

**An Assessment of the Effect of Season of
Grazing, Stocking Rate and Rainfall on the
Dynamics of an Arid Rangeland on the West
Coast of South Africa**

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DECLARATION

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

Signed.....
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Date..... 26. 09. 2006



ABSTRACT

A grazing trial investigating the effect of season of grazing and stocking rate initiated at the Nortier Experimental Farm in 1988 provided an opportunity to assess the response of the veld to both grazing and environmental influences in an arid environment. The trial allowed an assessment of the relative influence of internal (equilibrium) and external (non-equilibrium) forces on the dynamics of an arid rangeland. This study involved the analysis of a nine year data set stretching from 1988 to 1996 and served to provide evidence supporting the existence of an equilibrium/non-equilibrium continuum in rangeland dynamics. The most significant implication of this result is that rangeland systems should not be classified as either equilibrational or non-equibrational, but rather according to a continuum extending between equilibrium and non-equilibrium poles. The exact position of any system on this continuum is a function of the relative influence of internal and external forces on its species dynamics.

The dynamics of the veld at the Nortier Experimental Farm showed significant response to both grazing and environmental variables suggesting conformity to both equilibrational and non-equibrational paradigms. Both ordination and analysis of variance highlighted the importance of rainfall particularly in the fluctuations of the predominant grass species, *Ehrharta calycina*, which increased in abundance with rainfall. Partial ordination enabled the assessment of species variation following the removal of variation associated with rainfall. Partial ordinations revealed the gradual, directional movement of samples through multivariate space in response to grazing treatments. Individual plant species were also shown to be responding to grazing, the extent of which was influenced by season of grazing and stocking rate.

Both the partial ordinations and the ANOVA showed *Melothria* sp., *Tetragonia fruticosa* and *Hermannia scordifolia* as increasing and *Ruschia caroli* as decreasing in absolute abundance in response to grazing. Season of grazing was shown to significantly influence the abundance of *H. scordifolia* over time.

The 'shrub/herb complex', which constitutes the 'key resource' at the Nortier Experimental Farm displayed an increase in absolute abundance over the duration of

the trial. This increase in absolute abundance was accompanied by an increase in the relative abundance of the palatable component of this resource. The application of medium to heavy stocking rates during spring, summer and autumn and low stocking rates during winter resulted in elevated absolute abundances of palatable plants. Furthermore, low stocking rates, when averaged across all season of grazing treatments, resulted in a significantly higher absolute abundance of unpalatable plants. These findings provide the basis for the development of management principles for the Strandveld Vegetation Type.

The application of medium to heavy stocking rates within a rotational grazing system, as recommended by the literature dealing with grazing systems in the Karoo, is supported by the results of the Nortier grazing trial. Medium to heavy stocking rates should be applied during spring, summer and autumn and low stocking rates during the winter months. Furthermore, it is recommended that rests of between 12 and 14 months should be afforded to portions of the veld periodically due to the variability in growth, flowering and fruiting times of different plants in the Karoo.

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CHAPTER 1: INTRODUCTION

1.1 Aims and Objectives

The aims and objectives are to assess the relative influence of internal (equilibrium) and external (non-equilibrium) forces on the dynamics of an arid rangeland (Strandveld Vegetation Type on the west coast of South Africa) through the examination of the literature applicable to the equilibrium/non-equilibrium debate and the statistical analysis of the Nortier data set. Furthermore, this thesis aims to reach resolution on not only whether equilibrial or non-equibrial principles are applicable in the Strandveld Vegetation Type, but whether they are mutually exclusive or rather the poles of a continuum between which all rangeland systems exist. The secondary aim is to derive, from the relevant literature and the results of the statistical analyses applied to the Nortier data set, management principles for sustainable livestock production in the Strandveld Vegetation Type.

1.2 The Nortier Trial

1.2.1 Trial Background

In 1988, a grazing trial was initiated at the Nortier Experimental Farm (32°04'S; 18°22'E) to assess the response of vegetation to grazing by dry (not-pregnant) Dorper ewes at various stocking rates comprising light (0.216 Small Stock Units/hectare (SSU/ha)), medium (0.316 SSU/ha) and heavy (0.416 SSU/ha), during spring (September to November), summer (December to February), autumn (March to May) and winter (June to August). Each of the 12 treatments was replicated twice (Table 1.1). Species composition surveys were conducted four times a year (August, November, February and May) using the descending point method (Roux 1963) with 500 observations being recorded at 1m intervals along a length of non-stretch rope. As a result, each point observation was made in the same position in the landscape on each sampling occasion. At each point, direct hits (canopy interception) as well as the nearest neighbour were recorded.

Table 1.1: Nortier treatment combinations in terms of stocking rate and the season in which grazing was applied.

	Spring	Summer	Winter	Autumn
Low SR	Treatment 1 (Rep 1)	Treatment 4 (Rep 1)	Treatment 7 (Rep 1)	Treatment 10 (Rep 1)
	Treatment 1 (Rep 2)	Treatment 4 (Rep 2)	Treatment 7 (Rep 2)	Treatment 10 (Rep 2)
Medium SR	Treatment 2 (Rep 1)	Treatment 5 (Rep 1)	Treatment 8 (Rep 1)	Treatment 11 (Rep 1)
	Treatment 2 (Rep 2)	Treatment 5 (Rep 2)	Treatment 8 (Rep 2)	Treatment 11 (Rep 2)
High SR	Treatment 3 (Rep 1)	Treatment 6 (Rep 1)	Treatment 9 (Rep 1)	Treatment 12 (Rep 1)
	Treatment 3 (Rep 2)	Treatment 6 (Rep 2)	Treatment 9 (Rep 2)	Treatment 12 (Rep 2)

1.2.2 Climate

The Nortier Experimental Farm is located on the west coast of South Africa in the Strandveld Succulent Karoo (Low and Rebelo 1996) which typically experiences between 300 mm in the south to below 50 mm of rainfall annually, the majority of which falls in the winter months (Vorster and Roux 1983; Acocks 1988; Schulze 1994, Coetzee 2002). The Nortier Experimental Farm itself receives an average of 221 mm/annum (with a mean annual rainfall of 214 mm per year over the trial period (Venter, Lombard and Frey 1996). Fog, caused by the cold Benguela current is common, and can reach as far as 20 to 30 miles inland during the night, retreating seawards during the morning (Schulze 1994). The region experiences mean minimum and maximum temperatures of 10.9°C and 21.7°C respectively with highs during January reaching in the order of 35°C and lows during July reaching -10°C (Schulze 1994).

1.2.3 Vegetation

The Nortier Experimental Farm is situated within the Strandveld Vegetation Type (Acocks 1988; Low and Rebelo 1996) (Figure 1.1), which constitutes the west coast variation of the Succulent Karoo Biome (Coetzee 2002).

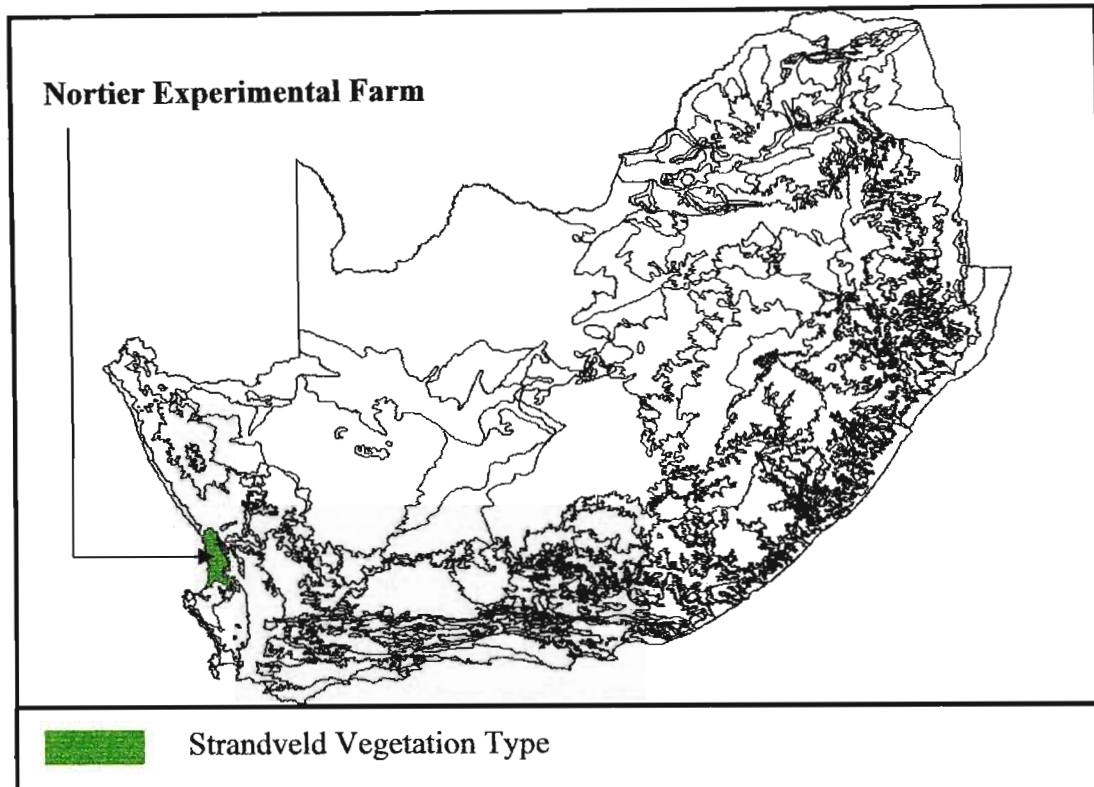


Figure 1.1: Map of South Africa showing the position of the Nortier Experimental Farm in relation to the Strandveld Vegetation type (Acocks 1988).

The Succulent Karoo Biome has global ecological significance with over half of its species considered rare and endemic (Coetzee 2002). Acocks (1988) distinguishes between two variations within the Strandveld Vegetation Type namely the Dense Scrub variety and the Strandveld Proper variety. The vegetation at the Nortier Experimental Farm conforms to that described by Acocks (1988) as Strandveld Proper. The Strandveld Vegetation Type comprises grasses which have the potential to become abundant if given the opportunity in vegetation described as open scrub dominated by low shrubs and small trees (Acocks 1988; Low and Rebelo 1996) (Table 1.2).

Table 1.2: Description of principle plant species in terms of mean relative abundance, plant type, morphology and palatability.

Botanical Name	Mean Relative Abundance	Plant Type	Morphology	Palatability
<i>Ehrharta calycina</i>	30.78%	Perennial tufted Grass	Leaves: Concentrated at the base of the plant. Leaf sheath	Palatable

			compressed. Flowers: Open panicle with secondary branches hanging downwards. Usually purple. (Van Oudtshoorn 1999)	
<i>Hermannia scordifolia</i>	16.03%	Creeping Shrublet	Leaves: Greyish-green and oval in shape. Up to 20mm long and 15mm wide. Flowers: Pale yellow, borne suspended from the branched tips of stems. (Van Breda and Barnard 1991)	Palatable
<i>Tetragonia fruticosa</i>	11.16%	Sprawling Shrublet	Leaves: Slightly fleshy, narrow with margins rolled under (Manning and Goldblatt 1996). Flowers: Elongated spikes, dull yellow with red tinge (Manning and Goldblatt 1996). Fruit: Strongly four-winged (le Roux and Schelpe 1981)	Palatable
<i>Zygophyllum morgsana</i>	9.97%	Shrub (up to 1.5m high)	Leaves: Unpleasant smelling, broad and short stalked. Stipules green and fleshy. Flowers: Pale yellow with a purple blotch (Manning and Goldblatt 1996). Fruit: Have four prominent membrane like wings (le Roux and Schelpe 1981).	Unpalatable
<i>Ruschia caroli</i>	4.61%	Succulent Shrub (up to 80cm tall)	Leaves: 1.5 – 7cm long, 2 – 8mm wide. Flowers: Purple, up to 2.5cm in diameter. (www.deserttropicals.com).	Unpalatable
<i>Chaetobromus schraderi</i>	3.58%	Perennial Grass	Leaves: Glabrous, except at the sometimes	Palatable

			<p>bearded sheath mouth. Flowers: Pannicle is long, contracted and usually dense. Lemmas awned and usually loosely hairy. (Chippendall 1955)</p>	
<i>Salvia lanceolata</i>	3.23%	Shrub	<p>Leaves: Narrow or broad, grey and hairy. May be coarsely toothed. Flowers: Occur at the tips of side branches. Dull rose to brownish crimson or grey-blue (Manning and Goldblatt 1996).</p>	Palatable

CHAPTER 2: APPLICABILITY OF EQUILIBRIUM AND NON-EQUILIBRIUM DYNAMICS IN THE STRANDVELD OF THE WESTERN CAPE

2.1 Introduction

Research that focused on equilibrium and non-equilibrium models of ecosystem functioning was reviewed to assess the applicability of these models to the interpretation of results obtained from grazing trials undertaken at the Nortier Experimental Farm in the Western Cape. At the centre of the contemporary debate surrounding the two conflicting paradigms is contention regarding the relevance of the equilibrium paradigm, including the range model, and the non-equilibrium paradigm, encompassing among others the state and transition model, to rangelands subject to different climatic conditions (Ellis and Swift 1988; O'Connor and Roux 1995; Fuhlendorf and Smeins 1997; Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Fynn and O'Connor 2000; Fuhlendorf *et al.* 2001; Briske *et al.* 2003). The conclusions drawn through consideration of opinions derived from trials and synthesis and opinion papers provide the theoretical background for the interpretation of the statistical analyses which constitute the core of this thesis.

2.2 The Contemporary Debate

Early concepts of vegetation succession were based on the development of an ecosystem from bare ground and the appearance of first pioneers through to the final or climax stage (Clements 1916). The climax forms the final stage in the succession process, existing in a state of dynamic equilibrium (Holechek *et al.* 1989) regulated by the climate (climatic climax) of a region (Clements 1916, Clements 1936). It has been generally accepted that rangeland systems, once at climax, are maintained in a state of dynamic equilibrium by negative feedback loops which control fluctuations in both animal and plant populations within a community (Ellis and Swift 1988). Ellis and Swift (1988) make reference to the appeal that this balance in nature has for rangeland scientists.

The past 20-30 years have seen a re-evaluation of the theory governing the management of rangeland systems and in particular, the role played by herbivores and the external environment. This re-evaluation was spurred on largely by the findings of Ellis and Swift (1988) who questioned the role of negative feedback loops and their

maintenance of dynamic equilibrium in systems characterized by highly variable external forces. Instead, they suggest that in 'systems dominated by external forces the opportunity for the development of feed-back control is much reduced and the persistence of the system depends on the development of other sorts of stabilizing mechanisms' (Ellis and Swift 1988). Since the work of Ellis and Swift (1988) a number of authors (O'Connor and Roux 1995; Fuhlendorf and Smeins 1997; Illius and O'Connor 1998; Fernandez-Gimenez and Allen-Diaz 1999; Fynn and O'Connor 2000; Fuhlendorf *et al.* 2001; Briske *et al.* 2003, Kochy and Wilson 2004) have undertaken studies or published reviews relevant to the contemporary re-examination of existing rangeland paradigms. The details of the equilibrium model and the non-equilibrium model and their applicability to the analysis of the Nortier data are relevant to this study.

2.3 The Equilibrium Model

An ecosystem is a 'functional unit consisting of organisms (including man) and environmental variables of a specific area' (Van Dyne 1966 (cited by Holechek *et al.* 1989)). It consists of abiotic (non-living) components which comprise soil and climatic factors (temperature and precipitation) and biotic (living) components which include primary producers, consumers and decomposers (Holechek *et al.* 1989). Succession is an ecological process described by Clements (1916) as being the 'movement of populations, the waves of invasion, which rise and fall through the habitat from initiation to climax and involves the directional development of an ecosystem, towards a climax stage'. The process of succession is in part caused by the impact which plants have on their own environment (both living and non-living), but is driven primarily by competition between plants (intra- and interspecific) and the influence of external factors such as organisms and the abiotic environment (climate, time, topography) (Jenny 1941 (cited by Holechek *et al.* 1989)). Jenny's (1958) triangle of interplay between climate, vegetation and soil neatly illustrates the independent effects of climate on soil and vegetation, and the interaction between soil and vegetation. Whittaker (1953) describes the role played by competition between plants in the directional movement of a community or the fluctuation of a community around the climax. Clements (1916) defined the essence of succession as lying in the 'interaction of three factors, namely habitat, life forms, and species in the progressive development of a formation' and incorporates both Jenny's (1958) and Whittaker's

(1953) assertions on successional theory. Furthermore, Tansley (1935), who criticised much of Clements' work, himself highlighted the role played by abiotic and biotic factors during succession and differentiates between what he termed autogenic succession, where community changes are a consequence of the influence of plants on the habitat, and allogenic succession, where changes in community composition are a consequence of external factors. While this distinction is made, Tansley (1935) does suggest that an interaction between the two does occur, with natural succession being driven by a combination of autogenic and allogenic influences. This interaction is further emphasised by Whittaker (1953) in what he terms 'the development of self-maintaining systems of interacting populations'. He likens the development of an ecosystem to the 'evolution of tides'; to the fluctuations of gene frequencies in a population through mutation, population changes and environmental selection; and to the 'varied, experimental adaptive responses of childhood' resulting in an adult, the personality of whom is a function of their environment (Whittaker 1953). The environment, claims Whittaker (1953), moulds and 'fashions the development or evolution' of a complex entity with the result (in this case a plant community) being a reflection of the environment to which it has been subjected (Whittaker 1953).

The final stage of succession is the climax stage proposed by Clements (1916) and further discussed by Phillips (1934; 1935 (cited by Tansley 1935)) and Clements (1936). Clements (1916) believed that for a region a single climax, termed the climatic climax exists towards which all vegetation will tend. Clements (1936) while emphasising his belief in a single climatic climax, acknowledges what he terms proclimax states which share the climax communities' characteristic of stability but which do not correspond to the climate of the region. Tansley (1935) criticizes monoclimate theory as described by Clements (1916), and discusses what he terms polyclimax theory. 'Polyclimax theory' assigns climax status to what appear to be permanent types of vegetation, which have adjusted to the influence of a particular disturbance under certain environmental conditions. Fire climax grasslands are an example of a polyclimax community, where the constant influence of fire leads to plant communities dominated by fire resistant species (Tansley 1935). Other examples of polyclimax communities include edaphic climax, mowing climax and physiographic climax (Tansley 1935). Clements (1936) disagrees and states that if climax communities are defined in this way then 'corn would constitute one climax,

wheat another and cotton a third'. On this basis, one is inclined to follow the assertions made by Clements (1936), which deal rather with proclimax states for communities influenced by disturbance. These proclimax states are subordinate to the true climax towards which the vegetation will tend following the removal of the hindering disturbance (Clements 1936). It is however, this multitude of what Whittaker (1953) refers to as 'ations', which has rendered Clements' theory of monoclimax questionable. Whittaker (1953) states that Clements' solution to the shortcomings in his monoclimax theory was the creation of new terms explaining non-conformism with the predicted climatic climax. Terms such as proclimax, subclimax, disclimax, preclimax and postclimax as well as associations, consociations, lociations etc. all explain variations to the climatic climax of an area (Whittaker 1953). Whittaker (1953) states that there is no such things as an 'absolute climax' in an area and that climax composition simply refers to the species composition of a community which has adapted to a particular environmental influence. Furthermore, the terms 'climax' and 'succession' are according to Whittaker (1953) only terms assigned to communities that differ according to their stability.

It is important for the purposes of analysing grazing trial data that a distinction between primary and secondary succession be drawn. While they both involve the 'progressive development of vegetation in an area, through a series of different plant groupings or communities' (Tainton and Hardy 1999) and while they are both driven by the same internal and external influences, they do have fundamentally different starting points which determine their relevance to the management of rangelands. Primary succession is succession, which begins on a bare surface and involves 'the colonization of a bare area' (Whalley 1994) which proceeds towards the relatively stable climax community (Tainton and Hardy 1999). The process of primary succession includes not only the development of the biotic plant and animal community but also the development of soil profiles characteristic of the climate and parent material in an area (Jenny 1958; Whalley 1994). This is in line with Holechek et al. (1989) who states that in reality an entire ecosystem (abiotic and biotic components) undergoes succession whether it be primary or secondary following a disturbance and that, while the macroclimate may remain the same, the microclimate within a system does undergo change as the soil and vegetation develop.

Secondary succession differs in that its beginning point follows a disturbance to the community and involves the development of the biotic community on previously developed soils following a disturbance (Holechek et al. 1989; Tainton and Hardy 1999). Secondary succession should not be confused with fluctuations as discussed by Smith (1996). Fluctuations are non-successional or short-term changes in species composition which are reversible in nature (Smith 1996). They constitute changes in the relative floristic abundance of species in response to environmental stresses such as soil moisture fluctuations, wind and grazing (Smith 1996).

Whalley (1994) makes reference in his discussion on succession to Sousa's (1984) definition of disturbance as being 'a discrete, punctuated killing, displacement or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established'. Sousa's (1984) definition incorporates both biological (predation, grazing) and physical processes (fire, flooding) of disturbance some of which are used by rangeland managers to manipulate the rangeland resource. The progression of an ecosystem through both primary and secondary succession is triggered largely by plant tolerance levels as defined by Shelford's Law (Figure 2.1).

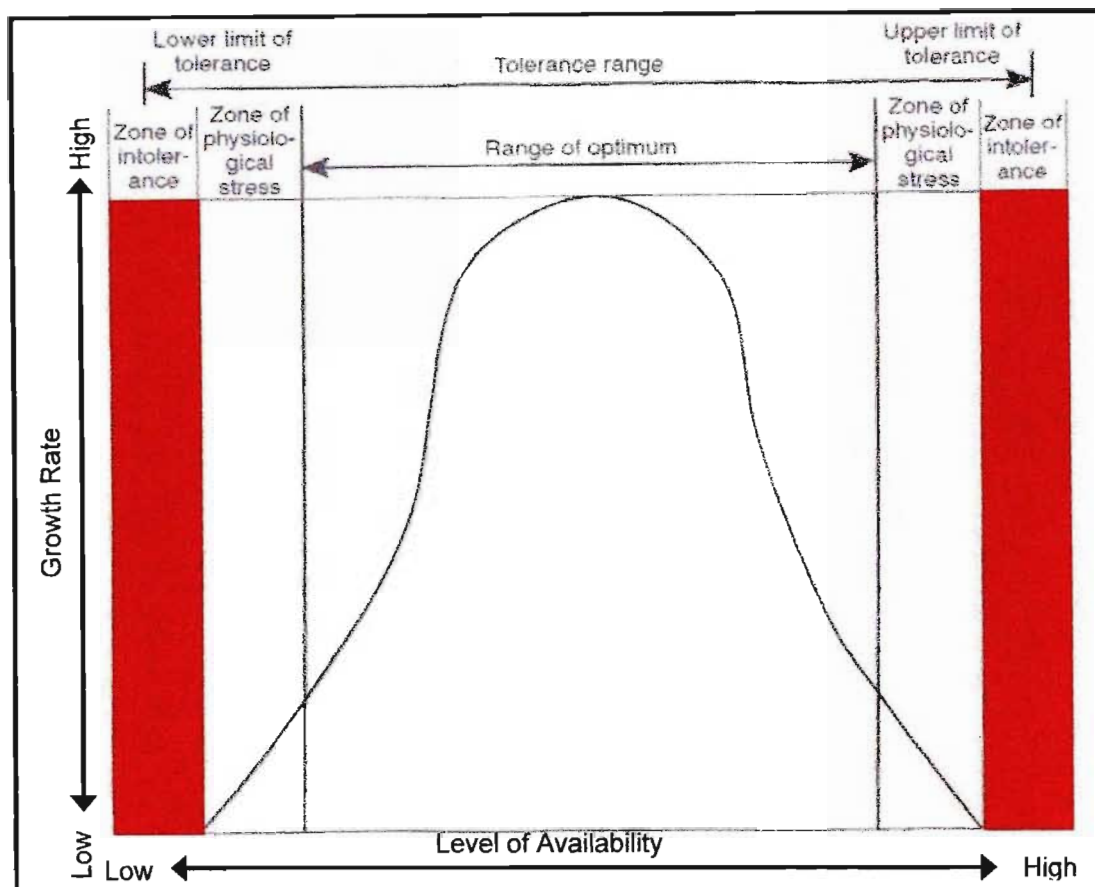


Figure 2.1: Schematic illustration of Shelford's law of tolerance (Boughley 1971 (cited by Tainton and Hardy 1999)).

Shelford's law of tolerance shows plant's limits and tolerance to the different levels (quantity, concentration, degree) of abiotic factors to which they are exposed (Tainton and Hardy 1999). Different tolerance levels among species lead to certain species being more dominant and abundant under different combinations of external variables. A change in any one factor (precipitation, stocking rate, soil chemistry) within a system will therefore result in a change in species composition. Indeed, the species composition within a system is representative of its position along the succession scale and is governed by competition, the influence of biotic and abiotic factors (as per Shelford's law) and time.

