonally propagated plants, where only those plants that survived throughout the experiment were included. Note the trend line fitted on the graphs is according to a logarithmic equation: y=clnx+b

5.4 Discussion

Both rainfall and light availability are recognized as important variables influencing the growth of populations of *Themeda* (Opperman and Roberts, 1978; Danckwerts, *et. al.*, 1984; O'Connor, 1985; Everson, *et al.*, 1985), as well as other andropogonoid grasses Risser, *et al.*, 1981; Towne and Owensby, 1984; Knapp and Seastedt, 1986; Milchunas, *et al.*, 1994; Knapp, *et al.*, 1998). Temperature is also recognized as having an effect on the growth and development of *Themeda* populations, with tiller production increasing with increasing temperature in plants grown under controlled conditions (Downing and Groves, 1985; Everson, 1994). This investigation aimed to find out whether there was a difference in plant response to, and the relative importance of, moisture and light availability in four populations of *Themeda*, and whether these were strong enough to result in ecological divergence, with adaptations to local conditions.

Productivity (defined as $B\Delta = \frac{Bt+1}{Bt}$) of *Themeda* in field populations at Ukulinga, Magangeni, Nqumeni and Kamberg was strongly related to initial biomass (see Figure 5.1), where the lower the initial biomass, the greater the productivity. This indicated that density-dependent factors (e.g. competition for light and space) significantly influence productivity and plant response in these populations, consistent with results from Knapp and Seatedt (1986). Other studies specifically on *Themeda* that demonstrated increases in productivity resulting from litter removal include Ndawula-Senyiba (1972), Everson, *et al.* (1985) and Everson, *et al.* (1988). Lunt and Morgan (2002) showed similar effects in temperate Australian grasslands where litter accumulation negatively impacted on productivity and even resulted in mortality in undisturbed plots of *Themeda,* and they concluded that "productive grasslands dominated by dense *Themeda* swards are not sustainable over long periods of time unless accumulated litter is periodically removed by burning, grazing, slashing …".

It should be noted that good rain fell at Magangeni and Nqumeni (tropical, variable) during this investigation. This area does, however, experience dry cycles and periodic droughts (Balfour and Howison, 2001). During dry periods, the relationship between initial biomass and productivity is likely to become less important, with moisture availability having a greater effect on productivity. This has been demonstrated by Balfour and Howison (2001) who showed a clear relationship between biomass production and rainfall variability in Hluhluwe-Umfolozi Park. Sternberg, *et al.* (2000), working in the Mediterranean herbaceous community in north-eastern Israel, found that inter-seasonal rainfall variation was the primary factor influencing the structure of plant communities under different grazing treatments. However, the effect of grazing on plant structure became more evident in wet years compared to dry years, demonstrating that in areas with variable rainfall cycles, the relative importance of rainfall and grazing (biomass removal/initial biomass) is dependant on the prevailing conditions at a given point within the cycle.

The semi-arid population at Trompsberg behaved quite differently, with no relationship between the initial biomass and productivity. There was very little rain at Trompsberg during the experiment, which may explain why plant productivity was negligible, regardless of initial starting biomass. It is not possible, from this field study, to say how productivity would be influenced by initial biomass in times of moisture availability. The experiment does, however, show that the primary limitation to productivity in the Trompsberg populations was lack of moisture and not competition for light or space. Other studies, however, showed that *Themeda* swards in this semi-arid environment are indeed highly responsive to moisture availability (Opperman and Roberts, 1978; Snyman and Fouché, 1993). Snyman and Fouché (1993) found that growth takes place "sporadically depending on the presence or absence of water". Opperman and Roberts (1978) also concluded: "rainfall is the most important limiting factor in the annual growth pattern and production of natural forage grass in the central Orange Free State". Danckwerts, *et al.* (1984) reported similar patterns in *Themeda* from the false thorn veld of the Eastern Cape, which is also a relatively dry area. This response is not limited to *Themeda*, but rather indicative of a general response of semi-arid grasslands. The importance of rainfall in determining productivity in semi-arid grasslands is also evident in Australia, where fuel accumulation in Spinifex grasslands, (typically arid or semi-arid), is strongly related to post-fire cumulative rainfall (and the time since the last fire) (Allan and Southgate, 2002).

Data from both this work and other studies reported here indicate that initial biomass (self-shading) is the most significant factor limiting productivity in mesic areas, whereas moisture availability is the most significant limiting factor in semi-arid and arid areas or regions where rainfall is unpredictable. The steepness of the slope (when productivity is graphed) indicates that density dependence was strongest at Ukulinga, followed by Magangeni, then Nqumeni, and negligible at Trompsberg, which is consistent with the predictions. Conclusions for the Kamberg population cannot be drawn since the data for the second season of growth could not be collected, but results reported in Chapter 4 indicate that density dependence was also strong at this mesic site.

It was necessary to verify whether differences in the relative importance of light and moisture availability for productivity among field populations of *Themda* had resulted in divergent adaptations to local conditions. This was done by growing plants sourced from the four main study populations in a common garden experiment where conditions were controlled.

Mortality in the propagated plants was high, but the resilience of populations varied considerably. The Trompsberg plants were most suited to successful propagation, having the lowest mortality, whereas the Kamberg plants were least suited to propagation, having the highest mortality.
Results indicated that there were inherent differences in plant response to treatments with respect to survival, biomass and tiller production among the populations tested, with different treatments favouring different populations. This was contrary to results investigating physiological adaptations to temperature among *Themeda* populations from different localities (Groves, 1975; Downing and Groves, 1985).

In terms of survival, Trompsberg plants generally showed least deviation from expected values in all treatments. This might be a function of the fact that there was greatest survival in this form, which may have biased the expected frequencies used in the analysis. A criticism of the chi-squared tests performed may therefore be that expected frequencies were biased towards populations with the highest number of survivors.

The effect of treatments on plant productivity may explain the patterns and causes of plant mortality. Mean biomass production was greater in cut plants compared to intact plants for all populations except Trompsberg. This data accords with field data where productivity was not related to initial biomass at the Trompsberg site. Plants propagated from the Trompsberg population were, however, most able to take advantage of increased water availability, reflected in significant increases in biomass and tiller production, regardless of shading or initial biomass. This supports the hypothesis that moisture availability, and not initial biomass or shading, is what limits productivity in semi-arid areas.