Holechek et al. (1989) suggest certain pitfalls associated with succession theory. The biggest of these pitfalls involves succession being depicted as a smooth process, a theory which in all but hypothetical circumstances does not hold true. This is particularly valid in semi-arid environments where climatic variability often plays a major role in the development of a sere (Figure 2.2). The natural progression of an ecosystem is illustrated by Heady (1973 (cited by Holechek et al. 1989)) as being

directional in nature moving towards a fixed climax. Heady (1973 (cited by Holechek et al.1989)) demonstrates clearly the influence of seasonal, yearly and longer cycles on the path of a plant community towards the climax state. This theory ties in with Jenny (1961) which refers to vegetation communities as being generally unstable due to the continual addition and removal of energy and matter from the system. It is this variable environment that prevents succession from being a smooth process (Figure 2.2).

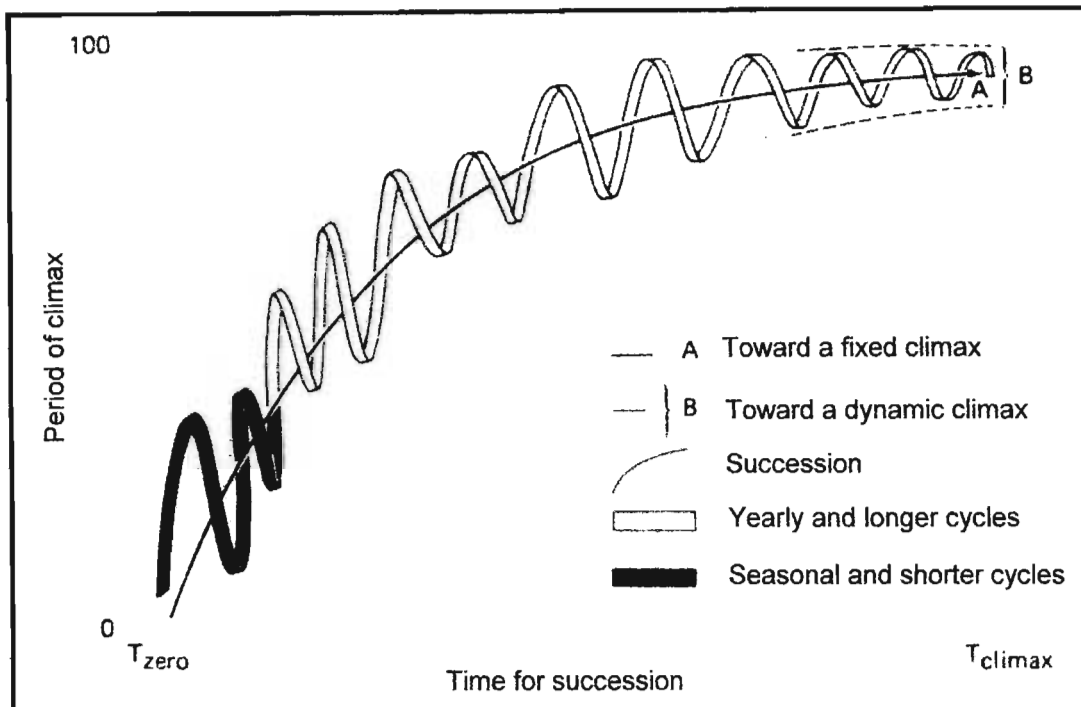


Figure 2.2: Diagram depicting the asymptotic development of a community towards a dynamic equilibrium including variations caused by daily, seasonal and yearlong phenomena (Heady 1973 (cited by Holechek et al. 1989)).

Succession from bare ground to a climax community (primary succession) takes in the order of hundreds or even thousands of years (Holechek et al. 1989) and can be difficult to detect, in the short term, beneath the often far greater fluctuations in ecosystem characteristics (e.g. plant species composition) caused by seasonal and year long cycles. Westoby et al. (1989) acknowledges this and states that the range succession model recognizes the variation in species composition caused by variable rainfall. This variation in species composition however is restricted to the path of the succession continuum through time and not perpendicular to the continuum as illustrated by Heady (1973 (cited by Holechek et al.1989)). Even once the vegetation has reached the 'grazing climax' or proclimax stage, the balance that exists between the pressure of grazing and the successional tendency of the vegetation cannot

produce a completely unvarying equilibrium (Whittaker 1953; Westoby et al. 1989), hence dynamic equilibrium.

The species composition of the producer component of an ecosystem is largely a function of the consumer component of the system and vice versa (due to the negative feedback relationship that exists between the two). Clements (1936) states that animals must also be 'considered members of the climax' hence the origin of the word 'Biome'. The relation between plants and animals begins early in the succession process and increases in complexity as the ecosystem progresses towards the climax stage, all the while being mediated by, and in some respects mediating, the micro and macroclimate within an area. The climax stage is reached once the plant and animal populations achieve dynamic equilibrium, at which point the system ceases its directional trend, fluctuating around a central point in response to annual and seasonal cycles in abiotic conditions (e.g. rainfall) (Whittaker 1953).

The range succession model postulates that for any rangeland there exists a single persistent state, the climax towards which, with the exclusion of grazing, the vegetation will tend (Westoby *et al.* 1989). The model is based on succession theory as detailed by Clements (1916) and supposes that the influence of grazing opposes the natural successional tendency inherent to all systems in such a way that an equilibrium associated with a particular stocking rate or grazing regime can be reached and maintained (Westoby *et al.* 1989). Clements (1916) recognizes that the successional tendency can be halted in a variety of ways and refers to proclimax communities which 'simulate the climax to some extent in terms of stability or permanence but lack the proper sanction of the existing climate'. These proclimax communities exist at any point between T_{zero} and T_{climax} (Figure 2.2) on the succession scale. Rangelands subjected to heavy grazing would according to the range succession model be positioned further from the climax (nearer to T_{zero}) than those under lighter grazing (nearer to T_{climax}). The technical term for the position of a rangeland upon this continuum according to Westoby *et al.* (1989) is condition, with rangeland condition deteriorating as one moves further from the climax. In addition to the influence of grazing on the condition of veld, numerous authors have attempted to incorporate the influence of rainfall into the range succession model. According to Westoby *et al.* (1989) dry periods are considered to have the same influence on a

rangeland in terms of succession as grazing does, forcing the system backwards in the successional process while above average rainfall has the opposite effect and promotes succession. The range succession model however, particularly its applicability in arid and semi-arid environments, has limitations. These limitations were highlighted by Ellis and Swift (1988) where the applicability of the range succession model, which relies strongly on the development of negative feedback relations between the producer and consumer components of an ecosystem, in non-equilibrium environments, where abiotic influences are predominant, was questioned. The state and transition model, which incorporates many of the principles of the range succession model, takes a different approach to modeling vegetation dynamics and is able to incorporate dynamics associated with environmental influence.

Succession theory is directly relevant to the Nortier grazing trials. This is because the introduction of disturbance (grazing) to an ecological system which is at or tending towards a climax state, or an alteration to an existing disturbance (change in stocking rate; change in season of grazing etc.) in an ecological system which is maintaining a proclimax state, fundamentally changes the system causing a reorganization in species composition to compensate for that disturbance. In a climax community, the introduction of a disturbance (Westoby et al. 1989) pushes the system backwards in the successional process, forcing it to accommodate the change, and move towards a new proclimax equilibrium incorporating the new disturbance. Westoby et al. (1989), in an article that set the foundation for the development of the state and transition model, states that 'the range succession model operates on the assumption that range condition can be modified continuously and reversibly...by adjusting the stocking rate to a constant level and giving time for the range to equilibrate with it'. In systems which are not yet at equilibrium, but tending towards a climax, the introduction or alteration of an existing disturbance, for example a different grazing regime from that which is in place, will alter the climax destination of the ecosystem and hence its successional path.

The development of multivariate statistical techniques, such as ordination, has made the tracking of a community's successional pathway and the influence of disturbance on these pathways relatively simple (Martens et al. 1995; O'Connor and Roux 1995; Fuhlendorf and Smeins 1997; Fynn and O'Connor 2000; Kirkman 2001). Monitoring

the progression of a plant community is achieved by plotting samples in multivariate space according to their species composition with similar plots being closer to one another than those which are dissimilar. By collecting species composition data along predefined transects at yearly intervals one is able to record changes in species composition, and through ordination create a visual representation of how a plant community is progressing in time. In a community where dynamic equilibrium and climax has been reached, according to the range model, samples gathered during consecutive years should be positioned close to one another in multivariate space, fluctuating around a central point ('fluctuate around an average' (Whittaker 1953)) in response to yearlong cycles in abiotic conditions such as rainfall. In contrast to this, samples gathered over time for a community to which a disturbance has been recently introduced, if joined together by a line, show a directional trend, with sporadic fluctuations around a mean trend line attributable to year long and seasonal fluctuations in abiotic conditions.

Numerous authors have undertaken trials that show how the application of grazing results in the alteration of plant species composition (Martens et al. 1996; Skinner 1996; Morris and Tainton 1996; du Toit 1998; Smit and Rethman 1999; Kirkman 2001). The evidence provided by these and other papers as to the relation between plant and animal communities suggests that the range model should not be disputed in terms of its applicability but rather the extent of its applicability. The extent of its applicability has recently been scrutinised by a number of authors (Ellis and Swift 1988; O'Connor and Roux 1995; Illius and O'Connor 1999; Fernandez-Gimenez and Allen-Diaz 1999; Fynn and O'Connor 2000; Briske et al. 2003) many of whom suggest that large fluctuations in environmental factors (high rainfall variability in semi-arid environments) hinder the internal regulation within an ecosystem to the extent that the range model, driven by internal regulation, becomes non-applicable. Illius and O'Connor (1999), for example, stated that 'environmental factors commonly disrupt the equilibrium of systems that would be stable under constant conditions'. Furthermore, it is argued that because of environmental variability, fluctuations in plant and animal populations are largely independent of one another (Ellis and Swift 1988). These revelations provide the basis for the rangeland debate and the focus of literature dealing with the non-equilibrium rangeland model.

2.4 The Non-equilibrium Model and ‘Continuums’

The belief of numerous African populations that illness is caused by spirits rather than harmful bacteria or viruses has led to the treatment of illness differing greatly to conventional western medicine (Ellis and Swift 1988). Ellis and Swift (1988) compared this to the manner in which the perception of ecological systems and how they operate influences the way in which they are manipulated to achieve certain objectives. It is through this analogy, that Ellis and Swift (1988) emphasize the importance of understanding a system’s dynamics, as it is this understanding which provides the basis for data analysis, model creation and ultimately the generation of management principles for specific ecosystems. Hoffmann (1988) states that the Karoo, in covering 427 015 km², constitutes over one third of South Africa’s surface area. Indeed, arid and semi-arid environments constitute one third of the Earth’s land surface area (Anderson and Inouye 2001) and in Africa alone support over 30 million livestock dependant people (Ellis 1994 (cited by Behnke and Kerven 1994)). Understanding the driving forces behind the dynamics of this biome, on which increasing demands are being placed (Anderson and Inouye 2001), is crucial if one aims to sustainably use the resource as a source of forage for livestock production in South Africa. Since the early reservations expressed by Ellis and Swift (1988), a number of authors (Westoby *et al.* 1989; O’Connor and Roux 1995; Fuhlendorf and Smeins 1997; Fernandez-Gimenez and Allen-Diaz 1999; Illius and O’Connor 1999; Fynn and O’Connor 2000; Briske *et al.* 2003) have examined the applicability and validity of the two dominant paradigms used to model dynamics within rangelands, namely the range model and the state and transition model. The range model and state and transition model are theoretically related to the equilibrium and non-equilibrium models respectively (Briske *et al.* 2003). Non equilibrium systems are defined by Wiens (1984 (cited by Sullivan and Rohde 2002)) as being ‘characterized by a general “de-coupling” of close biotic interactions where species should respond to environmental variations largely independently of one another.’ Equilibrium systems on the other hand are defined ‘primarily by stability in community components (and by rapid resilience – the ability of the system to return to a previous state following perturbation)’ (Wiens 1984 (cited by Sullivan and Rohde 2002)). Biotic coupling, density dependence, saturation and tight patterns of community organization are all traits characteristic of equilibrial environments (Wiens 1984 (cited by Sullivan and Rohde 2002)).

Ascertaining the extent to which a system's behaviour is equilibrational or non-equibrational is achieved through the examination of abiotic patterns, plant herbivore interactions, population patterns and community/ecosystem characteristics (Fernandez-Gimenez and Allen-Diaz 1999; Briske *et al.* 2003). In terms of abiotic patterns, areas which experience highly variable rainfall, similar to those which characterise the west coast of South Africa, are typically where one would expect to find a system in which non-equilibrium ecosystem characteristics are prevalent. Equibrational systems are usually predominant in areas where climatic conditions are relatively constant and stochastic events rare, both traits which are uncommon in the world's natural rangelands (Fernandez-Gimenez and Allen-Diaz 1999). Consistency in climatic conditions facilitates the tight coupling of plant and herbivore populations allowing the development of negative feedback loops that regulate the system in equilibrium. Where climate is highly variable, particularly in semi-arid regions, the development of negative feedback systems, customary in equibrational systems, is suppressed resulting in a loose coupling between plants and herbivores (Ellis and Swift 1988; Fernandez-Gimenez and Allen-Diaz 1999). This leads to plant and animal population dynamics appearing independent of one another (Illius and O'Connor 1999). The suppression of negative feedback regulation by variable climates has led to the postulation that ecological systems subject to variable climates are non-equibrational in nature while those which exist in regions subject to constant environmental conditions conform to an equibrational model.

Equilibrium and non-equilibrium systems are not mutually exclusive (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Briske *et al.* 2003) but rather extremes in between which rangelands exist. Indeed, even rangelands subject to relatively constant external forces display non-equilibrium traits and *vice versa* (Illius and O'Connor 1999). The direction towards which consensus on the topic seems to be tending, is that these two paradigms represent the poles of a continuum upon which individual systems are positioned according to the degree to which internal and external forces drive their dynamics (Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Briske *et al.* 2003).

The extent to which individual systems embody the principles of equilibrium and non-equilibrium models varies according to the temporal and spatial scales at which they are observed (Illius and O'Connor 1999) as well as which vegetation components are assessed (Fernandez-Gimenez and Allen-Diaz 1999). Fuhlendorf and Smeins (1997) go so far as to make specific reference to the spatio-temporal scale at which they assessed rangeland dynamics prior to discussing their results intimating that different conclusions could be drawn through observation at different scales.

2.4.1 *Spatial scale*

It is crucial to gaining a true understanding of a rangeland's dynamics that consideration is given to the spatial scale at which the rangeland is being observed (Briske *et al.* 2003). In spatially heterogenous landscapes, observation of system dynamics at different spatial scales can yield varying conclusions regarding the strength of relation between the plant component and internal and external influences. Illius and O'Connor (1999) refer to the existence of 'key resources' within spatially heterogenous landscapes which provide forage for herbivores during dry periods. The key resource may comprise vegetation growing in areas where soil moisture is retained, such as drainage lines, which provide animals with a source of forage during dry periods (Illius and O'Connor 1999). The key resource however is not necessarily spatially differentiated within the grazing resource, as is the case with drainage lines. Indeed the key resource can be a component of the veld which remains palatable during dry periods, such as grass species in the arid Karoid winter rainfall regions (Roux 1968), or evergreen species which provide forage throughout the year (Illius and O'Connor 1999). The development of a density dependant (equilibrial) relation between herbivore populations and the key resource precludes an equilibrial relation between the same herbivore population and the system as a whole (Illius and O'Connor 1999). Often annual irruptions of species responsive to rainfall (such as the herbaceous component in O'Connor and Roux (1995), Fynn and O'Connor (2000) and Kochy and Wilson (2004)) mask the density dependant relations between the key resource and herbivores. Closer investigation does however often reveal an underlying relation between herbivores and the vegetation or, at the very least, evidence in the plant dynamics of an interaction between grazing and climate (O'Connor and Roux 1995; Fynn and O'Connor 2000).

Therefore, it is crucial in research trials which are situated in spatially heterogeneous semi-arid landscapes that individual plots/samples contain both patches of veld which constitute the key resource and patches of veld which are driven by external forces such as variable rainfall. If trial design does not achieve this then a bias towards equilibrium or non-equilibrium processes may be introduced which could lead to inaccurate conclusions regarding the driving forces behind veld dynamics.

2.4.2 *Temporal scale*

Fuhlendorf *et al.* (2001) recognizes that the examination of systems at different temporal scales can be misleading when assessing the relative influence of grazing and climatic variability on vegetation. Fuhlendorf and Smeins (1997) adds further emphasis to the point stating that 'long-term data under varying grazing and weather regimes are essential to understand the multivariate patterns associated with vegetation change'. In addition to ensuring a temporal scale which allows adequate time for patterns to develop, it is vital that monitoring is structured in such a way that the patterns can be detected. For example, change within a system following a disturbance, whether that be the implementation of a new burning regime or a change in stocking rate, is greatest early on, tapering off as the plant component approaches an equilibrium with the new force or indeed a stable state as defined by Westoby *et al.* (1989). The decrease in magnitude of change within a rangeland as the system incorporates a disturbance means that the monitoring and assessment of change within a system should be at its most intense immediately following the application of a new treatment. O'Connor and Roux (1995) emphasized the importance of time and extended periods of monitoring by distinguishing between directional trends associated with grazing and those associated with rainfall cycles within the Karoo. Reference is made in their paper to Tyson (1986) who suggests an 18-year rainfall cycle in the Karoo. Discernment between species composition trends which are caused by grazing and trends caused by rainfall can only truly be made if a study extends over a period which incorporates two or more rainfall cycles, something which was not achieved by O'Connor and Roux (1995) and is rare among all trials.

2.4.3 *Vegetation components*

While the temporal and spatial scale at which rangelands are assessed has been emphasised by a number of papers, little formal emphasis has been placed on the

structuring of analyses to adequately assess various components within a system (shrubs, grasses, perennials, annuals, biomass, cover, etc.) (Fuhlendorf *et al.* 2001). For example, in the mountain steppe system assessed by Fernandez-Gimenez and Allen Diaz (1999) it was found that a number of measured variables (including grass and total biomass, total vegetative cover, the cover of grasses, weedy annuals and unpalatable forbs and richness and diversity) varied along grazing pressure gradients. They also revealed that within the same system total vegetative cover, species and functional group cover, as well as richness and diversity showed a correlation with inter annual rainfall variability. Had a variety of system components not been monitored, inaccurate conclusions may have been arrived at in terms of the systems' equilibrium or non-equilibrium nature. As a result, the authors in this particular instance were unable to assign equilibrium or non-equilibrium status to any of the systems which they investigated, in particular the mountain steppe. Instead, systems were classified in terms of the extent to which they displayed equilibrium and non-equilibrium traits, providing further evidence for classification according to a continuum. Similar variability in different system component response to internal and external influences was encountered by Kochy and Wilson (2004).

The operation of equilibrium and non-equilibrium processes within a system, and the prominence of each at different spatial scales, as contemplated above, corresponds with Wiens' (1984 (cited by Briske *et al.* 2003)) assumptions regarding the distribution of ecosystems along a continuum linking equilibrium and non-equilibrium extremes. The following are examples of recent publications supporting the existence of such a continuum:

1. Fynn and O'Connor (2000): In a trial, the objective of which was to evaluate the relative influence of rainfall and grazing on animal and vegetation dynamics, they found that while rainfall had the greatest impact on species composition its impacts were ameliorated by the different grazing treatments. The study states that the 'patterns of compositional change supported a state-and-transition model'.
2. Fernandez-Gimenez and Allen-Diaz (1999): The study investigates the applicability of non-equilibrium models to the desert steppe (Mean Annual Rainfall (MAR) – 95mm; Co-efficient of Variation (CV) = 47-50%), steppe (MAR – 200mm; 28%<CV%<50%) and mountain steppe (MAR – 230mm;

CV% = 28%) systems in Mongolia. The relative conformity of vegetation response to internal and external influences varied among these three steppe systems, each of which displayed equilibrium and non-equilibrium traits to varying extents.

3. O'Connor and Roux (1995): The study assessed vegetation changes in semi-arid (MAR = 361mm) grassy dwarf shrubland in the Karoo from 1949 – 1971. Different ecosystem components responded differently to internal and external forces. In particular, annual and short-lived perennials showed high correlation with inter annual rainfall while longer-lived perennial plants were influenced by the various grazing treatments.
4. Anderson and Inouye (2001): The study investigated long-term changes in abundance and distribution of major species and life forms in the sagebrush steppe of North America. In a typically semi-arid environment (MAR = 220mm) the authors found that there were no long term correlations between the changes observed in plant density and precipitation patterns as one would expect in a non-equilibrium environment. Furthermore, the authors state that while there were instances where high cover corresponded with wet periods, deeper investigation did not uncover individual species whose population closely tracked precipitation patterns.
5. Fuhlendorf and Smeins (1997): In a study undertaken at the Sonora Research Station (56km south of Texas – MAR = 600mm (range from 156mm to 1054mm) three grazing intensity treatments were applied to the veld to assess long term vegetation trends in relation to various grazing regimes and weather variation. At the spatio-temporal scale of the study, it was found that the dynamics of the veld were 'primarily driven by grazing intensity' but that 'precipitation was responsible for variation in production and basal area fluctuations'. The paper states that rainfall's primary influence was an 'accentuation of grazing intensity in the heavy grazed treatments' which is in direct contrast to the findings of Fynn and O'Connor (2000) where the influence of rainfall was ameliorated by grazing intensity. The study provides an example of a system where, because of slightly higher and perhaps less variable rainfall, relations have been able to develop to the extent that the system shows conformance more to the equilibrium model than the non-

equilibrium model. This conformance is expected in rangelands experiencing high mean annual rainfall.

The idea of a continuum draws away from the “either/or” classification of ecosystems and classifies systems rather according to the extent to which equilibrium and non-equilibrium principles prevail. An ecosystem’s position along the continuum contemplated above is determined largely by climate or more accurately, the extent to which climate allows a relation to develop between herbivores and the vegetation. Literature relevant to the contemporary debate, and experience gained in analysis of the Nortier grazing trial, has made it apparent that the classification of a rangeland system is often largely a function, in addition to the spatial and temporal scale, of both the trial/experiment design (which includes which vegetation components are monitored) and the analysis tools used to assess data. If a continuum is to be assumed, and communities are to be positioned along this continuum according to the relative influence of internal and external forces, then it is vital that trials are designed and analysed in such a way that they expose all variation within a system and record as many possible causes of this variation.

2.4.4 The State and Transition Model and the Continuum

‘The state and transition model (Westoby *et al.* 1989) describes vegetation...as a catalogue of alternative states’ (Whalley 1994). It is a model which has been developed to better account for non-linear, non-equilibrium plant community dynamics (Westoby *et al.* 1989). It is a common misconception that the state and transition model was intended to replace the range model. Rather, its design is able to incorporate both equilibrium and non-equilibrium principles of vegetation dynamics with transition between states being caused by both natural events such as weather or fire and by management actions such as a change in stocking rate or fertilization (Westoby *et al.* 1989; Briske *et al.* 2003). This misconception may have fuelled criticism of the rangeland model when in fact the state and transition model’s ability to incorporate many of the principles of the range model should have lead to an earlier realisation that the two models are not mutually exclusive. The incorporation of the range model into the state and transition model and the extent to which its principles apply in various systems is analogous to the notion of a rangeland continuum existing between equilibrium and non-equilibrium extremes.

The state and transition model differs from the range model in that it is multivariate rather than univariate, and incorporates, in addition to grazing, the influence of climate and fire (Westoby *et al.* 1989; Briske *et al.* 2003). The stochastic impacts of fire and climate, for example, may be followed by fluctuations in floristic composition during which negative feedback relations develop between certain plants or plant components and herbivores following the external disturbance (Whalley 1994). Furthermore, the transition between stable 'states' caused by, for example, inter annual variability in rainfall, may be underlain by a directional trend associated with the range model which also represents a transition between two stable 'states' (Figure 2.3) (Westoby *et al.* 1989; O'Connor and Roux 1995; Illius and O'Connor 1999). The degree of fluctuation in climate influences the extent to which negative feedback loops are able to develop and as a result the extent to which a system, when analysed, appears equilibril (dynamics driven by internal influences) or non-equibril (dynamics driven by external influences). In systems subject to dramatic inter annual climatic variation, key resources provide a consistent source of food for herbivore populations (Illius and O'Connor 1999). While analysis may show an insignificant relation between herbivore populations and the system as a whole, closer examination may reveal that beneath the veld component fluctuating in response to inter annual variability lies a resource or component of the veld, the key resource, which is more stable and which changes directionally over time in response to grazing.