Shading significantly reduced plant production in the Ukulinga plants, whereas water had no effect. Furthermore, plant production was lower in intact plants compared to cut plants. These results indicate that productivity in plants from the mesic populations was limited by self-shading and initial biomass, not moisture availability. This again is consistent with field observations where the greater the initial biomass, the lower the productivity was for this population. Results for plants from the Kamberg populations were inconclusive due to the poor replication resulting from high mortality in these plants in the greenhouse experiment, and the inability to sample effect of initial biomass on productivity in field populations.

In summary, results from means of survival, biomass and tiller production all indicated that populations from arid areas responded more to water, whereas populations from mesic areas were more limited by light availability and density-dependent processes. The difference in the relative importance of light, water and initial biomass on plant production among clonally propagated plants from the four populations tested indicated some extent of genetic divergence, reflecting ecological adaptations to local conditions, which can be correlated to rainfall. Patterns were consistent with the hypothesis that water limits production in populations from semi-arid areas, density-dependent processes limit production in plants from mesic areas, and that this difference in limiting factors has resulted in genetic divergence in the ecological response of populations occurring under different climatic conditions.

6 Variation in demographic characteristics of *Themeda* populations

6.1 Introduction

Important components of caespitose grass population demography include seed production (discussed in Chapters 3&4), seedling recruitment, vegetative propagation, tussock fragmentation, seed biology, seed bank dynamics and mortality (O'Connor, 1993). Recent studies focusing on population demography have provided conflicting results regarding the relative importance of such components in maintaining *Themeda* populations. Snyman et al., (1997) recorded up to 43% mortality of *Themeda* tussocks during a drought in a semi-arid area in the central Free State (just north of Trompsberg). O'Connor (1993), from work in semi-arid savannas, describes *Themeda* as an obligate reproducer by seed and demonstrated that rainfall promotes abundance, seedling recruitment and plant basal area of *Themeda*, but episodic droughts cause mortality resulting in a continual population turnover. These populations therefore have a dependence on seedling recruitment and seed banks for persisting in such an environment. Results showed that variation in annual rainfall had the greatest effect on population growth (O'Connor, 1993). Everson (1994), working in montane grasslands, however, concluded that vegetative tillering was the primary mode of reproduction for maintaining *Themeda* populations, with seedlings contributing little to the population structure. Population turnover here was due to tussock fragmentation, where light competition, as opposed to moisture availability, was a key determinant of tiller production (Everson, *et al.*, 1988). Likewise, studies on productive temperate *Themeda* grasslands in Australia show that seedling recruitment is rare in these areas (Lunt and Morgan, 2002). It has recently been suggested that *Themeda* populations occurring under different extreme environmental conditions may differ in their demographic characteristics (O'Connor and Everson, 1998), which would have significant implications for management. It is therefore of value to explore how different populations of *Themeda*, occurring over climatic gradients, have developed different strategies of persistence, depending on their local conditions.

There are not only differences in the mechanisms of persistence of different populations of *Themeda* but also in their basic seed biology, where numerous studies provided evidence that this varies, depending on the locality of the parent population (Creswell and Nelson, 1971; 1972; 1973; Lock and Milburn, 1971; Martin, 1975; Mott, 1978; Groves, *et al.*, 1982; Baxter, *et al.* 1993). Explanations relating these differences to adaptations to local conditions have been limited, since patterns of dormancy appear to be inconsistent over the environmental variables tested (e.g. temperature) (Groves, *et al.*, 1982; Baxter, *et al.* 1993).

The aim of the work presented in this chapter was firstly, to determine if and how the demographic structure of *Themeda* populations varies in relation to a rainfall gradient. Secondly, the mechanisms, particularly seed bank dynamics, recruitment and seed biology contributing to this variation, were investigated.

The general predictions made were that *Themeda* populations in semi-arid regions would be characterized by high population turnover resulting from mortality during drought and recruitment following rainfall events. This would lead to a variable population with few old individuals and many young plants depending on the frequency of drought and recruitment events. High seed production, seed banks and seedling recruitment would be important for maintaining and regenerating these populations. Stable high-rainfall environments would be characterized by low, consistent population turnover where recruitment and mortality are rare, with fragmentation of tufts being the primary cause of shifts in population structure and where vegetative propagation maintains the population. Seed germination requirements will vary depending on the conditions best suited for successful establishment in a particular area.

6.2 Methods

6.2.1 Population structure

The first step was to determine whether there were differences in the demographic/age structure of populations of *Themeda* occurring over a rainfall gradient. Due to the limited time available for the study, the fate of plants could not be studied accurately over time. Instead, tussock size was investigated in order to obtain a measure of demographic structure based on the assumption that tussock size is related to age (see O'Connor, 1993).

In semi-arid and variable rainfall sites a variable age structure reflecting periodic mortality and seedling recruitment events may be expected, with a higher concentration of individuals in smaller size classes. Populations from mesic areas would be expected to have a stable parent population structure with minimal evidence of recruitment and mortality (few small tussocks).

Age structure was investigated by measuring the basal circumference (in cm) of 100 randomly selected tussocks at each of the sites listed in Table 6.1. *Themeda* tussocks, however, fragment with age (Everson, 1994). Since the objective was to determine the size of the entire parent plant (capturing recruitment events), all tussocks within 2.5 cm of the selected tussock, or where there was evidence that they were once a part of the selected tussock were included and assumed to part of one single genetic individual.

Table 6.1 Sites and their post-burn age, where population structure was investigated.

Sites	Post-burn age
Magangeni	3 months
Nqumeni	3 months 7 days
Hillside (Trompsberg)	58 years, grazed 7 months prior
Flips farm (Trompsberg)	30 months
Ukulinga	2 months
Kamberg	2 months

Statistical analysis

Data were categorized into size classes (0.2-m intervals) and are presented as frequency distributions (number of observations per size class categories).

6.2.2 Seed banks

Large, viable, responsive seed banks and large numbers of seedlings would be expected in the sites where mortality is frequent, providing recruitment gaps as predicted for semi-arid and variable rainfall sites. The absence of *Themeda* from the seed bank and low numbers of seedlings were expected for populations with very persistent plants maintained by vegetative propagation, as predicted for the mesic areas.

Twenty-four replicates of soil (15 x 10 cm in area and 3 cm deep) were collected from ground between tussocks of *Themeda* in February 1997, from recently burnt sites where possible for each study area (Table 6.2).

Table 6.2 Details of sites where soil was collected and the estimated age of the seeds produced by the current year's flowers.