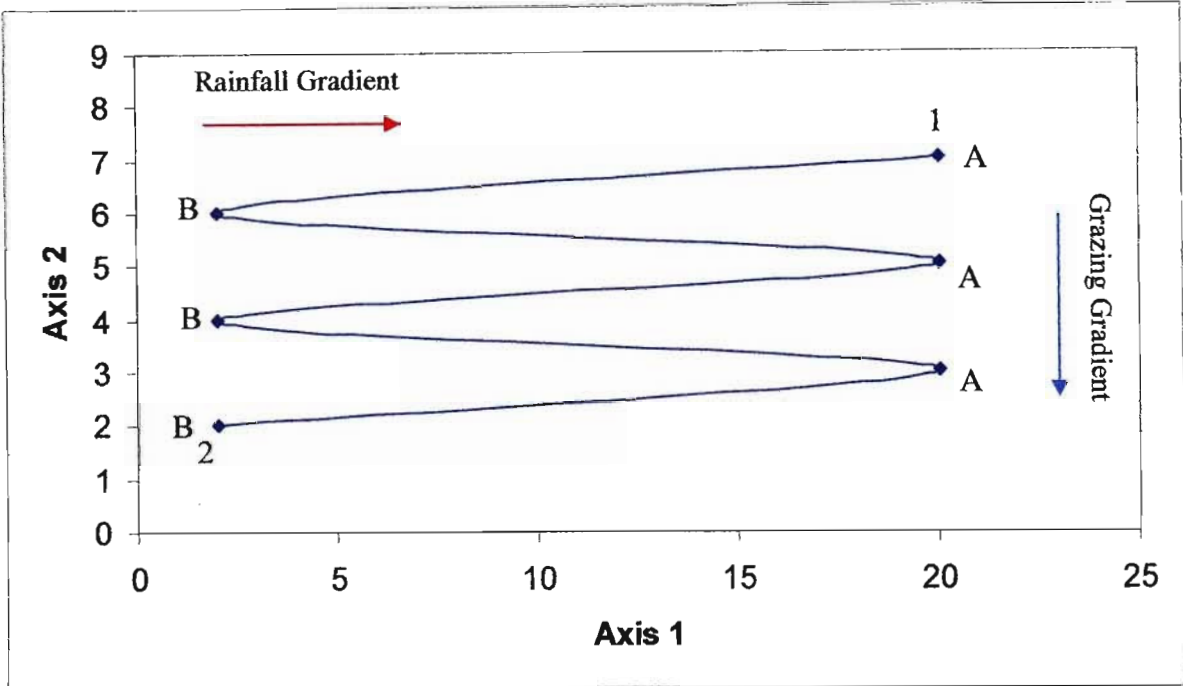


Figure 2.3: Ordination diagram showing typical trajectory of plots responding to highly variable rainfall (or other external variable) as well as the influence of grazing. Point 1 represents vegetation prior to the application of a grazing trial and point 2 vegetation after 8 years of grazing application (ordination based on hypothetical data to illustrate the point). Point A and B denote different stable states in high and low rainfall years respectively.

Figure 2.3 (conceptual ordination diagram for explanatory purposes) is included to illustrate how the state and transition model incorporates certain principles from the range succession model. The ordination diagram (Figure 2.3) depicts typical fluctuation along axis 1 (which captures the main variation in a data set) of a single treatment over time in response to fluctuating rainfall (especially in semi-arid systems). In the illustrated system, two dominant transitions exist between alternative states (transition between state A and state B; transition between state 1 and state 2). Alternative state A signifies veld in a year with above average rainfall (with a high abundance of annuals and short-lived perennials) and state B, veld in a year of below average rainfall (with a low abundance of annuals and short-lived perennials) (similar to that encountered by O'Connor and Roux (1995)). State A and state B, the two predominant alternative states, are a function of rainfall and are distinguishable by the relative abundance of annual and short-lived perennial grass species within the plant community. In addition to the observed inter annual fluctuation between state A and B, is a relation which develops between herbivore populations and the key resource (Illius and O'Connor 1999). This relation is illustrated by the directional movement of

the rangeland in ordination space from state 1 to state 2 along axis 2 in response to grazing, a transition which takes far longer than the transition between state A and state B. In systems subject to dramatic fluctuations caused by highly variable environments, in particular rainfall variability, these transitions (between state 1 and state 2) may only be revealed following the partialling out of predominant variation by means of specialised statistical techniques (O'Connor and Roux 1995).

A state and transition model would distinguish between state A and state B based on the relative abundance of species responding to inter annual variability, the transition between which would be based on above or below average annual rainfall. The long term directional trend however caused by grazing over time (transition from state 1 to state 2) would be made evident by gradual increases and decreases in the abundance of species responding to the grazing influence (Vorster 1999). The conceptual model (Figure 2.3), generated based on the review of various experiments in semi-arid systems, serves to highlight the importance of using both equilibrium and non-equilibrium models to describe trends and transitions within a system, both of which can be incorporated by the state and transition model (Westoby *et al.* 1989).

The extent to which the transitions within the state and transition model are a function of equilibrational processes i.e. grazing, or non-equibrational processes such as inter annual rainfall, would determine the position of a system on the equilibrium/non-equilibrium continuum. The system defined by Fynn and O'Connor (2000) for example, would lie nearer the non-equilibrium pole of the continuum while the system examined by Fuhlendorf and Smeins (1997) would be positioned nearer the equilibrium pole. While the relative influence of internal and external forces differs between the two systems, both systems can be described using state and transition models.

2.4.5 *Key Resources and the Catalogue of States*

Most rangelands as with most forms of vegetation have a catalogue of stable states (Westoby *et al.* 1989; Whalley 1994). Allen-Diaz and Bartolome (1998), in their assessment of the applicability of classical and state and transition models in the Sagebrush-Grassland in south eastern Oregon (MAR = 255mm and varied between 152mm and 406mm/annum), found that various transitions between states were instigated through the application of a variety of disturbances. These disturbances

included burning, ploughing and spraying each of which resulted in a transition, over a ten year period, to a distinctive stable state. Various states were classified according to the dominant species i.e. that species which responded positively to the relevant disturbance.

In systems comprising plants or plant groups (perennials vs. annuals; shrubs vs. grasses) which fluctuate in response to various external disturbances (which leads to transitions between states) there are suites of species which do not fluctuate to the same degree as others. These species constitute the key resource as described by Illius and O'Connor (1999). The key resource comprises those species which do not respond dramatically to external disturbances causing the transition between states. Because fluctuations (transitions) between different states are caused by different disturbances, key resources associated with different transitions differ in terms of their species composition. These key resources by means of their consistency provide a resource on which grazers can depend, particularly in semi-arid environments subject to high inter-annual rainfall variability (Illius and O'Connor 1999). As a result, these key resources may display a trend which correlates to grazing and which itself constitutes a transition to a new state. The state and transition model is able to incorporate both the dramatic fluctuations associated with inter annual variability and the underlying relation between herbivores and key resources and hence provides a useful means of describing and predicting occurrences in semi-arid environments.

Briske *et al.* (2003), in their comprehensive critique of current paradigms, suggests that a paradigm shift has not taken place but rather that the inadequacies of certain models in explaining certain systems has instigated a more 'comprehensive interpretation of vegetation dynamics along the equilibrium/non-equilibrium continuum'. They suggest that the 'rangeland debate should be redirected from the dichotomy between paradigms to one of paradigm integration' (Briske *et al.* 2003). This review, which has dealt with literature relevant to both equilibrium and non-equilibrium models, also points in the direction of a classification system which does not distinguish between equilibrium and non-equilibrium but rather the extent to which their principles apply in a given system. The likelihood of any natural system not being influenced by stochastic environmental events over the long term is as small as the possibility of a system existing where herbivores have no influence on the veld

resource. Instead, all systems exist somewhere in between these two extremes, the exact position of which is dependant on climatic variability. The interpretation of a system in terms of its equilibrium/non-equilibrium status is influenced by the spatial and temporal scale at which they are observed as well as trial design and analysis.

For systems to be effectively categorised the type and degree of analysis needs to ensure that it adequately exposes all the variation within a system and does not introduce any form of bias towards equilibrium/non-equilibrium principles. This bias can be predominant in systems dominated by non-equilibrial processes and can mask the less dramatic and often more long term variability induced by internal influences, most commonly grazing.

The Nortier data set is one which, based on criteria from Briske *et al.* (2003), due to the combination of semi-aridity and the highly variable rainfall, is expected to display non-equilibrial traits. Numerous investigations undertaken in semi-arid environments which are similar from a mean annual rainfall and rainfall variability perspective (O'Connor and Roux 1995; Fynn and O'Connor 2000) have yielded results which highlight the predominance of non-equilibrial behaviour. While this is the case, grazing has been shown to have an influence on species composition in grazing trials undertaken in the semi-arid Karoo (Donaldson 1986; Skinner 1996; du Toit 1998). The analysis of the Nortier data set aims to assess and expose variation within the Nortier rangeland, through appropriate statistical methods, and attribute as much of this variation to measured environmental variables and grazing treatments. The extent to which these two influencing factors account for the variation in species composition, exposed through ordination, will give an idea of the rangelands position on the equilibrium/non-equilibrium continuum.

2.5 Grazing Trials in the Karoo: Findings and Implications for Veld Management

Grazing trials undertaken in the Karoo were reviewed in order to obtain a better understanding of the influence of various grazing regimes (stocking rate, continuous versus rotational grazing) on veld condition and animal production. 'According to research and experience, it is clear that the application of correct stocking rates and rotational grazing as well as the diversification of stock (including game), are some of

the major veld management tools which can be used to achieve effective utilisation for optimal animal production without veld deterioration in the long term' (Vorster *et al.* 1983). This statement identifies not only the two main objectives in livestock production but also three tools with which to achieve them.

Of the various management principles implemented by livestock farmers in the Karoo, the strengths and weaknesses associated with continuous and rotational grazing regimes appears to have received the most substantial attention. Numerous authors (Coetzee 1937; Tidmarsh 1952; Acocks 1966; Roux 1968; Roux *et al.* 1981; Roux and Vorster 1983; Vorster *et al.* 1983; Hoffman 1988; O'Connor and Roux 1995; Skinner 1996; du Toit 1998; Beukes and Cowling 1999) provide insight into the impact of various grazing regimes on botanical composition, veld condition and animal production in the Karoo.

2.5.1 Continuous versus Rotational Grazing

The literature dealing with the topic of veld utilisation for animal production in the Karoo is focused largely on the implementation of different grazing regimes (i.e. continuous versus rotational) to manipulate both animal production and veld condition. The consensus among authors on the topic of continuous versus rotational grazing is that continuous grazing even at low stocking rates should not be applied to Karoo veld (Tidmarsh 1952, Roux and Vorster 1983, Donaldson 1986, du Toit 1998). The reason behind this recommendation, and why continuous grazing is considered to be detrimental can be attributed to the selective feeding that arises when herds of animals are kept continuously on large tracts of, often heterogenous, veld (Tidmarsh 1952). The negative influence of continuous grazing is further emphasized by Coetzee (1937), who states that selective grazing results in the 'gradual disappearance of the most nutritive and palatable plants' and consequent veld degradation. The problems associated with continuous grazing have lead to the development and implementation of various rotational grazing regimes in the Karoo. Hoffman (1988) states that rotational grazing involves the use of the group camp system whereby animals are moved in a structured, rotational manner between two or more paddocks for fixed periods during the year. It is believed that the structuring of grazing regimes in this manner has numerous advantages both in terms of maintaining veld condition (Coetzee 1937; Tidmarsh 1952; Donaldson 1986; du Toit 1999) and improving

animal production in terms of average daily gains (ADG) (Roux 1968; Roux et al. 1981; Vorster et al. 1983; Donaldson 1986). The success of rotational grazing, in terms of maintaining veld condition, is attributable to and indeed reliant on the partitioning of paddocks in such a way as to limit heterogeneity thereby reducing the degree of selective grazing. While rotational grazing regimes appear to be favoured by rangeland scientists for application throughout the Karoo, recommendations in terms of their design and implementation vary from region to region. Roux (1968) and Vorster (1999) make recommendations specific to the arid winter rainfall areas of the Karoo, the details of which are discussed later.

Hoffman (1988) paid significant attention to the principles of non-selective grazing (NSG) and short duration grazing (SDG) in the Karoo. Non-selective grazing involves the application of high stocking rates for relatively short periods of time (maximum of two weeks) following which animals are removed from the paddock, affording it a rest period of about six weeks up to a year (Hoffman 1988). The theory behind NSG is that the application of high stocking rates to restricted areas forces animals to graze on both palatable and unpalatable species thereby limiting selective grazing. By limiting selective grazing, any competitive advantage which unpalatable species may have over palatable species in systems to which grazing is applied is minimised. This would have positive implications for the maintenance of veld condition and as a result animal production. Hoffman (1988) does state however, that the application of NSG, should it be applied in the Karoo, would require significant expertise for it to be successful. The general feeling among authors who have dealt with the topic is that NSG has a negative influence on veld condition in the Karoo. In fact apart from Acocks (1966), whose interpretations were by his own admission based on 'data having an indirect bearing', most authors have condemned the use of NSG in the Karoo, most emphatically Roux and Vorster (1983).

2.5.2 *Species composition and veld condition*

One of the two major requirements for achieving sustainable livestock production outlined by Vorster *et al.* (1983) is that of maintaining veld condition over the long term. The importance of sustainable livestock production to farmers in the Karoo is highlighted by the numerous trials which have assessed the impact of various grazing regimes on veld condition, both species composition and structure. Indeed, the 28.4

million hectare extent of the Karoo Agricultural Region itself justifies the need to ensure productive and sustainable development in this region (Roux *et al.* 1981). The most notable and lengthy investigation into the influence of rotational and continuous grazing on Karoo veld was undertaken by du Toit (1998) and involves the renowned 'Camp Number 6' grazing trial at the Grootfontein Research Station near Middelburg in the Eastern Cape. du Toit (1998) assessed the impact of various forms of continuous and rotational grazing on the veld and the notion that a combination of rotational grazing and resting regimes outperforms continuous grazing, from both a veld condition and animal production perspective. Both Donaldson (1986) and du Toit (1998) agree that the evidence provided by the 'Camp Number 6' grazing trial confirms that the application of high and medium stocking rates on a continuous basis are detrimental to Karoo veld from a veld condition perspective. du Toit (1998) recommends the implementation of the three-paddock rotational grazing system combined with a rotational rest system and states that the implementation of this system surpasses continuous grazing in terms of maintaining veld condition.

Both du Toit (1998) and Vorster *et al.* (1983) found the application of continuous and high frequency defoliation detrimental to the veld, whereas the implementation of a rotational grazing regime, in which veld is afforded rest periods, appeared to have a positive impact on the veld's condition. Roux and Vorster (1983) state unequivocally that over the long term the rotational grazing regimes in the Karoo appear superior to continuous grazing from a veld condition perspective. The recommendation of rotational grazing strategies by both Roux (1968) and Vorster (1999) further illustrates the superiority of this grazing strategy in the Karoo environment.

In terms of species composition, Skinner (1996), in grazing trials applied near Graaff Reinet, found that under continuous grazing by sheep the palatable shrub component of the veld suffered a decrease in abundance causing a decline in veld condition. This impact of continuous grazing by sheep on the shrub component encountered by Skinner (1996) was also evident in du Toit (1998) where continuously grazed plots experienced a decrease in the shrub component in favour of grasses. From a veld condition perspective, the continuously grazed plots in du Toit (1998) exhibited further signs of veld deterioration such as the development of bare areas (a consequence of selective grazing) and an increased relative abundance of unpalatable

grass species. In the plots grazed under a rotational grazing regime it was found that the Karoo bush component flourished most in plots grazed during the growing season with the grass component becoming more dominant as grazing approached the dormant season (du Toit 1998).

Karoo veld subject to grazing, and particularly high intensity grazing, benefits from the implementation of extended rest periods (Beukes and Cowling 1999). Skinner (1996) states that 'Rest periods of 12 months or even longer should be a *sine qua non* for any system of veld utilisation in the lower rainfall areas of the Karoo'. du Toit (1998) also found that veld under rotational rest regimes (12 month rest periods) performed better in terms of veld condition than veld without rest, and in fact recommended the inclusion of rest periods in rotational grazing strategies. Furthermore, Vorster (1999) recommends that in all Karoo veld types receiving approximately 200 mm/annum of rainfall or less, that long rest periods (12 months or more) be implemented as a part of the grazing strategy.

Consensus on which grazing regime is most appropriate from a veld condition perspective undoubtedly favours rotational grazing regimes integrated with the application of suitable rest periods. Applying rotational grazing regimes however may not constitute a feasible alternative to all livestock farmers in the Karoo who may find it more convenient to continuously graze their livestock throughout the year or may find it impossible to implement a formal grazing rotation. In circumstances where continuous grazing is unavoidable, the application of moderate stocking rates (relative to the carrying capacity) is crucial (Roux 1975 (cited by Vorster *et al.* 1983)) in terms of maintaining veld condition and animal production (Roux 1964, Baard 1978 (cited by Vorster *et al.* 1983)).

2.5.3 *Animal production*

There are three variables that require consideration when attempting to optimise animal production: stocking rate, rotational versus continuous grazing and animal diversification (Vorster *et al.* 1983). Animal diversification, in terms of the species and/or the breed of livestock being stocked, is not relevant to the Nortier grazing trial as only Dorper ewes were grazed during the trial. In terms of stocking rate, Roux (1964 (cited by Vorster *et al.* 1983)) found that sheep flocks grazing continuously at

moderate stocking rate outperformed those at high stocking rates in terms of gains per animal (for body mass, carcass mass etc.). Flocks grazing the same veld at high stocking rates however outperformed those at moderate stocking rates in terms of gains per hectare (Roux (1964 (cited by Vorster *et al.* 1983))). This finding is anticipated, considering the Jones and Sandland model proposed in Jones and Sandland (1974 (cited by Morris, Hardy and Bartholomew 1999)) which depicts the relation between stocking rate and individual animal performance (Morris, Hardy and Bartholomew 1999), and is a theme evident in much of the literature assessing the benefits of rotational grazing over continuous grazing in terms of animal production. For example, Hoffman (1988) cites Tidmarsh (1951) as having concluded that rotational grazing regimes when compared to continuous grazing strategies did not improve animal production. Roux (1968), Bedford and Roberts (1975 (cited by Hoffman 1988)), Roux *et al.* (1981), Roux and Vorster (1983) and du Toit (1998) however, all found benefits to animal production under rotational grazing regimes.

It is important in terms of stocking rate, for all grazing regimes, that the 'economic optimum stocking rate' is achieved. The economic optimum stocking rate exists at a stocking rate where the balance that exists between gains per hectare (kg) and average daily gains per animal (kg) results in maximum economic return as depicted in the Jones and Sandland Model proposed by Jones and Sandland (1974 (cited by Tainton 1999)). From the literature, it would appear that the optimum point from both an animal production (i.e. economic optimum stocking rate) and veld condition perspective in the Karoo exists at a moderate to high stocking rate, relative to the carrying capacity, under a rotational grazing and resting regime.

Evidence in the literature supporting rotational grazing over continuous grazing in terms of animal production is inconclusive. The same cannot be said for literature assessing the advantages and disadvantages of continuous and rotational grazing by sheep on the condition of Karoo veld which indisputably supports rotational grazing and resting strategies. The maintenance of veld condition constitutes the cornerstone of sustainable livestock production and therefore must be prioritised if long-term utilisation of the veld in the Karoo is to be achieved.

2.5.4 Conclusion

The majority of research undertaken in the Karoo in terms of grazing management recommends the implementation of two, three and four paddocks per animal herd (Roux 1968; du Toit 1998; Vorster 1999) rotational grazing systems. While contradiction regarding the superior performance of this strategy over continuous grazing in terms of animal production is apparent, the benefit in terms of veld maintenance seems significant from the literature reviewed. Because the key to sustainable livestock production involves the maintenance of the rangeland resource, rotational grazing, if feasible, appears to be the most ecologically sustainable means of livestock production in the Karoo.

The recommendations made in terms of grazing strategies to be implemented at the Nortier Experimental Farm need to be tailored to deal with the aridity and winter rainfall experienced by the Strandveld Vegetation Type. The most significant consideration is that of the active growing season which extends between March/April and the end of August/early September (Roux 1968). To compensate for the low annual and winter rainfall, Roux (1968) recommends that each paddock be afforded a winter rest period once every three years. In addition to this, it is recommended that extended rest periods of 12-14 months be incorporated into the grazing regime, commencing at the beginning of the growing season (Roux 1968; Vorster 1999).

Roux (1968) recommends a three-paddock rotational grazing system integrating a 12-month rest once every three years for the arid Karoo winter rainfall areas (Table 2.1). Paddocks A, B and C as indicated below (Table 2.1) should be configured in such a way as to minimise veld heterogeneity and consequently selective feeding.

Table 2.1: A three-paddock rotational grazing system incorporating 12-month rest periods every three years (paddocks A, B and C) (Roux 1968).

Grazing Year	Months and Paddocks											
	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
1 st	A	A	A/B	B	B/A	A	A	B	B	B/C	C	C
2 nd	B	B	B/C	C	C/B	B	B	C	C	C/A	A	A
3 rd	C	C	C/A	A	A/C	C	C	A	A	A/B	B	B

The three-paddock system recommended by Roux (1968), in addition to providing the advantages shown by the literature to be associated with infrequent defoliation, allows flexibility during the frequent dry periods which characterise the arid Karoo winter rainfall areas. This flexibility allows animals to be moved into paddocks containing surplus feed in instances where prolonged dry spells have lead to a shortage of forage. Roux (1968) recommends that during dry periods herds should be placed in paddocks with the highest abundance of shrubs first, followed by paddocks dominated by grass species. The logic behind this recommendation is that shrub species lose their leaves early during periods of drought and need to be utilised as soon as possible. Grass species however, tend to remain palatable and edible for a longer period and should be utilised only once the shrub component has been exhausted (Roux 1968). Following drought the veld should, if possible, be afforded a six week period of no utilisation, during which time stock should be provided with supplementary feed (Roux 1968, Danckwerts and Stuart-Hill 1988).

The management principles recommended by the literature for sustainable livestock production in the arid winter rainfall regions of the Karoo provide the foundation upon which a grazing management plan for the Strandveld Vegetation Type can be developed. The integration of these principles with the findings of the statistical analyses investigating the influence of various season of grazing and stocking rate treatments on the dynamics of the Nortier rangeland, enable sound management recommendations to be made for sustainable livestock production in the Strandveld rangeland.

CHAPTER 3: METHODOLOGY

The Nortier data set consists of 12 treatments, each comprising a different combination of stocking rate (low - 0.216 SSU/ha, medium - 0.316 SSU/ha and high - 0.416 SSU/ha) and season of grazing (spring, summer, autumn and winter) applications, which have been monitored over a period of nine years. Species composition surveys were carried out using the descending point method (Roux 1963) with approximately 500 recordings being taken per sample at 1m intervals along a length of non-stretch rope. 'Bare ground' was included as a species (Species 74), which added an absolute abundance facet to the data set. Species composition data collected during the month of August was analysed for this project. A variety of statistical methods, particularly methods used to deal with multivariate data gathered over time, were reviewed prior to the analysis of data to ascertain which method best suited the Nortier data set. Each of the methods reviewed is based on different assumptions and can be used with varying success, depending on the requirements. Naturally, it is important that the most effective methods are chosen to obtain the required information.

The statistical procedures employed by Borcard *et al.* (1992) and Anderson and Gribble (1998), which partitioned variation in species composition into independent components (environmental, spatial, temporal), was given significant attention in the review of statistical literature undertaken prior to data analysis. The methods presented by Borcard *et al.* (1992) and developed by Anderson and Gribble (1998) did provide an initial overview of the Nortier data set by partitioning the explained variation into temporal, environmental (rainfall) and treatment categories. Their analysis however failed to provide a detailed understanding of the manner in which the various treatments influenced the species composition of the Nortier rangeland.

Min/Max autocorrelation factor analysis (MAFA) and dynamic factor analysis are related statistical tools designed specifically to deal with time series data. By extracting the main trends in the data and correlating response and explanatory variables to these trends the techniques expose both the dynamics which are taking place in the data set as well as the causal factors for these dynamics. Both of these methods however, have limitations when it comes to data sets which contain more

than one multivariate treatment, the dynamics of which are a function both of the treatment variable (which remains the same from year to year) and external variables such as rainfall (which fluctuates from year to year). The use of MAFA as a technique for analysing data is also suggested for data sets which stretch over a longer time frame than that which occurs in the Nortier data set. The combination of these two shortcomings meant that neither MAFA nor dynamic factor analysis were employed during the analysis of the Nortier data set.