Sites	Age of seed at watering
Trompsberg	1 year, 1–2 months
Magangeni	3–5 months
Nqumeni	3–4 months
Ukulinga	1–2 months
Kamberg	1–2 months

The procedure for setting out the samples followed that used by Everson (1994). Soil samples were first sifted in order to remove material that may have regenerated from rootstocks, then laid out in seedling trays (16 x 23 cm) that contained sterile sand. This ensured that all seeds in the sample were within 1–2 cm of the surface of the tray. The trays were watered three times a week and germination recorded every three days until no further germination was recorded for two weeks (38 days, with no further germination after the 24th day). At the end of the experiment, seedlings were extracted and the seed coat was examined in order to confirm that they were *Themeda* seedlings, and not that of another species. The experiment was conducted in a heated greenhouse at the University of Cape Town, maintained at 25/15°C (±3°C) temperature regime.

Statistical analysis

The non-parametric Kruskal Wallis ANOVA test was used to determine whether there was a difference in the mean values for seedling emergence from the seed banks for the five sites investigated.

6.2.3 Seedling recruitment

Sites listed in Table 6.3 were used to investigate seedling recruitment. At each of these sites, thirty 0.5 x 0.5-m quadratas were randomly placed ($n = 30$) over a 50m^2 area and the number of *Themeda* seedlings in each counted. *Themeda* seedlings have a distinctive seed coat, which is retained for a period after germination. Seedlings were therefore extracted and examined in order to verify that the seedlings counted were those of *Themeda*. Only those seedlings positively identified as *Themeda* were recorded. The Trompsberg and Hillside sites were sampled on two occasions. There had been no rain prior to the first sampling date in this area, whereas good rains were recorded prior to the second sampling date. Note that results are only an indicator of *Themeda* recruitment and number in the seed bank and are not necessarily indicative of establishment.

Table 6.3 Sites and their post-burn age, where seedling recruitment was investigated.

Sites	Post-burn age
Hillside (Trompsberg)	58 years, grazed 7 months prior
Hillside after rain	58 years, grazed 3 months prior
Flips farm (Trompsberg)	30 months
Flips farm after rain	34 months
Magangeni	3 months
Nqumeni	3 months 7 days
Ukulinga	2 months
Stillerust (Kamberg, annual burn)	2 months
Kamberg	2 months

Statistical analysis

Data were analysed using a one-way ANOVA. Sites where no seedlings were recorded were not included in the ANOVA. Only two seedlings were found in the Ukulinga site, hence this site was also excluded from the ANOVA in order that the assumptions of the test could be met.

6.2.4 Seed biology

6.2.4.1 Effect of seed age on germination percentages

Differences in the seed biology of *Themeda* are most often manifested in the effect of seed age on germination percentages (see Baxter, *et al.*, 1993; Groves, *et al.*, 1982). This was therefore investigated and results interpreted in terms of environmental conditions of source populations. Seed was obtained from the following sources:

Free State: Culms from a Free State form of *Themeda* were collected by staff of the Free State National Gardens in January 1997. These were air-dried on wire mesh racks in a laboratory in Cape Town. Mature seeds that dropped though the mesh were then collected and de-awned.

Hluhluwe-Umfolozi Park: Culms were collected by hand and sickle in January 1997 and dried, in the same manner as those of the Free State form, in a shed in the park.

Kamberg Nature Reserve: Dr Ed Granger (University of Natal Pietermariztburg) supplied seeds collected from Kamberg Nature reserve in December 1996/January 1997. Culms had been collected by hand and then put though a hammer and mill system to clean the seed. Ukulinga Research Farm: Unfortunately the 1996/1997 flowering season was missed for this site, hence culms were only collected in February 1998 from the Ukulinga Plateau. These were dried in the same manner as described for the Free State form.

All seed was stored in glass containers in the laboratory at Cape Town University. The effect of seed age of laboratory-stored seed on germination percentage was determined by germinating seed from the stocks described above at approximately 4 (6/97), 8 (20/10/97), 12 (1/3/98) and 16 (10/98) months after seed shed. While this does not provide direct information on the behaviour of seed in the field, it may provide an indication of inherent differences in seed germination characteristic among populations. Four replicates of 20 seeds each were used for each site in each experiment. Seeds were dusted with APRON and then germinated in plastic petri dishes on three layers of Whatman filter paper in a controlled chamber with a 12/12 day/night cycle and 15/25°C min./max. temperature cycle.

Germination was recorded daily until no further germination was recorded for 7 days. Only seeds weighing above 0.030 g were used in the experiment to ensure maximum viability. An initial viability experiment showed that seeds above this weight have 90–100% viability. Viability was determined using the tetrazolium method as described by Baxter (1997).

Statistical analysis

Statistical analysis was performed on arcsine-transformed data of the square root of germination percentages. Two 2-way ANOVAS were performed; the first included all sites and tested the effects of four- and eight-month-old seeds on germination. The second excluded the Ukulinga data, since data for 12- and 16-month-old seeds were absent for this site. Data were presented as percentage germination, with letters denoting the results from statistical analyses performed on transformed data.

6.2.4.2 Effect of seed mass on germination

In Chapter 3 differences were found in the seed mass of *Themeda* seed from the different source locations. The effect of seed mass on percentage germination of *Themeda* was therefore investigated in order to determine whether there was any advantage related to seed size that was being selected for at different sites. Seeds from stocks described above were divided into four weight categories in the case of Kamberg and Hluhluwe stock (≤ 0.003 g; 0.031–0.040 g; 0.041–0.050 g; 0.051+) and five categories in the case of Free State stock (≤ 0.003 g; 0.031–0.040 g; 0.041–0.050 g; 0.051–0.060 g; 0.061+). Seed from Ukulinga was not available at this stage. Viability for each weight group for each site was tested ($n = 20$). Four replicates, each containing 15 seeds, for each site were set out. Germination was recorded twice daily for four days and thereafter once daily until no further germination had occurred for 10 days.

Statistical analysis

An ANOVA was performed on arcsine square root-transformed data of total germination percentages.

6.3 Results

6.3.1 Population structure

Results provided evidence that there were differences in the age structure (recorded as tussock circumference) of the six populations investigated. The size classes for tussock circumference were most evenly distributed for Ukulinga and least evenly distributed for the two Hluhluwe sites (

Figure **6.1**). Ukulinga had the greatest range in size classes, followed by Nqumeni, then Kamberg and Magangeni, then Hillside, with Trompsberg having the fewest size classes. Trompsberg had the highest number of tussocks in the two smallest size classes (29%) followed by Hillside (27%), Magangeni (20%), Nqumeni (18%), Kamberg (8%) and Ukulinga (3%). Ukulinga had the highest number of tussocks in the larger size classes (≥ 1 m) (86%), followed by Kamberg (46%), Magangeni (45%), Nqumeni (36%), Hillside (36%) and Trompsberg (22%). Ukulinga plants had the largest mean tussock circumference followed by Nqumeni, Magangeni, Hillside, Kamberg and lastly Trompsberg.

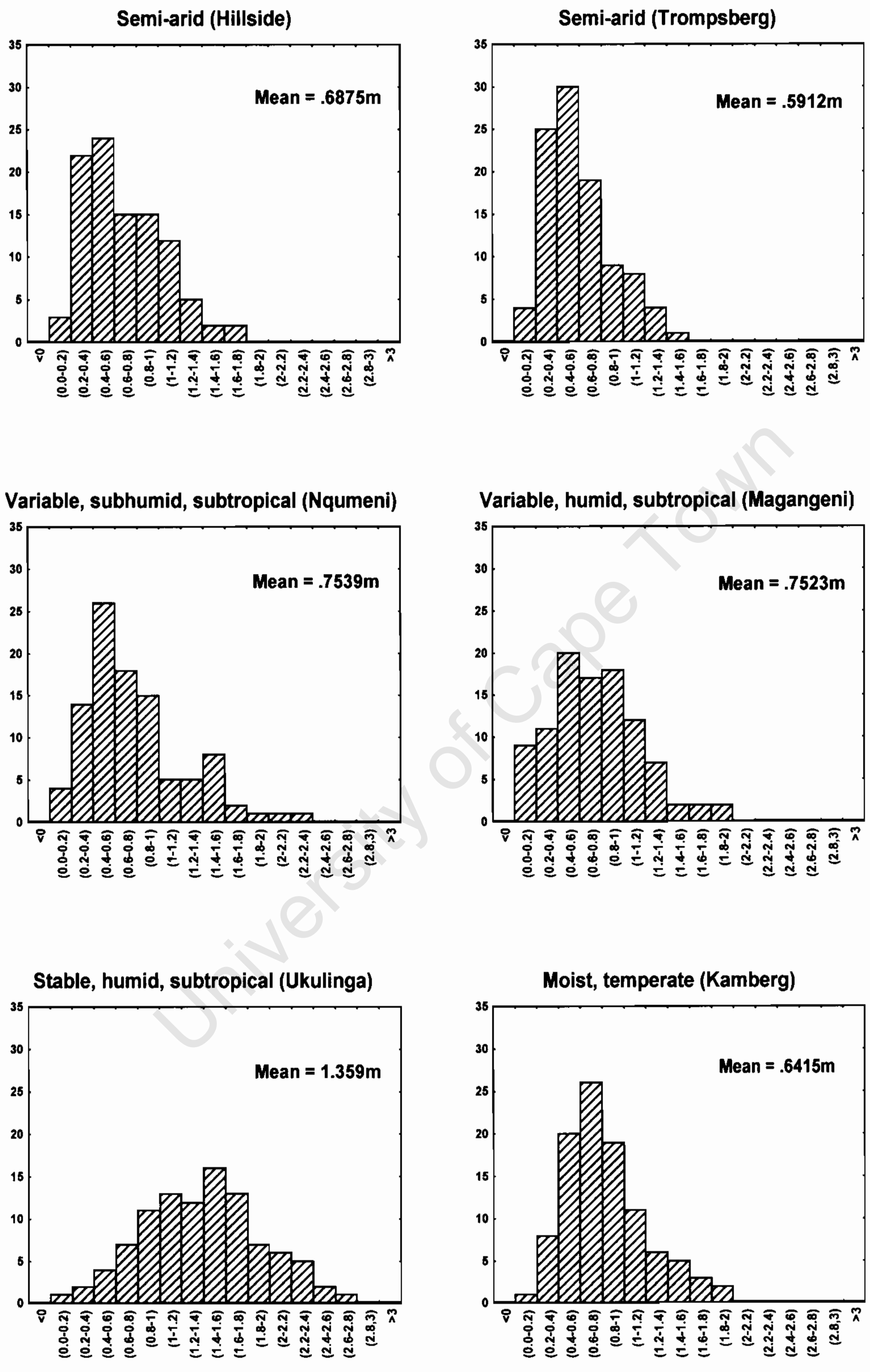


Figure 6.1 Frequency distribution of size classes as recorded for the sites listed in Table 6.1. X axis = circumference size classes in meters, Y axis = Number of tussocks in each size class (frequency).

6.3.2 Seed banks

Populations differed in the numbers of seedlings emerging from the seed bank in soil samples collected (Figure 6.2), (p = 0.0000; Chi-squared = 28.18; df = 4). Magangeni and Nqumeni (variable, subtropical) had higher seedling emergence of *Themeda* from soil samples than the expected values. Trompsberg (semi-arid) had slightly lower seedling emergence than expected, whereas mesic sites (Ukulinga and Kamberg) had much lower seedling emergence than expected.