The review of literature dealing with the analysis of multivariate data revealed ordination as being the one statistical tool with the capacity not only to accurately assess and quantify the variation within the species composition data but also to effectively attribute the variation to various internal and external forces. This characteristic was important in that it enabled the assessment of the extent to which equilibrium and non-equilibrium principles governed the dynamics of the Nortier rangeland. Furthermore, the ordination methods outlined by ter Braak and Šmilauer (1998) have the capacity to deal with the temporal component of the data set through the application of split plot design principles. The advantage of analysing the data set as a split plot design (with whole plots comprising the various treatments and split plots constituting samples collected at yearly intervals) is that one is able to account for temporal autocorrelation between whole plots (ter Braak and Šmilauer 1998).

The first step when analysing data using ordination is gauging whether the data conforms to a linear or unimodal response. The reason for this is that the two appropriate ordination methods, namely principal components analysis (PCA) and correspondence analysis (CA) are chosen according to this characteristic of the data. Typically, CA can analyse data sets conforming to a linear or unimodal response whereas the PCA is restricted to the analysis of linear data. Running a detrended correspondence analysis (DCA) gives an indication of the gradient lengths and in the case of the data set in question, gradient lengths were well below levels requiring the use of unimodal models (< 4 Standard Deviations (SD)). With gradient lengths below 4 SD the data can be analysed using PCA or CA. Experience however shows CA as being better suited to handling species composition data and the most appropriate method to use when dealing with data of an ecological nature.

The first routine applied to the Nortier data set was an indirect gradient analysis (correspondence analysis). The indirect gradient analysis reveals all variation within a data set and in the case of the Nortier data set facilitates the generation of trajectories depicting the movement of various treatments in multivariate space over time. The indirect gradient analysis plots samples relative to one another entirely according to species composition. As a result, it is unable to quantify the extent to which the measured explanatory variables explain the dynamics within the data set nor can it attribute any variability in the species data to these explanatory variables. Direct gradient analysis (canonical correspondence analysis (CCA)) plots samples and species as a function of the explanatory variables and while less variation in the species composition is displayed, the exact relation between variability in the species data and the various explanatory variables is exposed. The Monte Carlo permutation test, which is run as a part of the CCA, reveals whether the measured explanatory variables significantly account for the variation within the species composition data. Furthermore, examination of the correlation co-efficients and their respective t-values for each of the measured environmental variables and grazing treatments provides an indication of which variables are corresponding significantly to the main variation in the data set.

Preliminary tests (indirect analyses – correspondence analysis) showed rainfall as having a strong influence on the dynamics within the species composition data. This discovery is in line with the findings of the literature review in which the influence of rainfall on species composition in semi-arid rangelands was highlighted (O'Connor and Roux 1995; Fynn and O'Connor 2000; Briske *et al.* 2003). The correlation between rainfall and certain components within the species matrix can mask the relation which develops between grazing treatments and other components of the rangeland which do not respond to rainfall (i.e. the key resource (Illius and O'Connor 1999)). To determine the extent to which the various grazing treatments are influencing the species composition in the veld, the variation attributable to rainfall was removed from the data set (for certain analyses (partial analyses)). The partialling out of rainfall from certain analyses serves to remove, from the total variation, all variation that corresponds to measured rainfall patterns. In addition to the partialling out of rainfall variability, and in order to provide greater clarity in terms of the effect of treatment on vegetation dynamics, *Ehrharta calycina* and 'bare ground', shown by

preliminary ordinations to account for the majority of rainfall driven dynamics, were also removed from certain of the ordination analyses. The removal of *Ehrharta calycina*, the predominant grass species in the Nortier rangeland, and the 'bare ground' variable from the data set created what is referred to as the 'shrub/herb complex'. The shrub/herb complex constitutes that portion of the rangeland which responds less dramatically to rainfall and was created following the findings of initial ordinations which identified those species responding significantly to rainfall¹. The shrub/herb complex comprises predominantly large shrub species (>80% shrub species) in between which exist a variety of smaller bushes, annuals and grasses (Acocks 1988). It was created primarily to assess the trajectory of species composition samples over time in response to the various treatments without the drastic and confounding inter annual fluctuations caused by those species responding to rainfall. This allowed judgement on whether the remaining vegetation, which was not fluctuating as dramatically according to rainfall, was responding to grazing as a whole as well as during different seasons and at different stocking rates.

Prior to the application of routines suggested by O'Connor and Roux (1995) to the data, useful information about the extent to which the samples had changed and the significance of this change was obtained using Euclidean distance measures. Euclidean distance matrices were derived from the full data set (absolute abundance), relative abundance data set (re-relativised following the removal of bare ground) as well as the relative abundance data set from which *Ehrharta calycina* has been removed (re-relativised following the removal of bare ground and *Ehrharta calycina*). By using the upper confidence limit (UCL) value, obtained by averaging the Euclidean distance between samples at the beginning of the trial, it is possible to determine whether or not significant changes have occurred in the species composition of treatments over time relative to treatment 1. The UCL values are calculated by adding to the average Euclidean distance of initial samples a value, which is the product of the 1-tailed t-value (95%, n-1 d.f) and the standard error of the mean. If the Euclidean distance of samples relative to year 1 is greater than the UCL they can be considered significantly different at the 5% level.

¹ While certain other species did show a limited response to rainfall, none were as dramatic as *Ehrharta calycina* and 'bare ground'. Therefore, their removal was not required for the purposes of the analyses applied to the 'shrub/herb complex'.

The effects of rainfall are evaluated through examination of Euclidean distance graphs generated from the Euclidean distance matrix derived from the full data set. By comparing the magnitude of compositional change in the full absolute abundance data set over time (Euclidean distance) with rainfall patterns, the extent to which a relation exists between the two can be ascertained. Furthermore, examination of euclidean distance graphs generated from the shrub/herb complex enables the assessment of whether the more stable component of the vegetation is responding to grazing and the various season of grazing by stocking rate treatments.

A recent case study entitled 'Analysis of repeated observations of species composition from a factorial experiment' (Leps and Šmilauer 2003) provides important information on how repeated measure experiments should be analysed using ordination. The test recommended by Leps and Šmilauer (2003) involves a split-plot ANOVA with each repeated measure constituting a split plot within a treatment whole plot. Therefore, the repeated measures are in fact the 'within plot' factors. By structuring the analysis as such the interaction between treatment and time, which reflects the 'difference in the development of units between treatments' (Leps and Šmilauer 2003), is assessed. To extract this interaction between treatment and time Leps and Šmilauer (2003) recommends the use of plot identifiers (plot ID variables) as covariables. By adding plot identifiers as covariables (dummy variables) to the analysis, the average over years of each plot is subtracted and only the changes within each plot over time are analysed. For the purposes of the analysis, time variables were assigned to each year (0, 1, 2, 3 etc for year 1988/89, 1989/90, 1990/91, 1991/92).

The recommendations made by Leps and Šmilauer (2003) are implemented in CANOCO by restricting the CCA for 'spatial or temporal structure or split plot design'. Furthermore, the following interactions between treatment variables and time are stipulated to detect the influence of each treatment over time on each of the data sets analysed;

- Time*Spring
- Time*Summer
- Time*Autumn
- Time*Winter
- Time*Stocking rate

- Time*Stocking rate*Spring
- Time* Stocking rate*Summer
- Time* Stocking rate*Autumn
- Time* Stocking rate*Winter

The ordination methods applied to the data set are an extension of those employed by Fynn and O'Connor (2000) and O'Connor and Roux (1998) and refined according to recommendations made by Leps and Šmilauer (2003). The resulting analyses are as follows;

1. Correspondence analysis (indirect gradient analysis) applied to the entire data set.
2. Canonical correspondence analysis (direct gradient analysis) applied to the full data set, restricting for split plot design; using *plot ID* variables as covariables and stipulating interactions between explanatory variables (**CCA**).
3. Canonical correspondence analysis partialling out rainfall; using *plot ID* variables as covariables; restricting for split plot design and stipulating interactions between explanatory variables (**CCA-Rainfall**).
4. Canonical correspondence analysis partialling out rainfall; using *plot ID* variables as covariables, restricting for split plot design, stipulating interactions between explanatory variables and removing species 74 'bare ground' and species 9, *Ehrharta calycina* from the species matrix (i.e. the shrub/herb complex as defined above) (**CCA-Rainfall(-74); CCA-Rainfall(-749)**).

Ordination techniques are very useful in that they provide a means of gaining important information from large, complex data sets. While this is the case, it is important to back any findings up using other statistical procedures such as Analysis of Variance (ANOVA) (Genstat 6.1). ANOVA was used to assess the extent to which various individual species and species categories (shrub/herb complex, grasses, bare ground) increase or decrease in response to various treatments. ANOVA's were applied to the following data sets:

- Absolute abundance data set.
 - Palatable/Unpalatable component, grass component, shrub/herb complex, 'bare ground'.

- Prominent species (species which showed a response to grazing in the ordination analyses).
- Re-relativised shrub/herb complex.
 - Palatable/Unpalatable.

The analysis of the absolute abundance data set focussed on the shrub/herb complex, grasses, bare ground, prominent species as well as to a lesser extent palatable and unpalatable species. The analysis of the palatable and unpalatable categories of this data set was made difficult by the fluctuations in absolute abundance of *Ehrharta calycina* in response to rainfall. The more accurate analysis of these plant categories (palatable and unpalatable) was facilitated through the creation of the shrub/herb complex discussed later. The analysis of the absolute abundance of individual plant species shown to be changing in abundance along grazing gradients served to substantiate the findings of the ordination analyses which identified these species.

The shrub/herb complex analysed under the absolute abundance data set using ANOVA is similar to that assessed by the ordination. The difference is that it has not been relativised and hence provides an indication of how the more stable component of the vegetation is changing from a cover perspective in response to the various grazing treatments. This constitutes important information as it is the more stable shrub/herb complex that grazing animals rely on as a consistent source of forage from year to year. Because an increase in the abundance of the shrub/herb complex is only positive if the palatable component increases at a rate equal to or higher than the unpalatable component, a re-relativised shrub/herb complex is also analysed by means of ANOVA in terms of the relative abundance of palatable and unpalatable plants. The analysis of this data set provides an indication of whether the more stable shrub/herb complex is improving or degrading in terms of its palatable plant composition in response to the various grazing treatments. Through assessment and comparison of means obtained from the ANOVA applied to the absolute abundance shrub/herb complex and the relative abundance shrub/herb complex it is possible to gauge the impact of grazing on the condition of the veld (from a palatable species abundance perspective) and to make recommendations in terms of which stocking rates should be applied during which season.

As with any ANOVA, 'Repeated measures ANOVA' tests the equality of means. ANOVA procedures, however, require slight modification when looking at cases where all variables in a random sample are measured under a number of different conditions, as is the case for the Nortier data set. As the sample is exposed to each condition in turn, the measurement of the dependant variable is repeated. The use of the standard ANOVA under these circumstances is not appropriate because it fails to model the correlation between repeated measures i.e. the data violates the ANOVA assumption of independence. As a result, the 'Repeated measures ANOVA' option is applied to the data set providing results which are both more accurate and statistically sound.

The combination of multivariate (ordination and euclidean distance) and univariate (ANOVA) statistical tools ensures that not only the obvious, surface correlations between rangeland dynamics and explanatory variables are detected but also those which are less dramatic and cumulative over the long term. In so doing, the choice of statistical tools should provide a comprehensive understanding of the Nortier rangeland and insight into the role played by equilibril and non-equibril forces.

CHAPTER 4: RESULTS FROM ORDINATION

4.1 Correspondence Analysis (CA)

The correspondence analysis (CA) showed clear evidence of the importance of rainfall as an explanatory variable in semi-arid environments. The first four axes (Table 4.1) of the CA accounted for 46.3% of the variance in the species data and 56.4% of the species environment relation. Examination of the regression coefficients (Previous season (PS) rainfall: PS = -0.38 (Previous Season rainfall refers to the amount of rainfall which fell in the season prior to sampling being undertaken (e.g. winter rainfall for spring season samples)) and their respective t-values (PS rainfall = -6.13²) suggests that PS rainfall significantly explains the main variation in the data set.

Figure 4.1 gives an indication of those species with a high cumulative fit along the rainfall gradient that corresponds with axis 1 i.e. those species whose absolute abundance correlates with the PS rainfall variable. These species are 'bare ground' (Cumulative fit = 0.76), *Ehrharta calycina* (Cumulative fit = 0.76), *Tetragonia fruticosa* (Cumulative fit = 0.42), *Chaetobromus schraderi* (Cumulative fit = 0.13), *Exomis microphylla* (Cumulative fit = 0.11) and *Lebeckia multiflora* (Cumulative fit = 0.10). Examination of the various treatment trajectories (Figure 4.2) generated by this analysis shows fluctuation along axis 1, shown to be a rainfall (PS rainfall) gradient. *Ehrharta calycina*, *Tetragonia fruticosa*, *Chaetobromus schraderi* and *Exomis microphylla* increase in cover with high levels of PS rainfall while the cover of 'bare ground' and *Lebeckia multiflora* decreases (Figure 4.2). All the treatments (Figure 4.2) respond in a similar manner along axis 1 suggesting that rainfall has an overriding effect on species composition across all treatments.

² The CANOCO 4 (Ter Braak and Šmilauer 1998) manual states that explanatory variables with t-values > 2.1 along a particular axis correlate significantly with the variation along that axis.

**Table 4.1: Results of unconstrained ordinations using plot ID as a covariable
Summary**

Axes	1	2	3	4
Eigenvalues:	0.168	0.139	0.126	0.069
Species-environment correlations:	0.798	0.424	0.464	0.673
Cumulative percentage variance of species data:	15.5	28.3	39.9	46.3
of species-environment relation:	31.7	39.1	47.2	56.4

Regression/canonical coefficients for standardized variables

Time	0.1817	-0.3498	0.1552	-0.6681
SR (Stocking Rate)	0.1592	-0.3388	-0.3051	0.3966
Spr (Spring)	0.678	-0.5127	-0.0736	0.2589
Sum (Summer)	-0.4926	-0.3882	-0.056	-0.245
Aut (Autumn)	0.586	-0.486	-0.2919	0.7531
Win (Winter)	0.5896	-0.3213	-0.8261	0.9968
CS (Current Season Rainfall)	0.0567	0.1076	0.031	0.1087
PS (Previous Season Rainfall)	-0.3829	0.12	-0.1289	0.1147
CS.PS	0	0	0	0
YrP (Year Prior Rainfall)	-0.0257	-0.0802	0.0296	-0.1513
Time*SR	-0.2381	0.4458	-0.0475	0.7802
Time*Spr	-0.6123	0.4022	-0.2561	0.2747
Time*Sum	0.0407	0.1846	0.0741	0.4735
Time*Aut	-0.6033	0.4004	-0.3093	0.7497
Time*Win	-0.3046	0.3809	-0.2889	0.5139
SR *Spr	-0.5117	0.7296	0.1516	-0.2591
SR *Sum	0.6181	0.6013	0.1821	0.2421
SR *Aut	-0.3388	0.8175	0.2723	-0.8944
SR *Win	-0.2258	0.4894	0.8701	-0.9647
Time*SR *Spr	0.4477	-0.4118	0.0439	-0.2388
Time*SR *Sum	-0.1806	-0.2175	-0.2314	-0.4222
Time*SR *Aut	0.473	-0.4798	0.1741	-0.8415
Time*SR *Win	0.1921	-0.3866	0.0998	-0.5426

Table 4.1 cont.

T-values of regression co-efficients:

Axes	1	2	3	4
Time	0.3083	-0.4141	0.1924	-1.1525
SR	0.5947	-0.8828	-0.8327	1.5058
Spr	1.4707	-0.7758	-0.1166	0.5708
Sum	-1.5525	-0.8536	-0.1289	-0.7847
Aut	1.106	-0.6398	-0.4024	1.4445
Win	1.1934	-0.4537	-1.2215	2.0505
CS	1.4713	1.9471	0.5885	2.8651
PS	-6.1293	1.3397	-1.507	1.8665
CS.PS	0	0	0	0
YrP	-0.4082	-0.89	0.3446	-2.447
Time*SR	-0.3827	0.4999	-0.0558	1.2745
Time*Spr	-1.2679	0.581	-0.3873	0.578
Time*Sum	0.1225	0.3873	0.1627	1.4474
Time*Aut	-1.0636	0.4924	-0.3983	1.3431
Time*Win	-0.5756	0.5023	-0.399	0.9872
SR *Spr	-1.2997	1.2928	0.2812	-0.6689
SR *Sum	1.5701	1.0654	0.3379	0.6249
SR *Aut	-0.6161	1.0372	0.3618	-1.6533
SR *Win	-0.4739	0.7167	1.3342	-2.058
Time*SR*Spr	1.0895	-0.6991	0.0781	-0.5907
Time*SR*Sum	-0.4393	-0.3691	-0.4112	-1.0439
Time*SR*Aut	0.8078	-0.5716	0.2171	-1.4606
Time*SR*Win	0.3791	-0.5323	0.1439	-1.0884

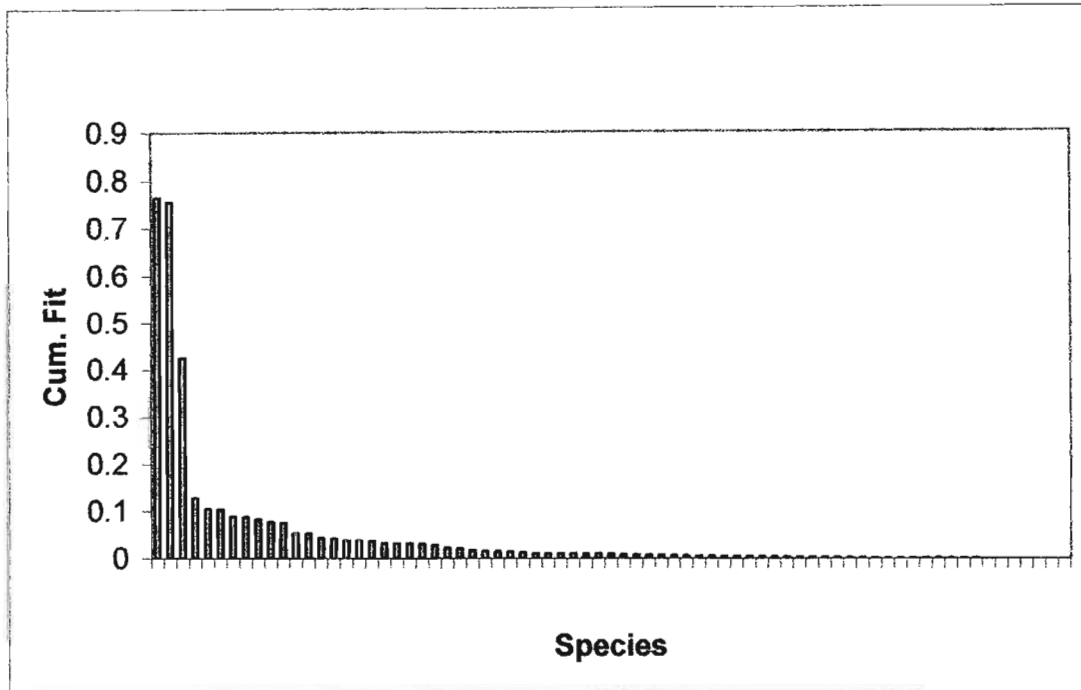


Figure 4.1: Cumulative fit along axis 1 for Correspondence Analysis applied to full data set with plot ID variables used as covariables. The first six species with the highest cumulative fit values are; 9 = *Ehrharta calycina* (0.76), 74 = bare ground (0.76), 44 = *Tetragonia fruticosa* (0.43), 5 = *Chaetobromus schraderi* (0.13), 13 = *Exomis microphylla* (0.11), 23 = *Lebeckia multiflora* (0.10).

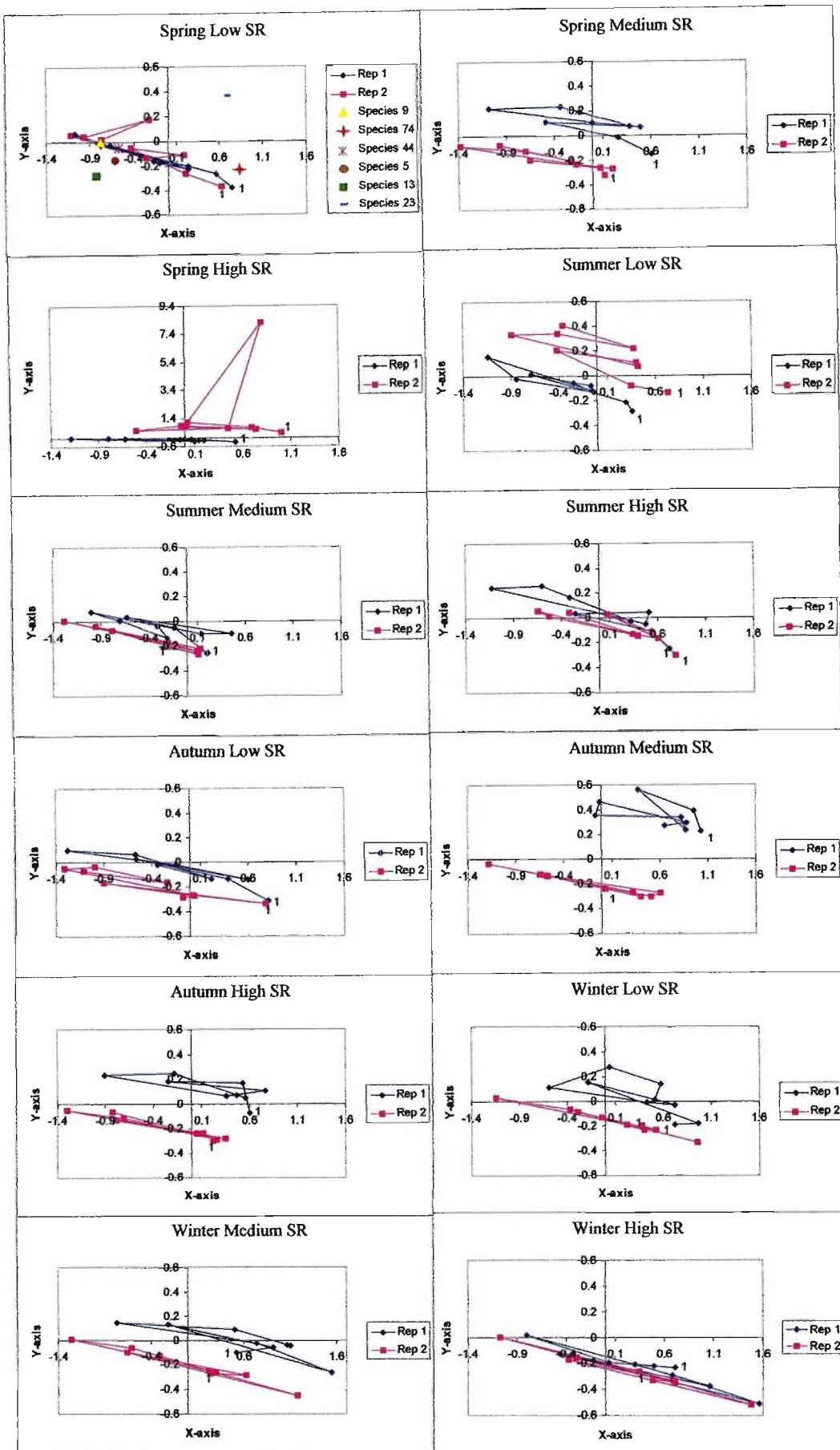


Figure 4.2: Ordination trajectories obtained from unconstrained correspondence analysis applied to full data set for treatments 1-12. Species 9, *Ehrharta calycina*, 44, *Tetragonia fruticosa*, 74, bare ground, 5, *Chaetobromus schraderi*, 13, *Exomis microphylla* and 23, *Lebeckia multiflora* show high cumulative fit values to axis 1. Previous Season rainfall explains the most variance along axis 1 with a correlation coefficient of -0.38 (t -value = -6.13). 1= treatment in year 1. Rainfall increases from right to left in each graph. Species positions depicted in Spring Low graph remain constant in all ordination plots.

4.2 Canonical Correspondence Analysis (CCA)

4.2.1 Canonical Correspondence Analysis applied to full data set

The results of the canonical correspondence analysis (CCA) applied to the full data set (Table 4.2) confirm the findings of the correspondence analysis (Table 4.1). The application of the CCA to the full data set included the use of *Plot ID* variables as covariables. The first four axes of the analysis accounted for 21.3% of the species variation and 86.9% of the species-environment relation. The most important of these axes, axis 1 (which accounts for the main gradient of variation) accounts for 15.9% of the species variation and 64.8% of the variation explained by the environmental variables. While a drop in eigenvalues from the unconstrained to the constrained analysis is evident, it is not substantial, suggesting that the explanatory variables chosen are significant in relation to the species variation (see results of Monte Carlo test). The results of the Monte Carlo tests (Table 4.3) show that both axis 1 ($p = 0.0150$) and all canonical axes ($p = 0.005$) significantly account for the variation in the absolute abundance data set. This indicates that the measured explanatory variables significantly account for the variation in the species composition data set. Examination of the canonical coefficients and their t-values for the various explanatory variables along axis 1 show PS rainfall (Canonical coefficient = 0.48, t-value = 7.88) as significantly corresponding with the main variation in the absolute abundance species composition data. The combination of the findings of the Monte Carlo test and the evidence provided through examination of the canonical coefficients and their respective t-values serve to further accentuate the importance of PS rainfall and its significance in explaining the dynamics in the Nortier rangeland.