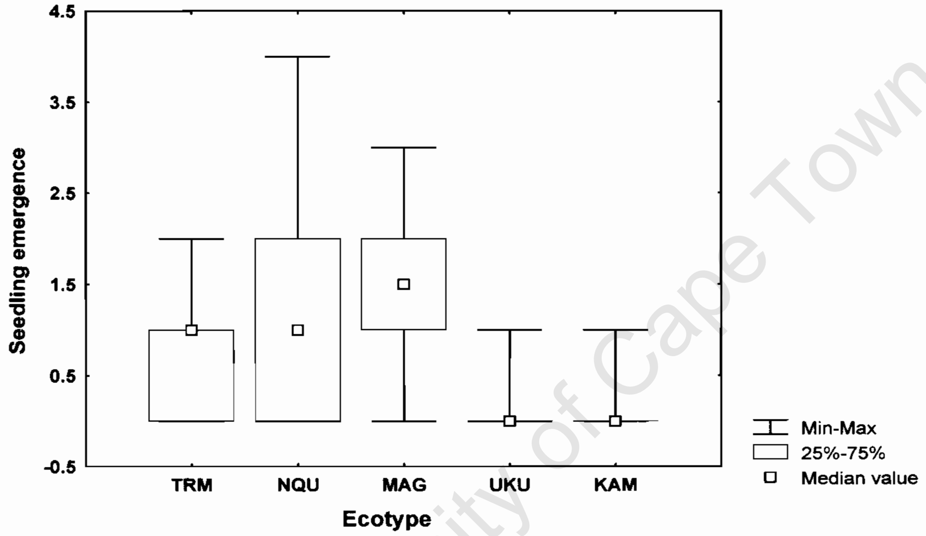


Figure 6.2 Seedling emergence under greenhouse conditions from soil samples collected from the field to determine relative seed bank size among populations, (n = 24). TRM = Trompsberg (semi-arid, frost prone); NQU = Nqumeni (variable, sub-humid, subtropical); MAG = Magangeni (variable, humid, subtropical); UKU = Ukulinga (stable, humid, subtropical); KAM = Kamberg (moist, temperate, frost prone).

6.3.3 Seedling recruitment

Seedling emergence was significantly different among the sites (F = 18.3, df = 174, $p <$ 0.001). No seedlings were found at the semi-arid sites, Flips farm (Trompsberg) or Hillside (Trompsberg) at the first sampling date. There was a significant increase in the number of seedlings in this area when sampled after rain. The number of seedlings found at Magangeni (variable, tropical) was significantly higher than all other sites investigated. The Trompsberg sites and the biannual burn site at Kamberg (mesic) had significantly more seedlings than Nqumeni (variable, tropical), which had significantly more than the annually burnt site at Kamberg (Stillerust). Only two seedlings were found at Ukulinga (moderately mesic).

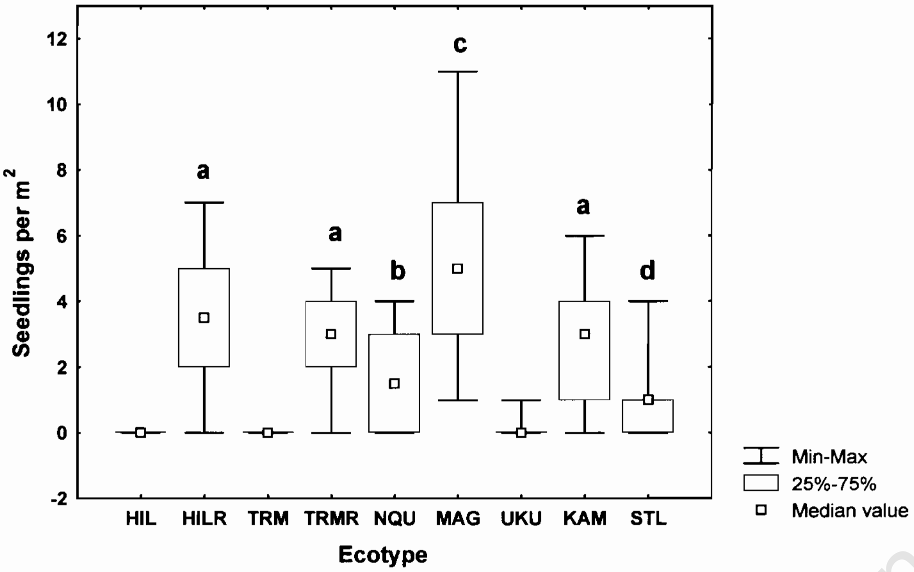


Figure 6.3 Field measurements of seedling emergence per m^2. Populations with the same letters indicate no statistically significant differences among the means (LSD test on log transformed data). HIL=Hillside farm at Trompsberg(semi-arid, frost prone); HILR= Hillside farm after rain; TRM= Flips farms at Trompsberg (semi-arid, frost prone); TRMR=Flips farms at Trompsberg after rain; NQU = Nqumeni (variable, sub-humid, subtropical); MAG = Magangeni (variable, humid, subtropical); UKU = Ukulinga (stable, humid, subtropical); KAM = Kamberg (moist, temperate, frost prone); STL=Stillerust (Kamberg annual burn).

6.3.4 Seed biology

6.3.4.1 Effect of seed age on germination percentages of *Themeda* from different parent populations

Viability, as tested using the tetrazolium dye method, was similar among all ecotypes at 8 months (Magangeni = 95%; Trompsberg = 85%; Ukulinga = 100%; Kamberg = 80%).

Analysis of data from 4 and 8 month old seed from all populations showed that, study populations of *Themeda* exhibited significantly differential potential success in seed germination, as reflected by percentage germination under controlled conditions (Table 6.4)., Magangeni and Ukulinga had the highest germination percentages. Magangeni and Trompsberg were comparable for 12- and 16-month-old seed, due to a reduction in the percentage germination in Magangeni seed, and an increase in percentage germination in the Trompsberg seed. Kamberg seed had the lowest germination percentages overall, Mean total percentage germination was highest for Magangeni (68.5%), followed by Ukulinga (62.5%), Trompsberg (48.4%) and Kamberg (34.7%).

There was no overall pattern on the effect of age on the germination percentages of *Themeda* seed (Table 6.4) but rather indications that the effect of age on germination percentages differs among ecotypes. Germination percentages for Magangeni and Ukulinga seed were initially high but declined with age. Germination percentages for Trompsberg were lowest at 4 months but increased significantly by 8 months Likewise, Kamberg had low germination initially, increasing significantly in 12-month-old seeds, but then reduced significantly in 16-month-old seeds.

Table 6.4 Results from an ANOVA performed on arcsine-transformed data of germination percentages where the effect of seed age on germination percentages was tested at 4 and 8 months for all sites.

	df Effect	MS Effect	df Error	MS Error	F	*p*-level
Ecotype	3	0.4278	24	0.0219	19.59	0.0000
Age	1	0.0492	24	0.0219	2.25	0.1466
Ecotype x age	3	0.1851	24	0.0219	8.48	0.0005

When data from ages 4, 8, 12 and 16 months were included in the analysis, but Ukulinga data was excluded (Table 6.5), the different ecotypes still exhibited differential potential success in seed germination, as reflected by percentage germination under controlled conditions. Furthermore, the effect of age on germination percentages becomes more evident with older seed included. However, as with the first test, this effect differs significantly among ecotypes (Table 6.5).