Figure 4.3 shows the same species as having high cumulative fit values along axis 1 for the constrained analysis (CCA) as for the unconstrained analyses (CA). The cumulative fit value identifies those species whose variation corresponds most with a particular axis and gives an indication of which species are responding to the explanatory variables which correlate with that axis. It is not surprising that the same species are identified along axis 1 of the CCA and the CA as each of these axes correlated significantly with the same explanatory variable, namely PS rainfall. The similarity in the output of the two forms of analysis substantiates the significance of the influence of rainfall on the dynamics in the absolute abundance data set. Species that fluctuate significantly in response to rainfall in this system are 'bare ground'

(Cumulative fit = 0.57), *Ehrharta calycina* (Cumulative fit = 0.36) and *Tetragonia fruticosa* (Cumulative fit = 0.43) (Figure 4.3).

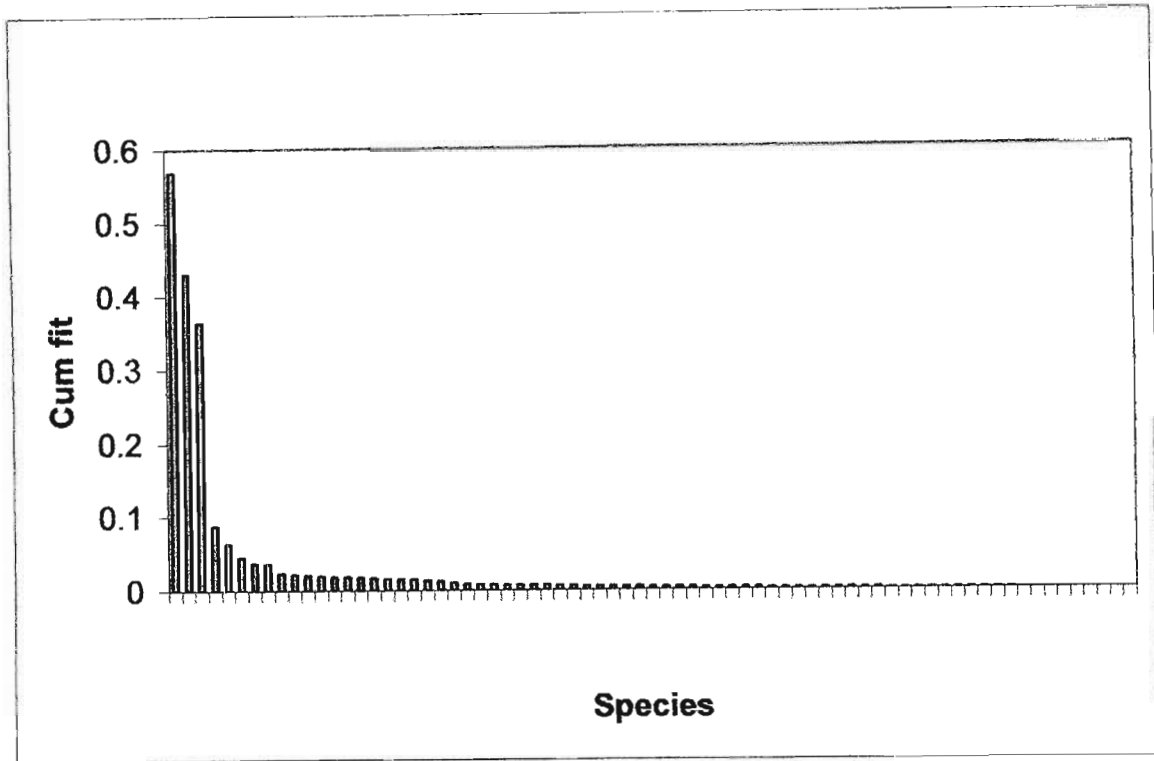


Figure 4.3: Cumulative fit along axis 1 for Canonical Correspondence Analysis applied to full data set with plot ID variables used as covariables. The first three species are 74 = bare ground (0.57), 44 = *Tetragonia fruticosa* (0.43), 9 = *Ehrharta calycina* (0.36).

Examination of the various treatment trajectories along axis 1, in both the unconstrained and constrained analysis shows very little differentiation between the treatments. The similarity of each trajectory indicates that it is not the treatments which are causing the dominant change from year to year but rather an explanatory variable common to all treatments. The CCA and CA shows this variable to be PS rainfall which causes treatment samples to move back and forth along axis 1 according to the abundance of 'bare ground', *Ehrharta calycina* and *Tetragonia fruticosa*. The results of the CCA show categorically that rainfall, and in particular PS rainfall, has a significant influence on the dynamics of the Nortier rangeland.

While the ordination diagrams (Figure 4.4) and canonical coefficients (Table 4.2) provide testimony to the dominant influence of rainfall on the dynamics within the Nortier rangeland, gradual trajectory trends and significant canonical coefficients for certain treatments along axis 2 reveal the underlying influence of grazing on the veld resource. The underlying directional trend of samples beneath the fluctuations caused by variable rainfall constitutes the most important finding of the multivariate

statistical analyses. The significance of the time*spring ($t = -3.19$), time*summer ($t = -2.93$), time*autumn ($t = -2.93$) and time*winter ($t = -3.07$) treatment variables confirm that this directional trend along axis 2 is attributable to the various season of grazing treatments and highlights the prevalence of both equilibrial and non-equilibrial dynamics in the Nortier rangeland. Thus, while the main variation is a function of rainfall, an underlying relation does exist between the veld and the various grazing treatments.

Table 4.2: Results of constrained ordinations using plot ID as a covariable

Axes	CCA				CCA-Rainfall			
	1	2	3	4	1	2	3	4
Eigenvalues:	0.104	0.022	0.008	0.006	0.039	0.006	0.006	0.005
Species-environment correlations:	0.844	0.833	0.346	0.418	0.763	0.471	0.493	0.325
Cumulative percentage variance of species data:	15.9	19.2	20.4	21.3	7	8	9	10
of species-environment relation:	64.8	78.3	83.3	86.9	58.1	67.1	75.5	83.3

Regression/canonical coefficients for standardized variables

Time	-0.1262	1.0849	2.742	-3.3105	-0.5081	4.6489	-1.2675	0.5739
CS (Current Season Rainfall)	-0.0649	-0.1398	-0.2689	-0.0368				
PS (Previous Season Rainfall)	0.4773	-0.0683	-0.2671	-0.1226				
CS.PS	0	0	0	0				
YrP (Year Prior Rainfall)	0.007	0.2457	0.2109	0.1287				
Time*SR	0.1525	-1.0531	-3.0469	2.7359	0.513	-4.3098	1.1421	-1.393
Time*Spr (Spring)	0.7158	-1.0573	-1.7418	2.97	1.1857	-3.4925	1.567	-0.186
Time*Sum (Summer)	-0.1399	-0.6684	-1.33	0.2941	0.0734	-1.8519	-0.8363	-0.5588
Time*Aut (Autumn)	0.6328	-1.14	-2.7535	3.2991	1.0816	-4.3925	1.7457	-1.0231
Time*Win (Winter)	0.3421	-1.1139	-2.1157	2.6138	0.788	-3.5051	1.2042	-0.5602
Time*SR *Spr	-0.4987	0.7101	1.6895	-2.1737	-0.794	2.7745	-1.2754	0.6435
Time*SR *Sum	0.335	0.3206	1.5307	-0.1233	0.2996	1.5942	0.5947	1.0184
Time*SR *Aut	-0.4466	0.956	3.1583	-2.6893	-0.7748	4.1767	-1.4734	1.7877
Time*SR *Win	-0.159	0.8569	2.2366	-1.9954	-0.4682	3.0442	-0.9634	1.0817

Table 4.2 cont.

T-values of regression coefficients	1	2	3	4	1	2	3	4
Time	-0.2208	2.6843	2.1329	-3.475	-0.8516	5.6121	-1.6554	0.461
CS	-1.7344	-5.2889	-3.1968	-0.5903				
PS	7.8771	-1.5933	-1.9597	-1.2138				
CS.PS	0	0	0	0				
YrP	0.1155	5.7001	1.5382	1.2662				
Time*SR	0.2527	-2.4675	-2.2444	2.7197	0.8143	-4.927	1.4126	-1.0598
Time*Spr	1.5278	-3.1913	-1.6528	3.8033	2.4246	-5.1435	2.4968	-0.1823
Time*Sum	-0.4338	-2.9305	-1.8331	0.5471	0.2181	-3.9614	-1.9354	-0.7955
Time*Aut	1.1498	-2.9295	-2.2245	3.5968	1.883	-5.5074	2.3681	-0.8537
Time*Win	0.6665	-3.0689	-1.8326	3.0553	1.4709	-4.712	1.7514	-0.5012
Time*SR *Spr	-1.2512	2.5192	1.8844	-3.2719	-1.9084	4.8028	-2.3885	0.7413
Time*SR *Sum	0.8399	1.1369	1.7065	-0.1855	0.7197	2.7583	1.1132	1.1726
Time*SR *Aut	-0.7862	2.3799	2.4719	-2.8405	-1.3068	5.0735	-1.9362	1.4451
Time*SR *Win	-0.3235	2.4656	2.0232	-2.4358	-0.9126	4.2737	-1.4633	1.0105

CCA

Analysis of full data set using a split plot experiment design

CCA-Rainfall(A)

Analysis of full data set using a split plot experiment design using rainfall covariable

Table 4.2: Results of constrained ordinations using plot ID as a covariable cont.

Axes	CCA-Rainfall(-74)				CCA-Rainfall(-74-9)			
	1	2	3	4	1	2	3	4
Eigenvalues:	0.026	0.008	0.007	0.006	0.036	0.01	0.01	0.007
Species-environment correlations:	0.769	0.385	0.39	0.504	0.788	0.369	0.424	0.521
Cumulative percentage variance of species data:	3.9	5	6.1	7	4.1	5.3	6.5	7.2
of species-environment relation:	41.9	54.6	66.4	76	43.4	56.2	68.2	76.2
Regression/canonical coefficients for standardized variables								
Time	0.701	-3.7433	-2.6915	-0.1757	0.3663	-2.6055	-3.8868	-2.672
CS								
PS								
CS.PS								
YrP								
Time*SR	-0.5252	3.8556	1.9196	0.3775	-0.2797	3.0883	3.1019	3.6713
Time*Spr	-1.4132	3.5103	2.6378	0.7184	-1.2053	2.2999	3.6587	0.0026
Time*Sum	0.1161	1.7418	0.3042	-1.4649	0.0253	1.8202	1.1596	0.9606
Time*Aut	-0.9433	3.9718	2.6712	0.7806	-0.6836	2.8971	3.7608	3.1306
Time*Win	-0.964	3.0648	2.1416	0.7136	-0.5912	2.1361	3.202	2.6626
Time*SR *Spr	0.9582	-3.1548	-1.7342	-0.8173	0.8123	-2.3323	-2.6505	-0.2173
Time*SR *Sum	-0.5997	-1.7176	0.0436	1.0484	-0.4653	-2.0083	-0.7152	-1.8305
Time*SR *Aut	0.46	-4.1661	-1.8891	-0.7785	0.2471	-3.46	-3.0759	-3.8286
Time*SR *Win	0.4616	-2.8278	-1.4626	-0.6715	0.1743	-2.1889	-2.3647	-3.0571

Table 4.2 cont.

T-values of regression coefficients

	1	2	3	4	1	2	3	4
Time	1.3528	-3.3792	-2.5095	-0.2371	0.6797	-2.0348	-3.6315	-3.6084
CS								
PS								
CS.PS								
YrP								
Time*SR	-0.9518	3.2685	1.6807	0.4784	-0.484	2.2492	2.7026	4.6234
Time*Spr	-3.0877	3.5877	2.7845	1.0974	-2.6025	2.0903	3.9781	0.0041
Time*Sum	0.3645	2.5577	0.4613	-3.2152	0.0763	2.3093	1.76	2.1073
Time*Aut	-1.7936	3.5328	2.454	1.0379	-1.2666	2.2593	3.5088	4.2217
Time*Win	-2.0163	2.9987	2.1642	1.0437	-1.1607	1.7654	3.1659	3.805
Time*SR *Spr	2.4543	-3.7798	-2.146	-1.4636	2.0308	-2.4541	-3.3364	-0.3953
Time*SR *Sum	-1.5244	-2.0421	0.0535	1.8632	-1.1074	-2.0118	-0.8571	-3.1706
Time*SR *Aut	0.849	-3.597	-1.6846	-1.0047	0.4406	-2.5973	-2.7623	-4.9696
Time*SR * Win	1.0269	-2.9429	-1.5721	-1.0446	0.371	-1.9615	-2.5352	-4.737

CCA-Rainfall(-74)

(A) with species 74 removed from analysis

CCA-Rainfall(-74-9)

(A) with species 74 and 9 removed from analysis

Table 4.3: Results of the Monte Carlo permutation tests

CCA

Test of significance of first canonical axis: eigenvalue = 0.104

F-ratio = 33.824

P-value = 0.0150

Test of significance of all canonical axes : Trace = 0.160

F-ratio = 4.473

P-value = 0.0050

CCA-Rainfall

Test of significance of first canonical axis: eigenvalue = 0.039

F-ratio = 13.404

P-value = 0.0050

Test of significance of all canonical axes : Trace = 0.067

F-ratio = 2.438

P-value = 0.0050

CCA-Rainfall(-74)

Test of significance of first canonical axis: eigenvalue = 0.026

F-ratio = 7.226

P-value = 0.0650

Test of significance of all canonical axes : Trace = 0.062

F-ratio = 1.825

P-value = 0.0900

CCA-Rainfall(-74-9)

Test of significance of first canonical axis: eigenvalue = 0.036

F-ratio = 7.690

P-value = 0.0450

Test of significance of all canonical axes : Trace = 0.082

F-ratio = 1.878

P-value = 0.0950

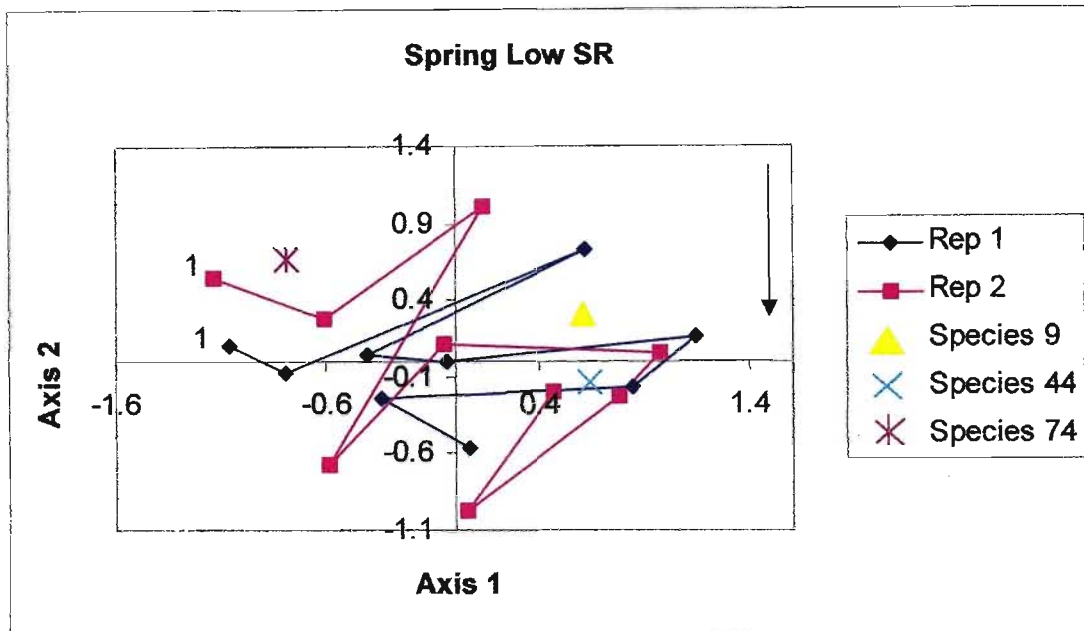


Figure 4.4a: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 1. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1. Arrow indicates grazing gradient. Species positions depicted in Spring Low graph remain constant in all ordination plots (Figure 4.4b to 4.4l).

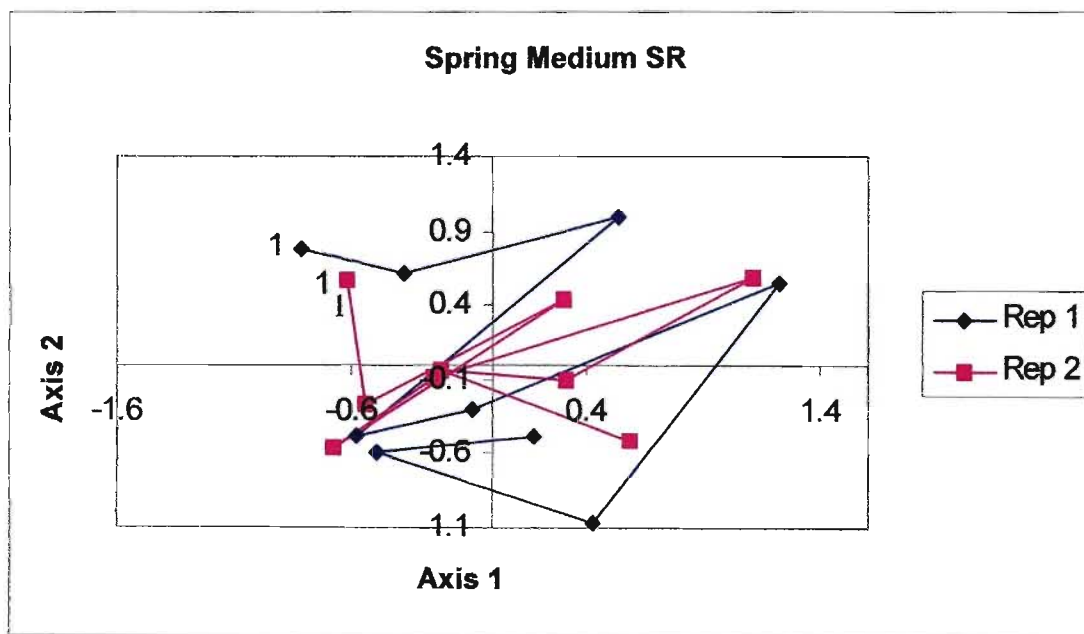


Figure 4.4b: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 2. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

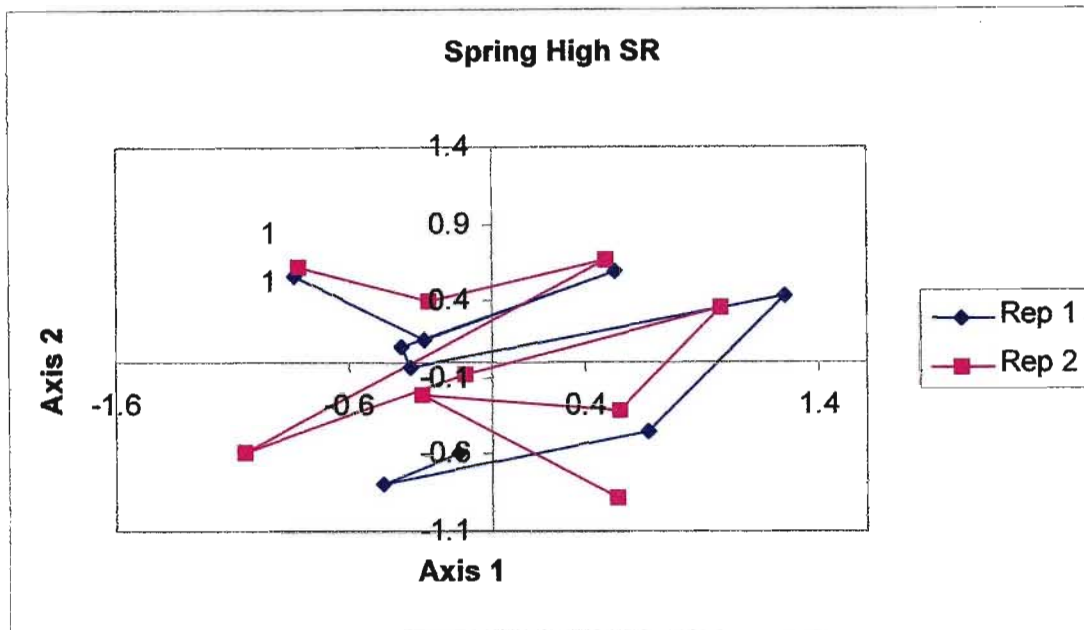


Figure 4.4c: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 3. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

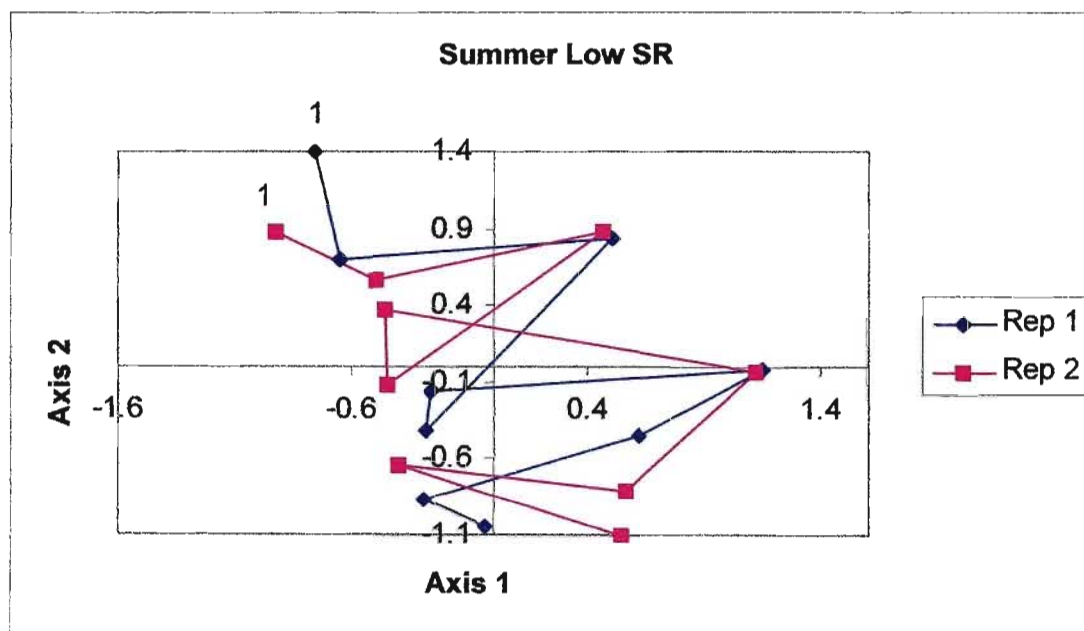


Figure 4.4d: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 4. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

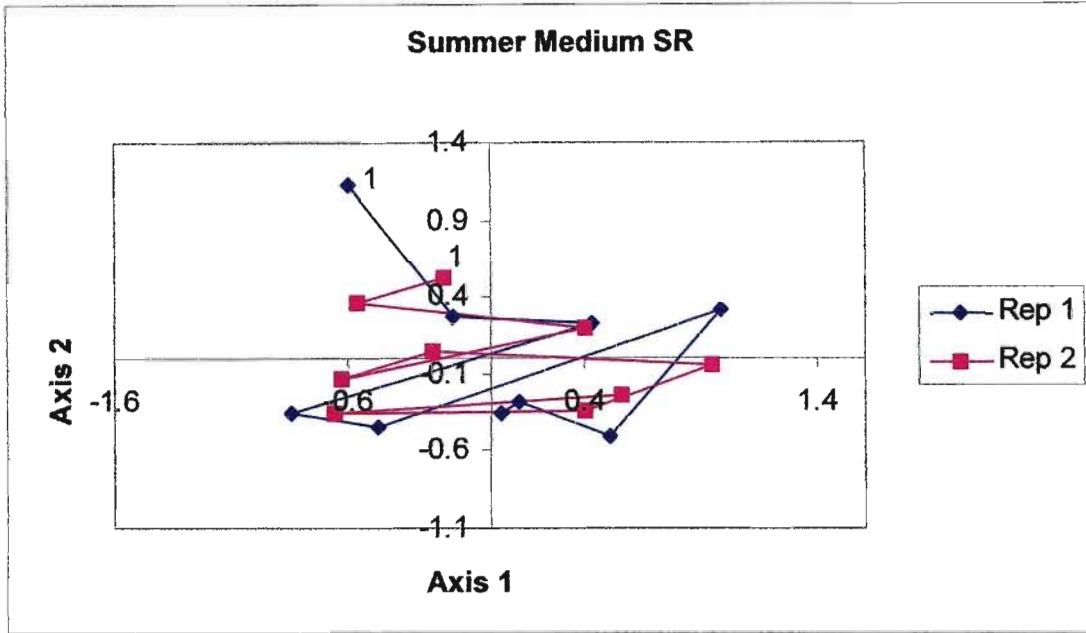


Figure 4.4e: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 5. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