Table 6.5 Summary of the two-way ANOVA performed on percentage germination in different populations (excluding Ukulinga) and with different-aged seeds.

	df Effect	MS Effect	df Error	MS Error	F	*p*-level
Ecotype	2	0.5317	36	0.01205	44.13	0.0000
Age	3	0.1246	36	0.01205	10.34	0.0001
Ecotype x age	6	0.0879	36	0.01205	7.3	0.0000

6.3.4.2 Effect of seed mass on germination of *Themeda* seed from different parent populations

Patterns of viability were similar among ecotypes, except for seeds weighing less than 0.0030 g, where Magangeni seeds had a higher percentage of viable seeds. Kamberg seeds showed a slight increase in viability with seed mass (Figure 6.4).

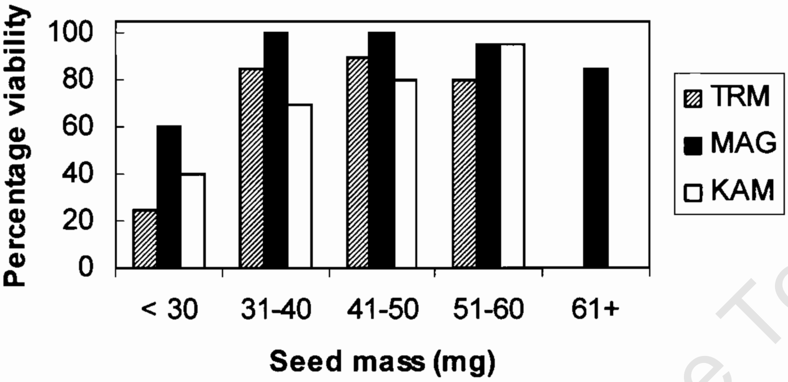


Figure 6.4 Percentage viability of seeds in different weight classes, for three ecotypes tested, as determined using the tetrazolium dye method. TRM= Trompsberg (semi arid, frost prone), Magangeni (variable, humid, subtropical), KAM = Kamberg (moist, temperate, frost prone).

Results from the analysis of variance (Table 6.6) showed that the effect of mass and ecotype on seed germination percentages was significant. Germination percentages of seed weighing less than 0.0030 g were significantly lower then all other weight classes whereas heavier seeds (> 0.0051 g) had consistently higher germination percentages than all other weight classes tested. There was, however, no significant interaction between seed mass and ecotype indicating that the effect of seed mass on germination is similar among ecotypes

Table 6.6 Summary of all effects from the ANOVA performed on arcsine-transformed germination data testing the effect of seed mass on germination percentages.

	df Effect	MS Effect	df Error	MS Error	F	*p*-level
Mass	3	0.6188	40	0.0391	15.82	0.0000
Ecotype	2	0.5952	40	0.0391	15.22	0.0000
Mass x ecotype	6	0.0525	40	0.0391	1.34	0.2617

6.4 Discussion

As predicted, the population dynamics and mechanism of persistence differ among the study populations of *Themeda*. These differences reflect differences in the allocation patterns, phenological development and relative importance of rainfall among population reported on in previous chapters, making them ecologically meaningful.

This study provided evidence that recruitment is relatively common in populations from semi-arid and variable environments (Trompsberg and Hluhluwe), whereas there was a lack of recruitment in populations from the mesic stable environments, (Ukulinga and Kamberg). This was reflected in the demographic structure of the populations as well as seedbank and seedling emergence studies.

At the driest sites, (Trompsberg sites), tussock mortality was common, occurring regularly enough to limit the size these plants could attain. Tussock persistence was most evident at the moderately mesic site (Ukulinga), which had the greatest number of large tussocks. The low frequency of larger tussocks in the mesic site (Kamberg) was unexpected. This may be explained in terms of competition with other species, since species diversity was high at this site and inter-tussock distances were small.

As predicted, mesic sites (Ukulinga and Kamberg) had the most normally shaped frequency distributions for tussock size classes, indicating low, stable population turnover. This accords with data presented by Everson, *et al.* (1985) who also observed stable population turnover rates in mesic montane grasslands. Variable and semi-arid sites had left skewed frequency distributions, suggesting more frequent recruitment and low survival rate.

Themeda is considered to be poorly represented in the seed bank relative to its abundance in the vegetation, with minimal carry-over though successive seasons (Everson 1994). However, results from this study indicated that although the representation of *Themeda* in seed banks was generally low, there were still significant differences in seedling emergence from seed banks among sites. These were reflected in the demographic structure of the populations. As predicted, the largest seed banks were in variable and semi-arid environments (Magangeni, Nqumeni and Trompsberg) and the lowest in the moderately mesic area (Ukulinga). The high seedling numbers recorded for semi arid and variable environments after rainfall, indicated an opportunistic response to moisture availability. This accords with productivity responses observed for this form (Chapter 5). Likewise, O'Connor (1993) found rainfall to be a primary determinant of population growth in semi-arid regions.

O'Connor and Pickett (1992) showed that variation in *Themeda* seed production is a major determinant of variation in abundance of its seeds in the seed bank. Seed production data in Chapter 3 show that populations in semi-arid and variable environments (Trompsberg and Magangeni) had the highest seed production which correlated with good seedling emergence as predicted for these areas. The stable, humid subtropical site (Ukulinga) had the lowest seed production and, as predicted, was poorly represented in the seed bank and had the lowest seedling emergence. Results for the mesic site (Kamberg) for seed production, seedbank and field seedling emergence were inconsistent. This may be due to the apparent variability in seed production in this area (Pers Obs,). Everson (1994), working in the same region, found very few seedlings and reported that seedling mortality was very high.

Observed differences in the emergence of seedlings and the representation of *Themeda* in seed banks may also be attributed in part to differences in seed biology found among populations. Fresh seed of *Themeda* is generally considered to exhibit embryo dormancy, requiring a 6- to 15-month dry after-ripening period, with only a small proportion the seeds being non-dormant at seed shed (Groves, *et al*., 1982; Baxter, *et al*., 1993; Lock and Milburn, 1971). Several studies indicate that dormancy of *Themeda* seeds is reduced through after-ripening, storage at high, altering temperatures or cold stratification (Hagon 1976; Groves, *et al*., 1982; Baxter, *et al*., 1993) with best germination occurring in temperature regimes of 30/20°C or 35/25°C (Hagon, 1976). These studies form the basis of a "general" understanding of the seed biology of *Themeda.* More detailed work on this is required with more careful consideration given to time of sampling soil for seed bank studies and looking at seedling emergence through time in field as apposed to under laboratory conditions.