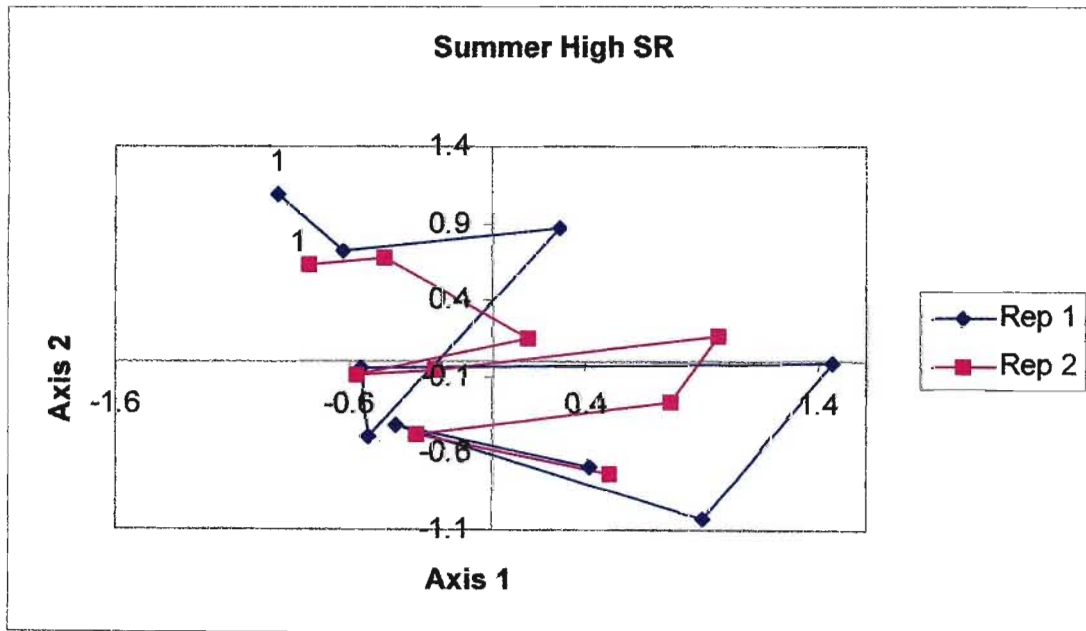


Figure 4.4f: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 6. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

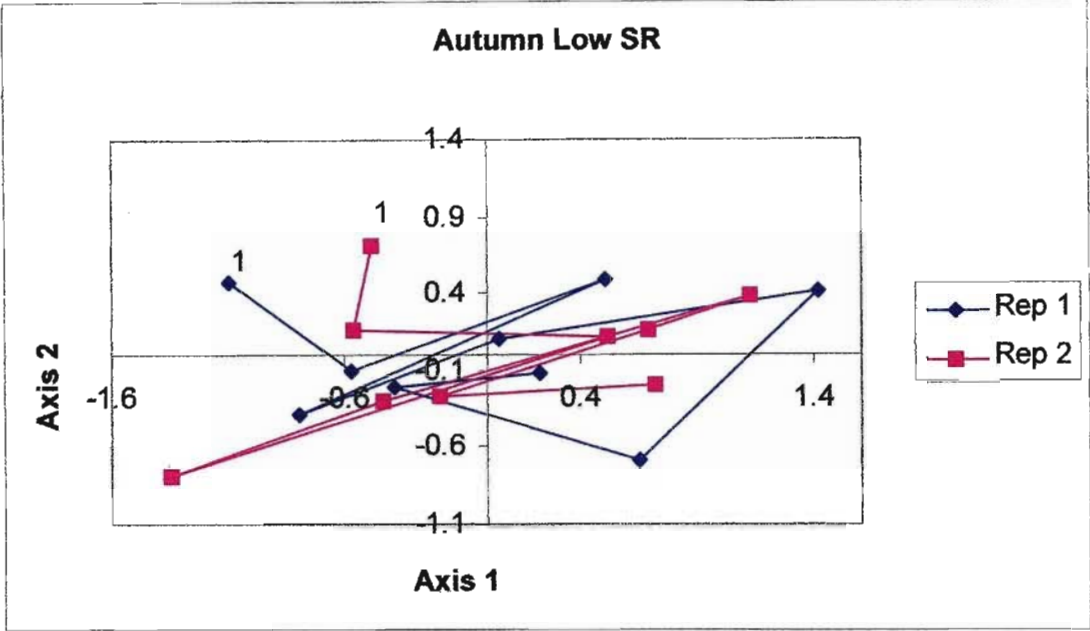


Figure 4.4g: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 7. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

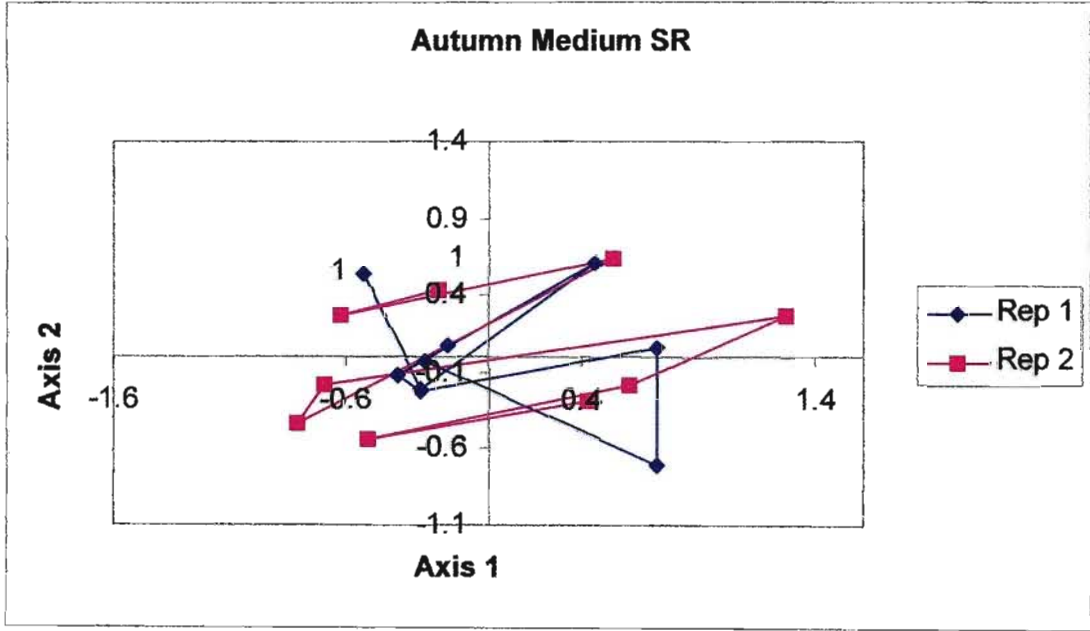


Figure 4.4h: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 8. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

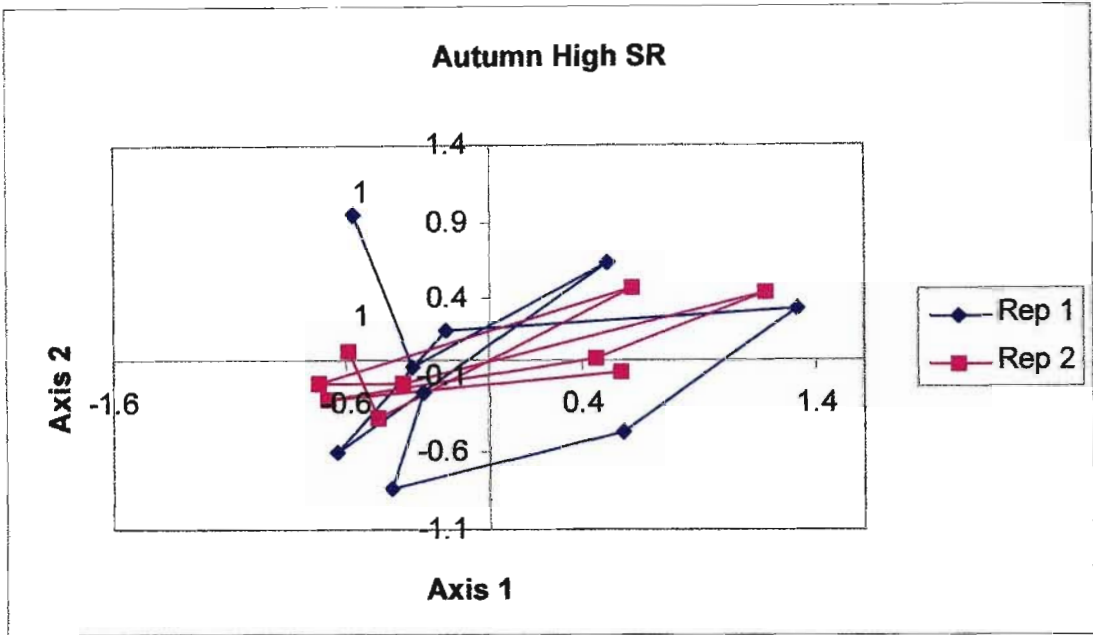


Figure 4.4i: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 9. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

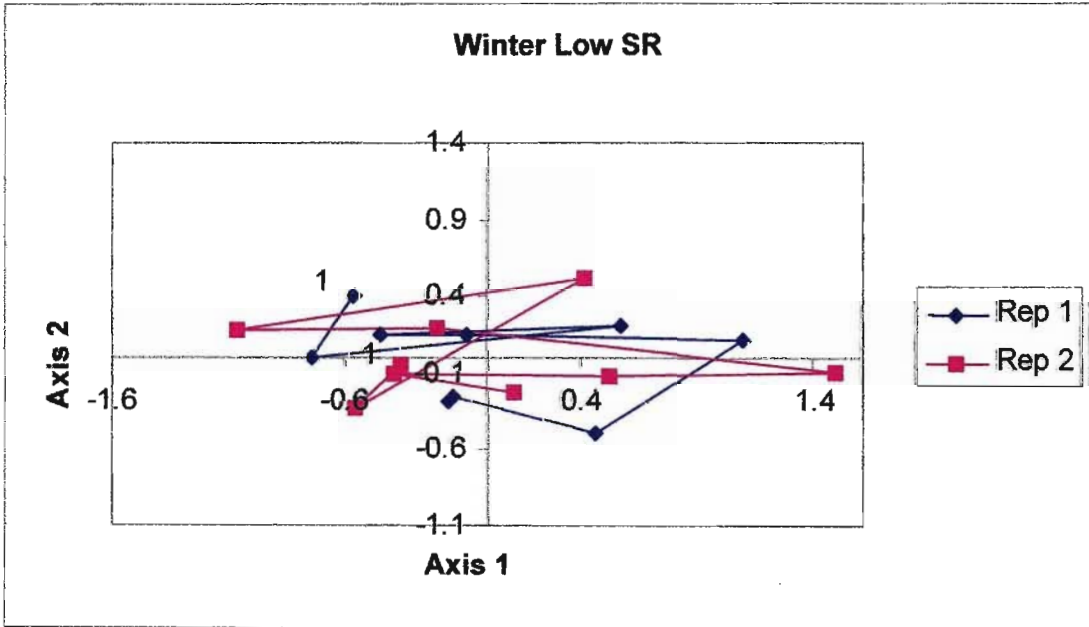


Figure 4.4j: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 10. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

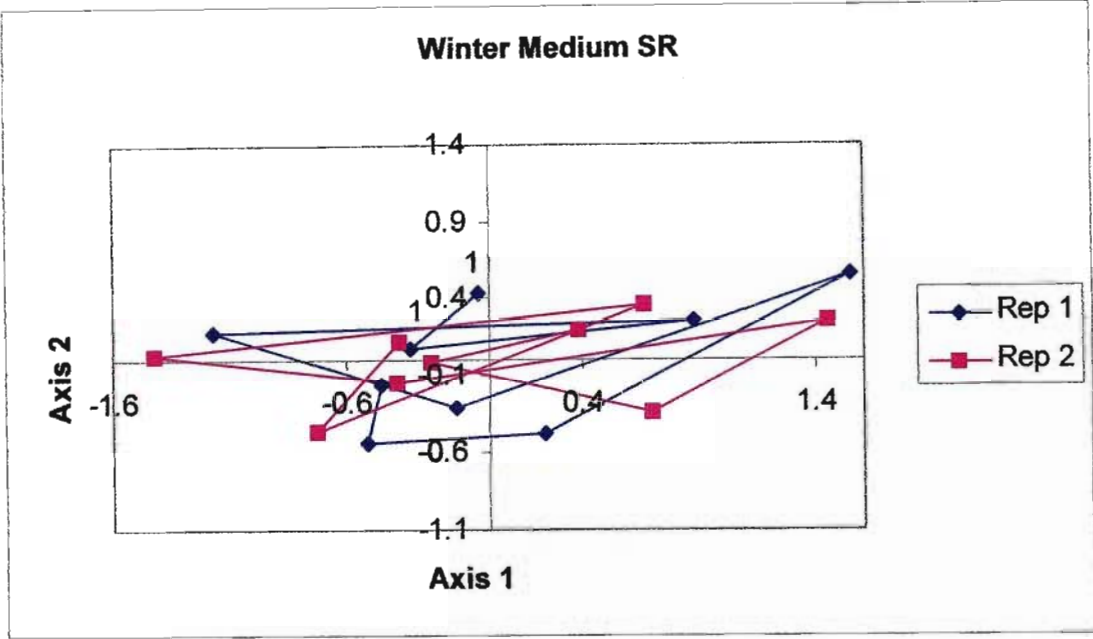


Figure 4.4k: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 11. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

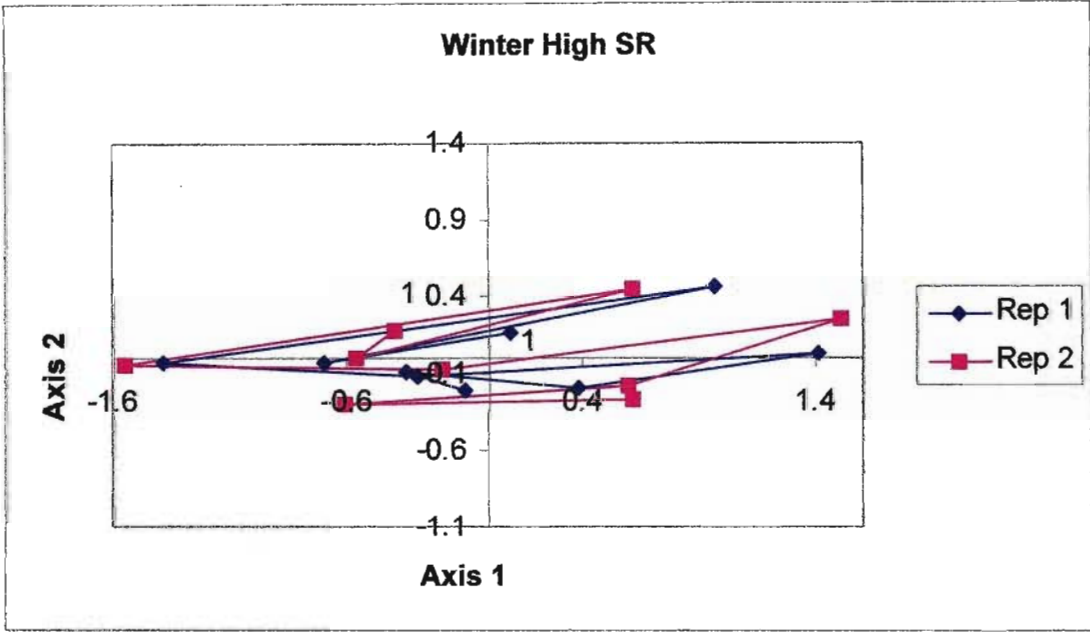


Figure 4.4l: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix with plot ID variables used as covariables, for treatment 12. Species 9, *Ehrharta calycina*, Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' show high cumulative fit values to axis 1. PS rainfall explains the most variance along axis 1 with a canonical coefficient of 0.72 (t-value = 7.88). 1= treatment in year 1.

Species description graphs (Figure 4.5) were generated for species which showed a high cumulative fit along axis 1 (cumulative fit > 10%), a PS rainfall gradient. The species description graphs highlight the increase in absolute abundance of *Ehrharta*

calycina and *Tetragonia fruiticosa* and a decrease in the 'bare ground' variable during years of high PS rainfall.

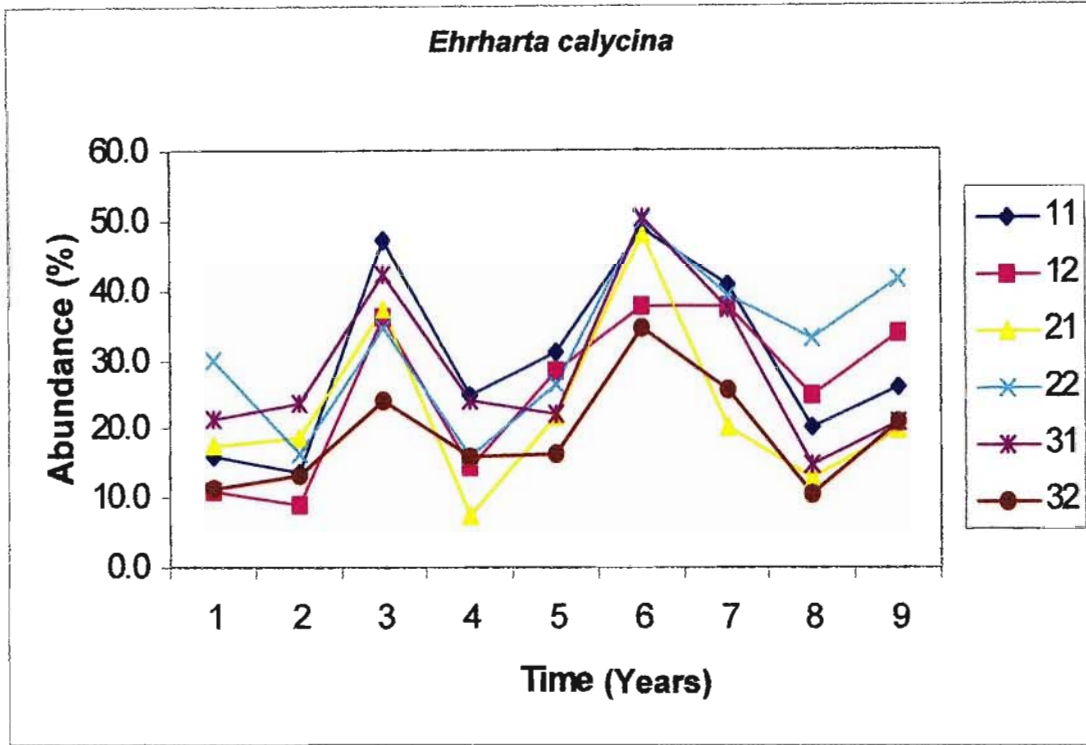


Figure 4.5a: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set** using 'Plot ID' variables as covariables. Absolute abundance of species 9, *Ehrharta calycina* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

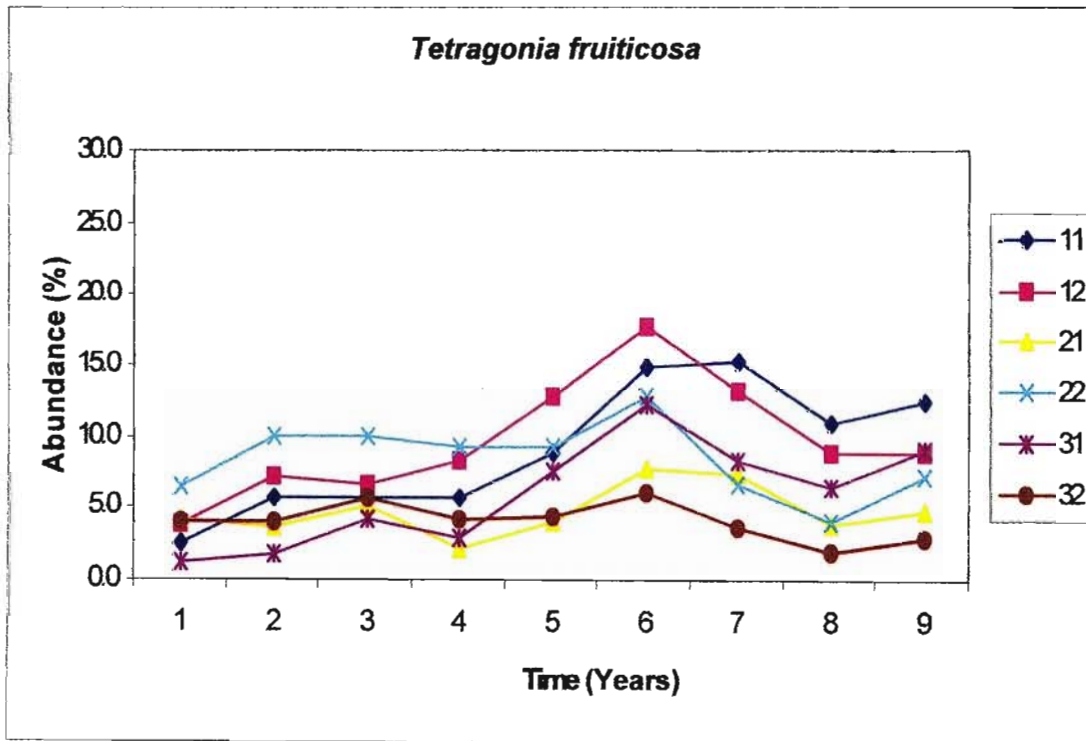


Figure 4.5b: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set** using 'Plot ID'

variables as covariables. Absolute abundance of species 44, *Tetragonia fruticosa* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

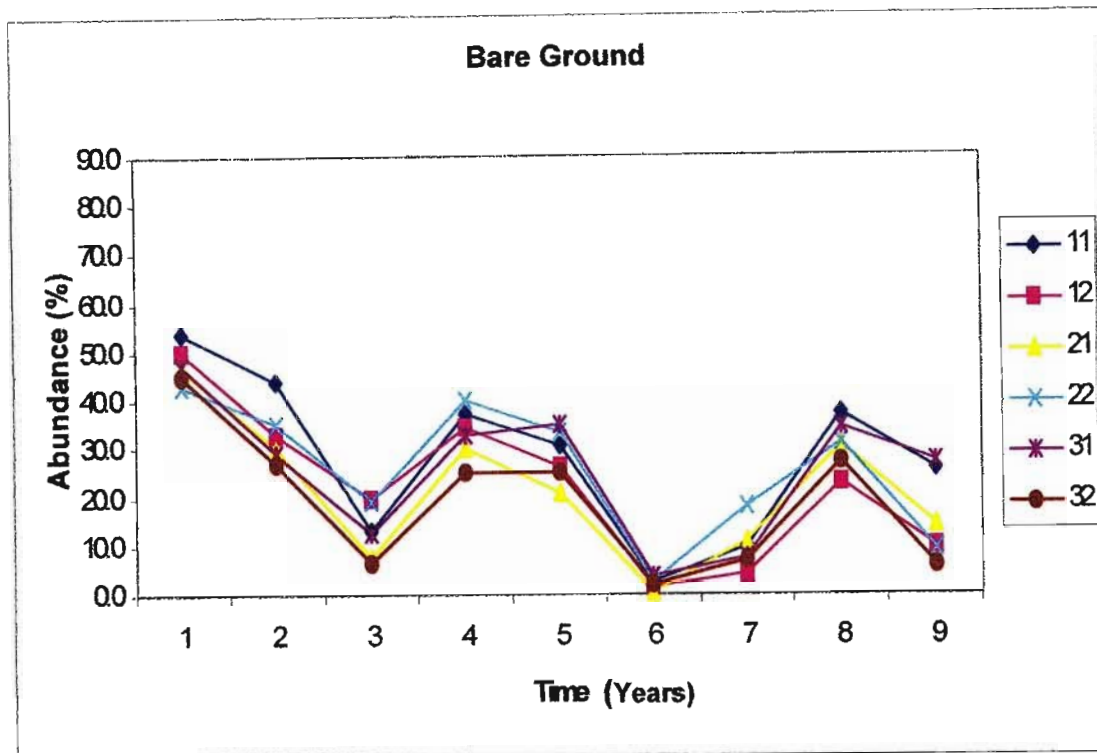


Figure 4.5c: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the full data set using 'Plot ID' variables as covariables. Absolute abundance of species 74, bare ground for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

4.2.2 Partial Canonical Correspondence Analysis (Absolute Abundance)

The results of the first partial constrained analysis (rainfall removed) applied to the absolute abundance data set showed a substantial decrease in the amount of species variation accounted for by the first four axes (Table 4.2). While the first four axes of the CCA applied to the full data set (without the variation corresponding to rainfall removed) accounted for 21.3% of the species variation, the first four axes of the CCA applied to the absolute abundance data set, from which variability associated with rainfall had been partialled out (CCA-Rainfall), accounted for only 10.0%. However, even though a marked decrease was observed in the species variance accounted for, these four axes did account for 83.3% of the species environment relation remaining following the partialling out of variance associated with rainfall. While less variation is accounted for, it should be noted that the variance of the data set being analysed is reduced due to the partialling out of rainfall effects. As a result, the treatment variables, according to the Monte Carlo test, still account for a significant portion of

the remaining variation in the absolute abundance data set ($p = 0.005$ for axis 1, $p = 0.005$ for all canonical axes). With the rainfall variables removed, the partial ordination (Table 4.2) reveals the significance of the time*spring treatment variable (Canonical coefficient = 1.19; $t = 2.42$) in explaining the variance along the environmentally constrained axis 1. Axis 1 however is essentially a grazing gradient with all treatment trajectories moving in a similar direction over time (Figure 4.6). The different effect of individual treatments is revealed by the second ordination axis, which differentiates between the effects of the various treatments (all treatment*time variables have significant canonical coefficients along axis 2). This finding suggests that the variation in species composition following the partialling out of rainfall effects is significantly correlated with grazing over time with small variations occurring between the different season of grazing treatments.