The percentage germination and the effect of age on dormancy differed significantly among populations and could not be attributed to differences in the viability of seed. This provides further evidence for adaptations of *Themeda* populations to local conditions and challenges the concept that a general seed germination biology literature for *Themeda* as a species can exist without reference to the parent population and environmental conditions thereof. Other studies have also found differences in the dormancy strategies among populations of *Themeda* from different origin (Groves, *et al.*, 1982; Baxter, *et al.*, 1993). It should be noted however that the germination behaviour of laboratory stored seed may differ to actual seed behaviour in the field. Further studies are required to understand the ecology of *Themeda* seeds in field situations.

Independent attempts to relate differences in seed biology of *Themeda* to certain local environmental conditions have often been inconclusive. When reviewed in combination, including results presented in this thesis, the general pattern that emerged was that seeds from tropical populations are initially less dormant (i.e. germinate earlier) than seeds from temperate, cold or dry areas (Lock and Milburn, 1971; Groves *et al.,* 1982; Baxter, *et al.*, 1993). Further studies replicated across environmental gradients are needed for discerning dormancy patterns more clearly.

An interesting result was that germination percentages were higher in heavier seed, despite similar viability among size classes. This pattern was common to all populations tested. The Ukulinga populations produced the heaviest seeds (see Chapter 4). Large seeds are thought to be an advantage in shady environments (Leishman and Westoby, 1994; Westoby, 1996). Although these were inter-species studies, this may in part explain the heaviness of the Ukulinga seeds. Seeds from the semi-arid population (Trompsberg) were also relatively heavy, consistent with the notion that larger seeds are also considered to be an advantage in arid environments (Jurado and Westoby, 1992). The advantage of seed size and its relationship to dormancy in *Themeda* populations requires further investigation.

Summary

The characteristics and relative importance of seedling recruitment, seed bank dynamics and seed biology differed among the study populations investigated. These differences were evident in, and supported by differences in the demographic structure for the populations studied. These data provide clarity to apparently conflicting results reported previously in the

literature when interpreted in conjunction with the environmental conditions of parent populations.
In semi-arid, frost-prone sites (Trompsberg and Hillside), the population structure, seedling emergence from seed banks and in the field, as well as seed production data are consistent with the prediction that mortality is common, and seeds are important propagules for maintaining these populations.

In variable, sub-humid and humid, subtropical sites (Nqumeni and Magangeni) there was convincing evidence for population turnover in terms of recruitment and mortality. High seed production, well-established and responsive seed banks, combined with high germination percentages and good seedling emergence observed for these sites, are clearly, as predicted, important demographic characteristics maintaining these populations.

The size-class structure of *Themeda* in the moderately moist site (Ukulinga) was consistent with the hypothesis that there is little population turnover in this site, with minimal evidence of recruitment or mortality. Despite good germination percentages under laboratory conditions, seed bank studies, seedling emergence in the field, and seed production data all provide further evidence that recruitment through seed is rare, and the inferences made from tussock circumference data are likely to be a true reflection of the demographic characteristics of this area.

The tussock circumference data indicate a stable parent population, with some recruitment and a limit to the size *Themeda* can attain in the moist, temperate, frost-prone site (Kamberg). Data for seedling emergence suggests recruitment can occur in these populations, however, *Themeda* was poorly represented in the seed bank and germination percentages were low. These data provide evidence that seeds may contribute to the population structure, but the importance of this is unclear.

Livestock farmers often allow rest periods during flowering and fruiting seasons of *Themeda* to allow good seed production in the belief that seedling recruitment is important for maintaining *Themeda* swards. The data reported here suggest that such rest periods are of lesser importance in maintaining Themeda swards in mesic, frost-prone areas where populations are largely maintained by vegetative propagation.

7 Synthesis

Since *Themeda* is a valuable forage resource and its presence and abundance in rangelands is considered indicative of good rangeland management practice, the scientific work conducted on this species in the past has influenced much of rangeland management philosophy. This has however occurred without a coherent acknowledgment of the diversity of ecotypes to be found or their associated divergent ecologies. Management recommendations have sometimes therefore been broadly and perhaps inappropriately applied.

Burning regimes recommended for *Themeda* are an example of this. There is a common perception that if *Themeda* is not burnt every 2-4 years it will go moribund (starts to self shade resulting in tussock mortality) and be replaced by other, often less desirable, species. This is true for the more mesic areas of the country where, in the absence of burning, *Themeda* declines from the system as a result of self shading (Everson *et. al.*, 1985). Results from field and glass house experiments for Ukulinga and Kamberg, the two mesic-stable sites investigated, are consistent with this pattern. However, in more arid areas, where productivity is limited by moisture availability rather, than density-dependant processes, burning is not necessary to prevent *Themeda* plants from going moribund. Fire in fact may negatively impact on the grassland resource by removing valuable forage material. Another type of response has developed in frost-free areas. The absence of frost provides an opportunity for grasses to develop an inherent tendency to spread tillers vertically (aerial tillers) instead of laterally. This is evident in plants from Hluhluwe, which have a “bamboo-like” growth form supporting new aerial tillers on large perennial culms. These populations remain productive for long periods without defoliation by grazing or fire. As a consequence, the burning strategies applied can be more flexible and incorporate a greater array of objectives.

Differences in the demographic processes among *Themeda* populations provide a second example of where, if not taken into account, management applications extrapolated among areas may be inappropriate. O’Connor (1993) argued that the survival of *Themeda* populations, following mortality of adults resulting from drought, is dependant on seedling survival. Results from this thesis indeed demonstrate that populations from arid areas or areas which experience periodic drought are reliant on reproduction by seed for population persistence. This was not true for populations from mesic areas where persistence was through vegetative means rather then through seed. This highlights the importance of understanding the demographic processes within a particular area so as to apply the appropriate management. It would only be necessary to manage rangelands for seeds, seed banks and recruitment events in r-selected genotypes of *Themeda*, such as the Trompsberg and Hluhluwe forms.