The identity of the species that respond to grazing during spring and to a lesser extent grazing during the remainder of the year can be obtained by observing the cumulative fit values for axis 1. Figure 4.7 shows that species 61, *Melothria* sp. (Cumulative fit = 0.21), species 44, *Tetragonia fruiticosa* (Cumulative fit = 0.18), and species 74, 'bare ground' (Cumulative fit = 0.16) all respond to grazing during spring. Figure 4.6 illustrates how these species respond to the various grazing treatments with *Melothria* sp. and *Tetragonia fruiticosa* increasing with grazing over time while 'bare ground' decreases under the influence of grazing. Figure 4.8 depicts the change in abundance experienced by the aforementioned species in response to grazing during the spring months. These results are consistent with results obtained through the application of ANOVA to plant species in this data set.

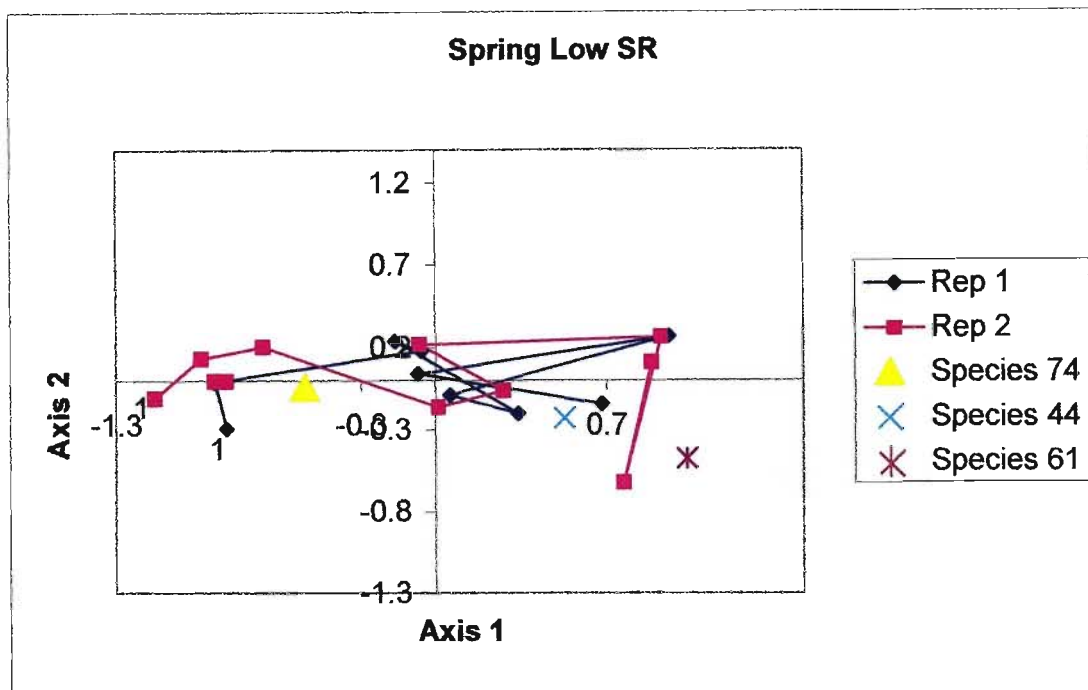


Figure 4.6a: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 1 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1. Species positions depicted in Spring Low graph remain constant in all ordination plots (figure 4.6b to 4.6l).

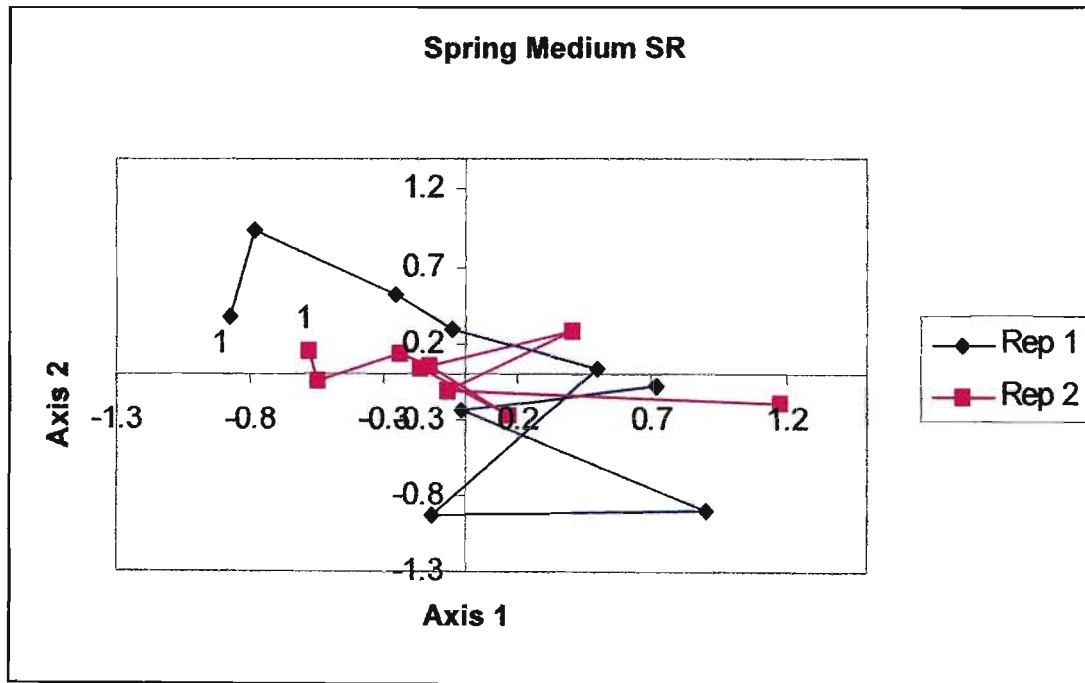


Figure 4.6b: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 2 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

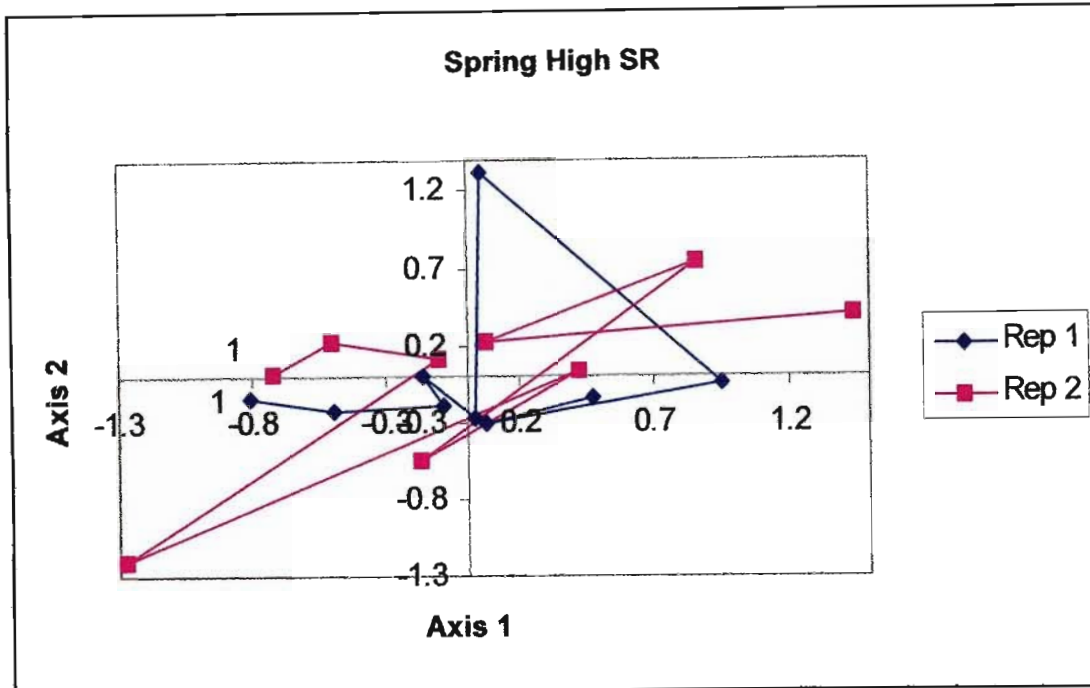


Figure 4.6c: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 3 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

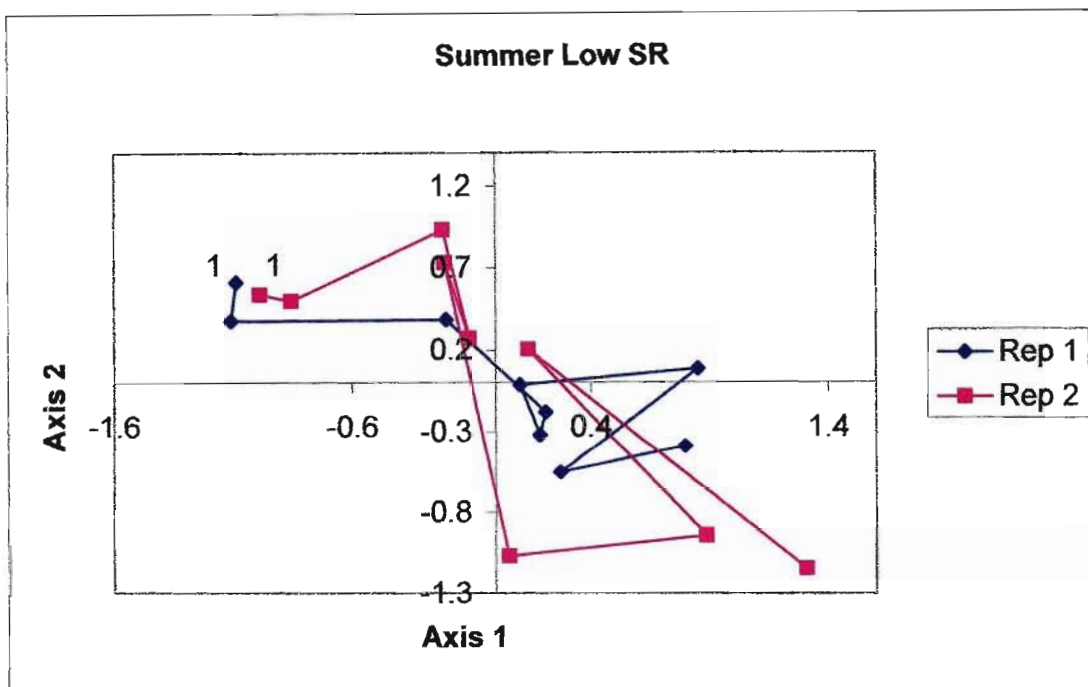


Figure 4.6d: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 4 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

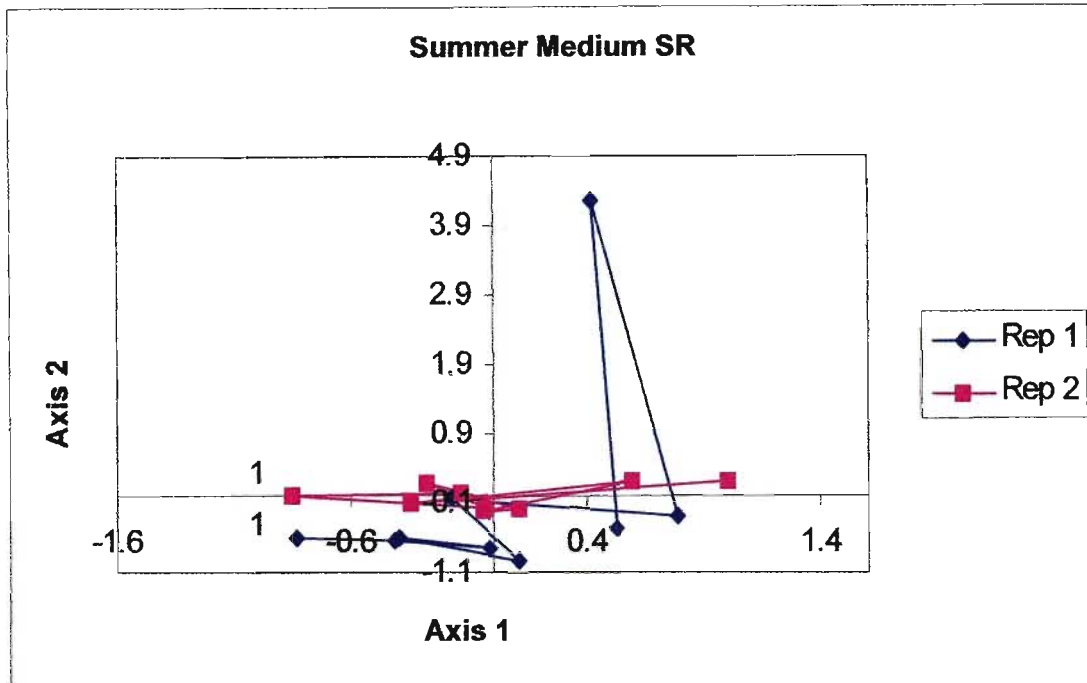


Figure 4.6e: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 5 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

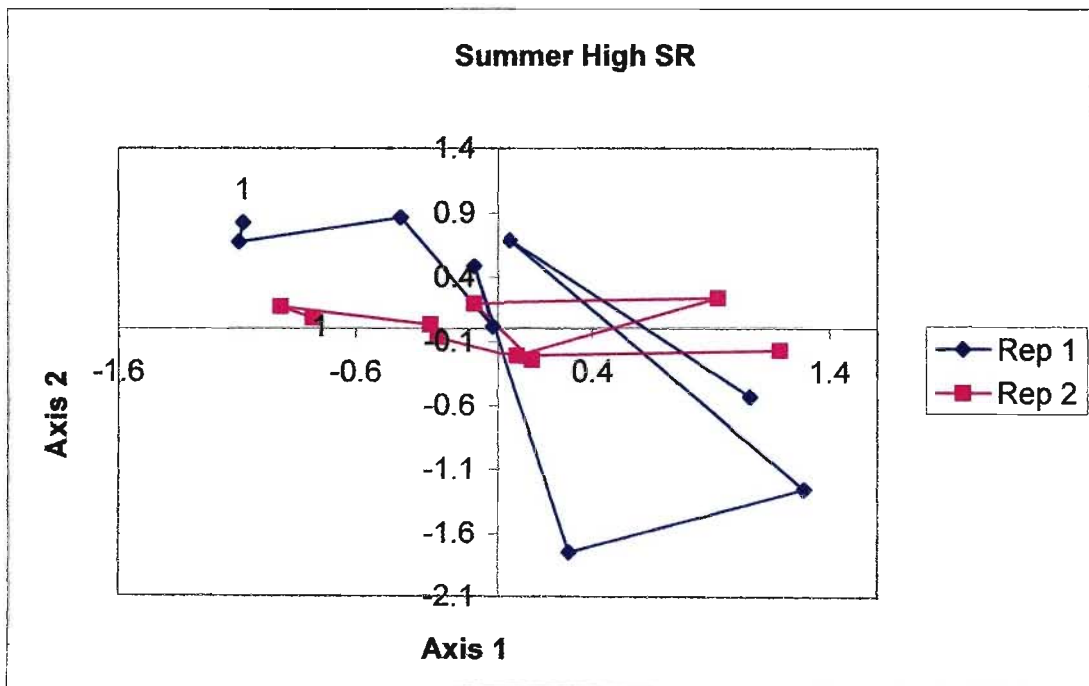


Figure 4.6f: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 6 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

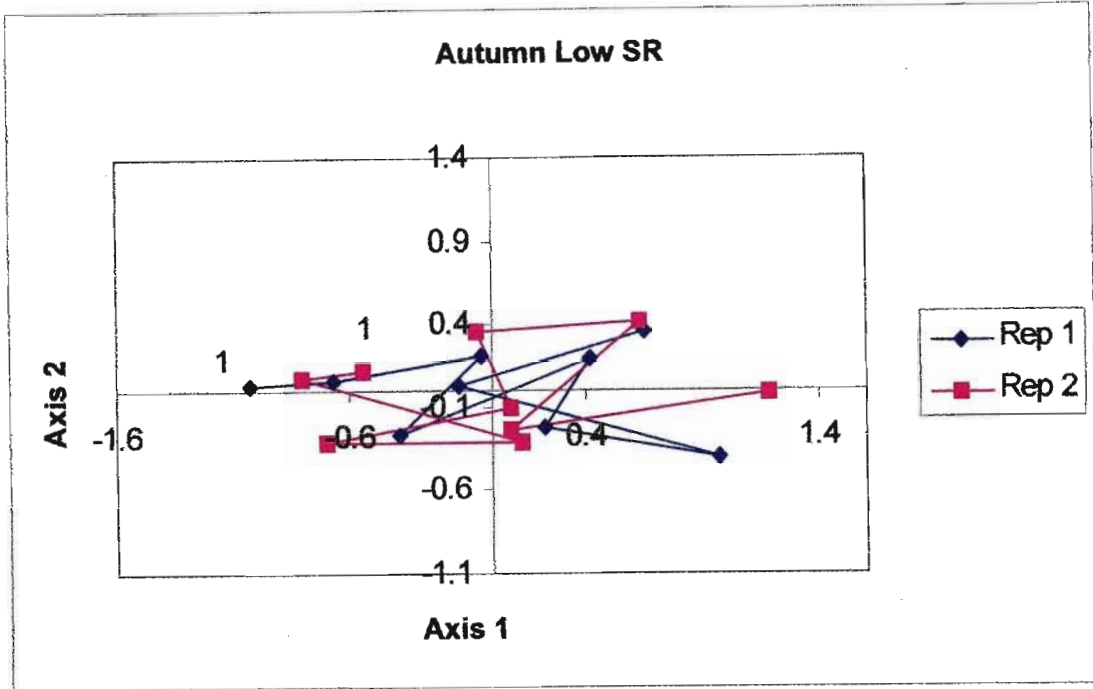


Figure 4.6g: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 7 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

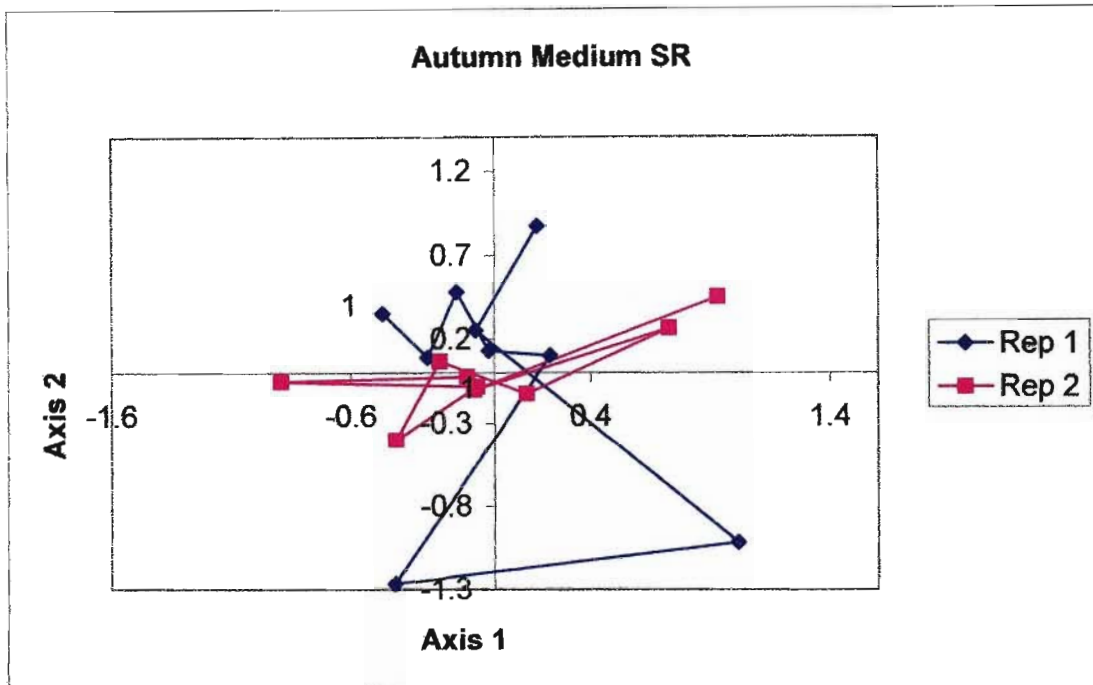


Figure 4.6h: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 8 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

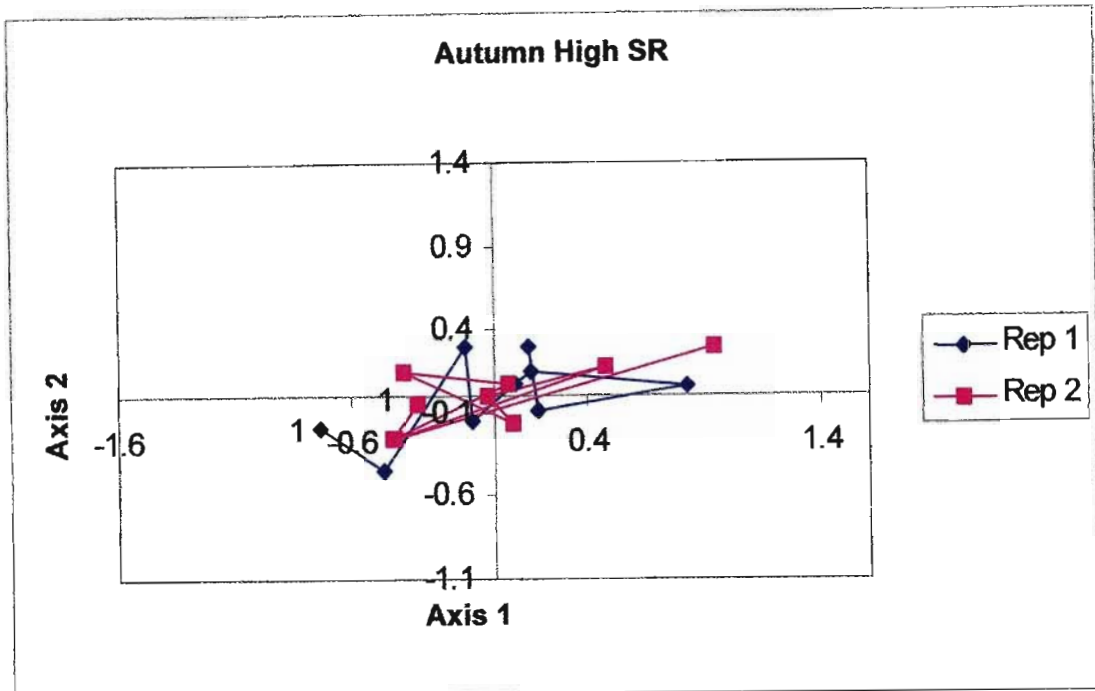


Figure 4.6i: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 9 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