The apparently conflicting reports on *Themeda* ecology and management recommendations in the literature are largely a function of the fact that a single species name is used to refer to a divergent set of grass functional types. The results from this study suggest that a clear understanding of a few key traits of *Themeda*, in conjunction with knowledge of the prevalent climatic conditions, may provide a useful way for distinguishing among ecological types which would be more meaningful and useful in guiding grassland management. Several authors have highlighted the need for a functional approach to classifying rangelands that is ecologically meaningful (Theunissen, 1992; Campbell, *et al.*, 1999, Duckworth, *et al.*, 2000). *Themeda* provides a novel opportunity whereby such classification may be derived from this single species rather then establishing a few functional types from an array of species:

Plants from semi-arid areas or areas where rainfall variability is relatively high and droughts occur would be expected to have fast relative growth rates under optimum moisture conditions, rapid phenological development associated with early apex elevation followed rapidly by stem elongation and flowering. Recruitment and mortality would be common associated with a high allocation to reproductive structures, in terms of biomass and seed production. Various studies provide supportive evidence that these traits are consistently found in semi arid populations of *Themeda* or populations that experience periodic drought (Groves, 1975, Downing and Groves, 1985, Dankwerts, et. al. 1984, Dankwerts, 1987, Snyman, 1993; Snyman and Fouche', 1993). Results from this work and the work of others show that populations from such areas are able to respond opportunistically to moisture availability (Opperman and Roberts, 1978; Dankwerts, et al. 1984, Dankwerts 1988; Snyman and Fouche', 1993, Snyman, et. al, 1997), a trait apparently absent in more mesic populations. Management practices in semi-arid areas or areas experiencing periodic drought would have to be adaptive. There should be careful consideration of demographic processes (e.g. seedling establishment, tussock mortality) and factonmrs effecting seed production when considering management strategies in these areas. The options available to management would be largely dependant on the prevailing moisture conditions and the objectives that need to be achieved.

Lower relative growth rates, delayed flowering and high tiller production are expected traits for populations from mesic areas. Several studies provide further evidence that these are common features of mesic populations (Tainton and Booysen, 1963, Groves, 1975, Downing and Groves, 1985). The majority of tillers in these populations would typically remain vegetative until the second season of growth. The reproductive output when flowering occurs appears to be variable, ranging from moderate to low seed production among populations (pers. obs, see Everson 1994). With biannual burns and low risk of total plant destruction, seeds would not be as important as vegetative growth for maintaining populations, since plant mortality is expected to be low. In the absence of a defoliation agent, populations from these mesic areas would become less productive and in time would be replaced by later successional species. The loss of *Themeda* from these grasslands would be serious since it would be more difficult to restore such populations due to the lack seed available for recruitment. In mesic areas there is therefore a need to manage density dependent processes such that *Themeda* maintains its productivity and competitive advantage over other species, in terms of light and space acquisition. There is not necessarily a need for adaptive management; instead a burn cycle or a set carrying capacity could be applied that achieves the objectives required.

Comparing studies that investigate the effects of permutations of fire, grazing and season on *Themeda* populations from different areas provide much evidence for differences in the defoliation response of *Themeda* populations (Rethman and Booysen, 1968; Opperman, *et al.*, 1970; Tainton, 1972; Coetsee, 1975; Van den Berg *et. al.*, 1975; Van den Berg, *et al.*, 1976; Tainton, *et al.*, 1978; Coughenour, *et al.* 1985; Oesterheld, and McNaughton, 1988; Dankwerts and Nel, 1989; Snyman, 1993). The grazing response of different ecotypes was conspicuously not addressed in this thesis. It was hoped that through identifying the key traits and processes associated with different populations of *Themeda* this information would enable one to predict the grazing response of different forms. What is now apparent is that differences in grazing response will have different implications depending on the life history strategies of the populations. For example, loss of seed production resulting from applying grazing at the "wrong" stage of apex elevation would be irrelevant in mesic areas, but potentially serious in populations in semi-arid regions. Differences in the phenological development, extent and rate of apex elevation were some of the key traits distinguishing populations of *Themeda*, which are important traits determining grazing response. Thus, it seems likely that an understanding of the life history strategies and associated key traits will assist in predicting and interpreting grazing response among populations of *Themeda*.

An important recommendation from this thesis is therefore that when reporting on work conducted on *Themeda*, a description of the climatic conditions and associated key traits of the plants should be presented in order to determine the applicability of the work to different areas of South Africa where this remarkable species dominates.

Table 7.1 List of some key traits distinguishing *Themeda* ecotypes, likely climatic conditions and implications thereof.

Characteristic	Conditions under which may be found	Implications
Apex elevation (Extent/number of nodes)		
• Long, robust culms/many nodes. • Aerial tillering likely • Regular inter-nodal distances. • Rapid apex elevation.	Frost free.	Less chance of going moribund because there is less self-shading of leaves in plants with aerial tillers.
• Few Nodes • Short thin culms • Ability to initiate aerial tillers on upper nodes absent or limited. • Tillers condensed around base or second node when light is limiting.	Winter frost common.	Depending on rainfall, potential for becoming moribund exists
Seed production		
• High seed production in wet years • Relatively large numbers of seedlings, depending on moisture availability	High co-efficient of variation (C.V.) of rainfall, periodic droughts, semi arid areas.	Seeds likely to be important in population persistence, therefore careful application of grazing so as to maximise seed production, avoiding damage during vulnerable stages. Adaptive management required. Seedling recruitment important
• Consistently low seed production • Few seedlings	Low C.V. of rainfall. Mesic	Seeds unlikely to play a major role in population persistence. Less need to worry about effect of grazing on seed production. However, restoration work may be slow and difficult, if populations are lost.

Characteristic	Conditions under which may be found	Implications
Population structure (tussock size classes)		
• Variable • High population turnover • Recruitment and mortalities occur • Evidence of seedlings and mortality, depending on moisture availability..	High co-efficient of variation (C.V.) of rainfall, periodic droughts, semi arid areas.	Recruitment though seed likely to be important. Managing for optimum seed bank is important. Apply adaptive management
• Mainly large/fragmented • Stable population. • Low recruitment and mortality.	Low C.V. of rainfall. Mesic.	Population persistence most likely through vegetative spread. Managing for optimum productivity is important for persistence.
Productivity		
• Density dependence (self shading) strongly evident • Intense light and space competition.	Moderate to High rainfall, low C.V. of rainfall.	Requires burning and/or grazing to prevent populations from going moribund Predictable forage availability.
• Productivity responsive to rainfall • Forage availability and fuel load varies.	High C.V. of rainfall, periodic droughts, semi arid regions.	Variable forage flow Requires adaptive management Fire regime dependent on amount and frequency of rain and management objectives.

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