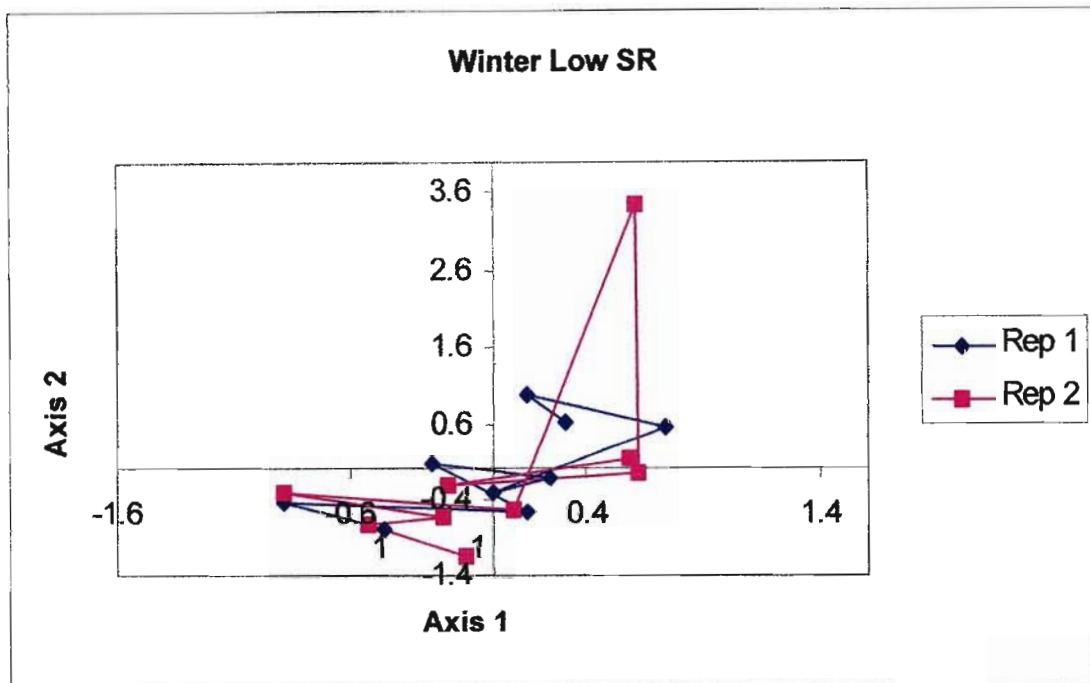


Figure 4.6j: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 10 with the effects of rainfall removed. Species 44, *Tetragonia fruticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

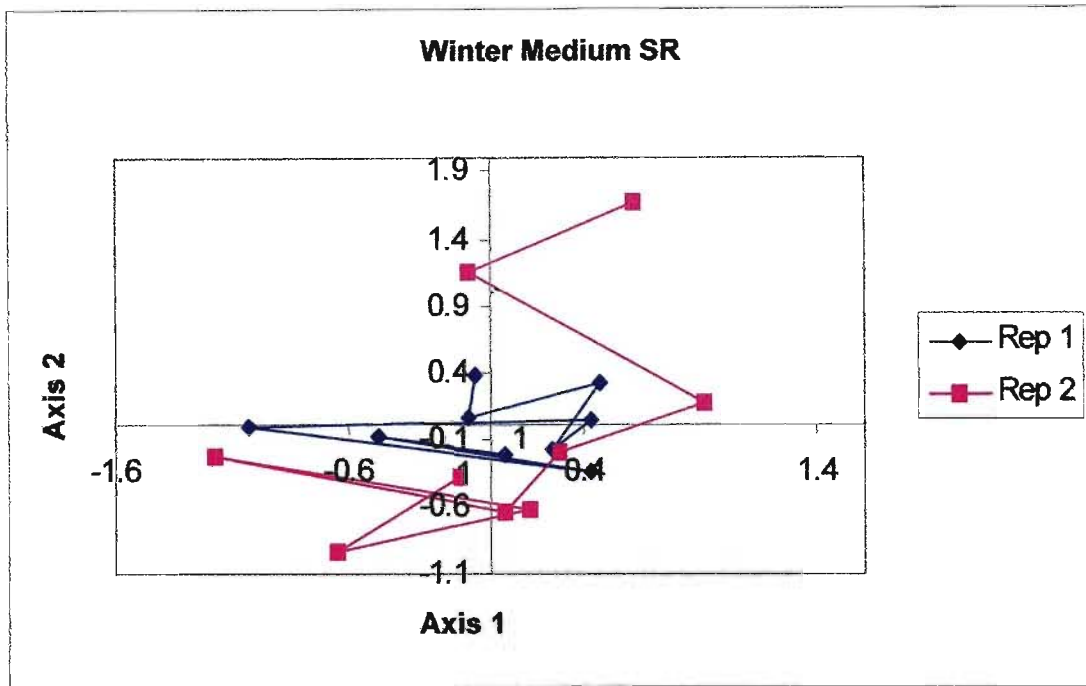


Figure 4.6k: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 11 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

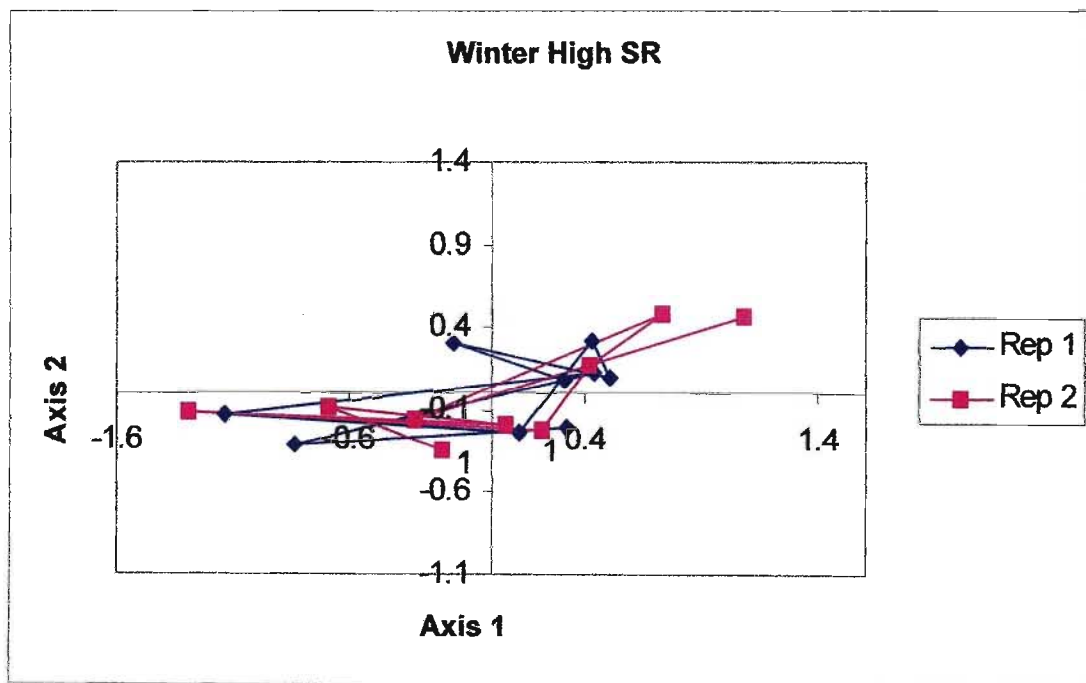


Figure 4.6l: Ordination trajectory obtained from Canonical Correspondence Analysis applied to absolute abundance matrix for treatment 12 with the effects of rainfall removed. Species 44, *Tetragonia fruiticosa* and Species 74, 'bare ground' and species 61, *Melothria* sp. show high cumulative fit values to axis 1. The spring*time treatment variable significantly explains the variation along axis 1 with a canonical coefficient of 1.19 and t-value of 2.42. 1= treatment in year 1.

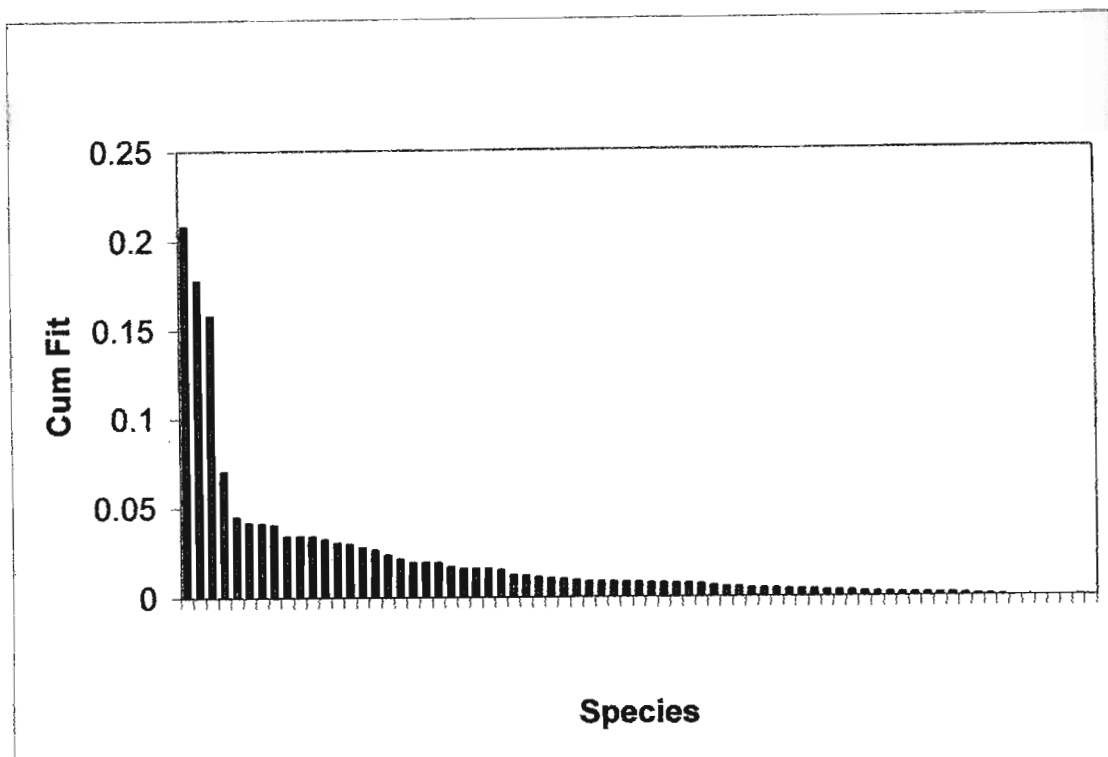


Figure 4.7: Cumulative fit along axis 1 for Canonical Correspondence Analysis applied to full data set with plot ID variables and rainfall variables used as covariables. The first three species are 61 = *Melothria* sp. (0.21), 44 = *Tetragonia fruticosa* (0.18), 74 = bare ground (0.16).

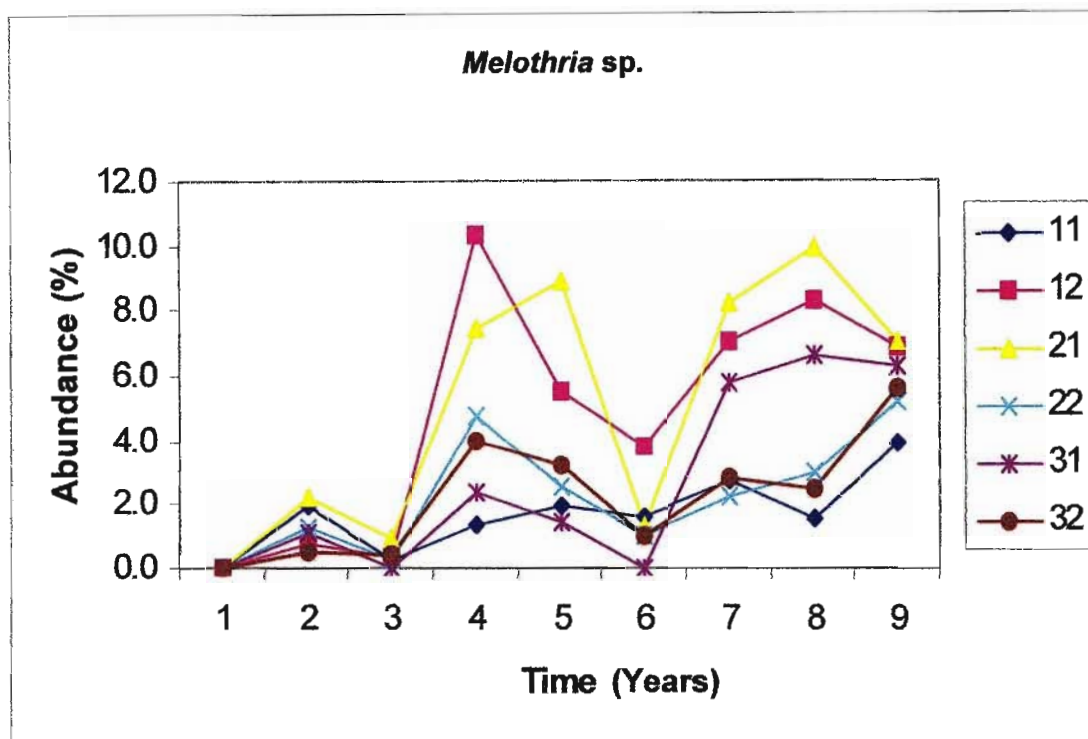


Figure 4.8a: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the full data set using 'Plot ID' variables and rainfall variables as covariables. Absolute abundance of species 61, *Melothria* sp. for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

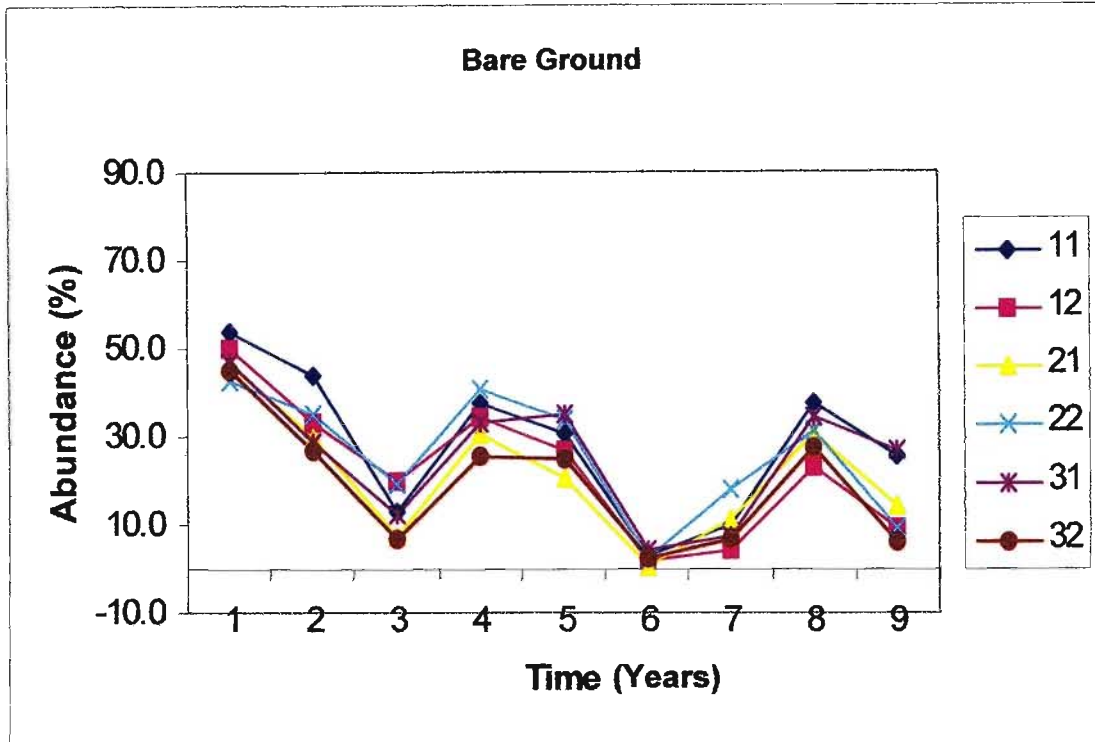


Figure 4.8b: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set** using 'Plot ID' variables and rainfall variables as covariables. Absolute abundance of species 74, bare ground for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

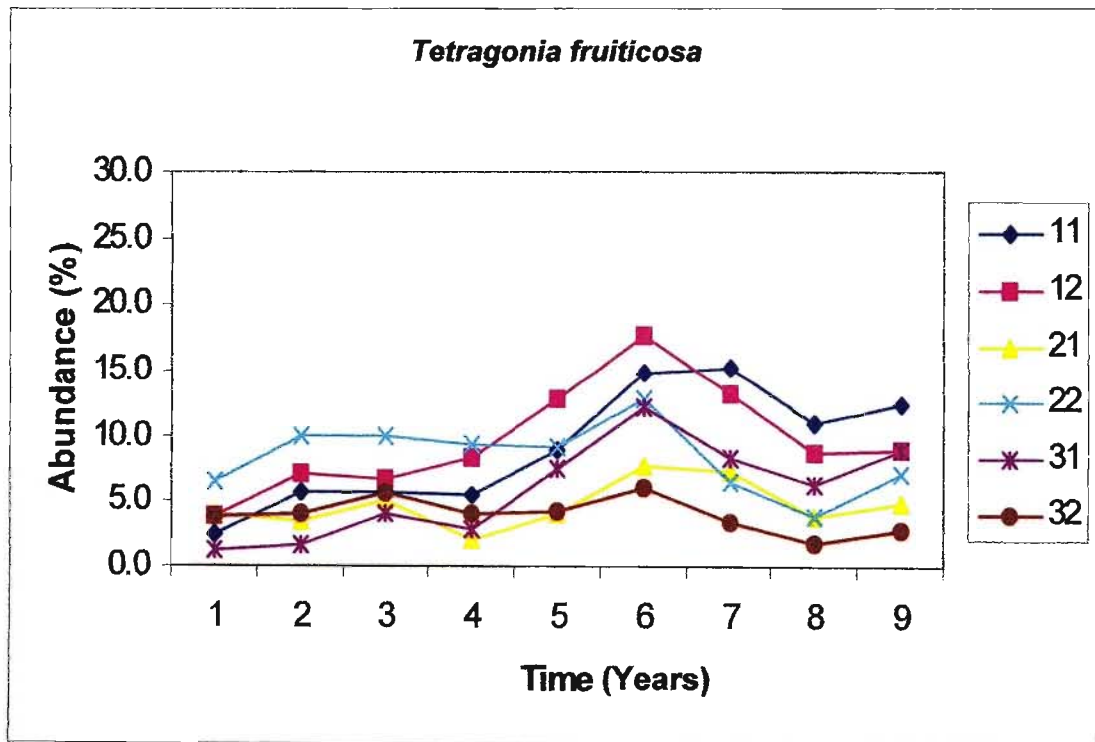


Figure 4.8c: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set** using 'Plot ID' variables and rainfall variables as covariables. Absolute abundance of species 44, *Tetragonia fruticosa* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

4.2.3 *Partial Canonical Correspondence Analysis (Relative abundance)*

The removal of species 74 (bare ground) enabled the analysis to be altered from one which assessed the influence of treatment variables on absolute abundance to one which assessed the influence of these variables on relative abundance. Analysis of the absolute abundance data set has shown clearly the relation between the variability in species composition and both non-equilibrium (rainfall) and equilibrium (grazing treatments) variables. The removal of the absolute abundance facet served to further remove that portion of the variability, which coincides with rainfall (i.e. cover) and provides a different perspective on how the species dynamics were influenced by the various treatments. To achieve this, partial canonical correspondence analysis (effects of rainfall removed) was applied to relative abundance data set (CCA-Rainfall (-74)) to establish whether changes in the relative abundance could be attributed to treatment. The partial CCA output showed a further drop in the amount of variance being accounted for by the analysis, with axis 1 accounting for only 3.9% and the first four axes only 7.0% of the variation in the species composition data (Table 4.2). Of the treatment variables assessed, time*spring (canonical coefficient = -1.41, t-value = -3.09) significantly explains the variation along axis 1 and SR*time (Canonical coefficient = 3.86; t = 3.27), time*spring (Canonical coefficient = 3.51; t = 3.59), time*summer (Canonical coefficient = 1.74; t = 2.56), time*autumn (Canonical coefficient = 3.97; t = 3.53) and time*winter (Canonical coefficient = 3.06; t = 3.00) the variation along axis 2. This suggests that grazing during the spring season is having the most substantial influence on species composition.

The results of the Monte Carlo permutation test (Table 4.3) show that the variation explained by axis 1 and subsequent axes are non-significant ($p > 0.05$) relative to the total variation in the relative abundance data set ($p = 0.065$ for axis 1, $p = 0.09$ for all canonical axes). The removal of the 'bare ground' variable and in essence the absolute abundance facet of the data set leads to a dramatic decline in the amount of variation accounted for by the treatment variables. While neither axis 1 nor subsequent axes significantly explain ($p > 0.05$) the variation in the relative abundance data, it is worth noting that the same treatments that explain the variation along axis 1 and 2 for this analysis explained the variation along axis 1 and 2 of the partial ordination applied to

the absolute abundance data set (CCA-Rainfall analysis). This provides further evidence of the impact of grazing on species dynamics.

The same species which have high cumulative fits along axis 1 of the partial ordination analysis applied to the absolute abundance data set (CCA-Rainfall) have high cumulative fit along axis 1 of this analysis. These species include *Tetragonia fruticosa* (Cumulative fit = 0.11) and *Melothria* sp. (Cumulative fit = 0.12) (Figure 4.9). Furthermore, the relative abundance of *Zygophyllum morgsana* (Cumulative fit = 0.15) and *Ruschia caroli* (Cumulative fit = 0.12) was also shown to change in response to grazing. *Tetragonia fruticosa* (Figure 4.10b) and *Melothria* sp. (Figure 4.10d) increase under the influence of spring grazing while *Zygophyllum morgsana* (Figure 4.10a) and *Ruschia caroli* (Figure 4.10c) decrease with grazing during spring over time from a relative abundance perspective. These results are consistent with the findings of the analysis of variance.

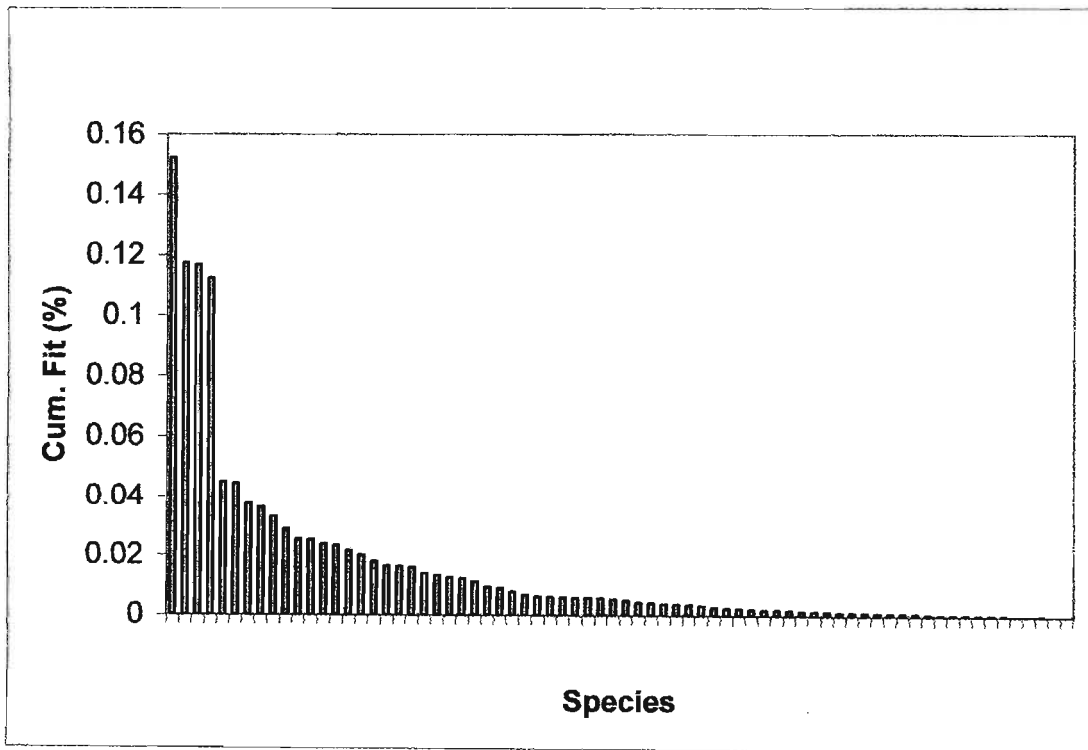


Figure 4.9: Cumulative fit along axis 1 for Canonical Correspondence Analysis applied to full data set with plot ID variables and rainfall variables used as covariables. Species 74 (bare ground) was removed from species matrix. The first five species are 73 = *Zygophyllum morgsana* (0.15), 44 = *Tetragonia fruticosa* (0.11), 65 = *Ruschia caroli* (0.12), 61 = *Melothria* sp (0.12).

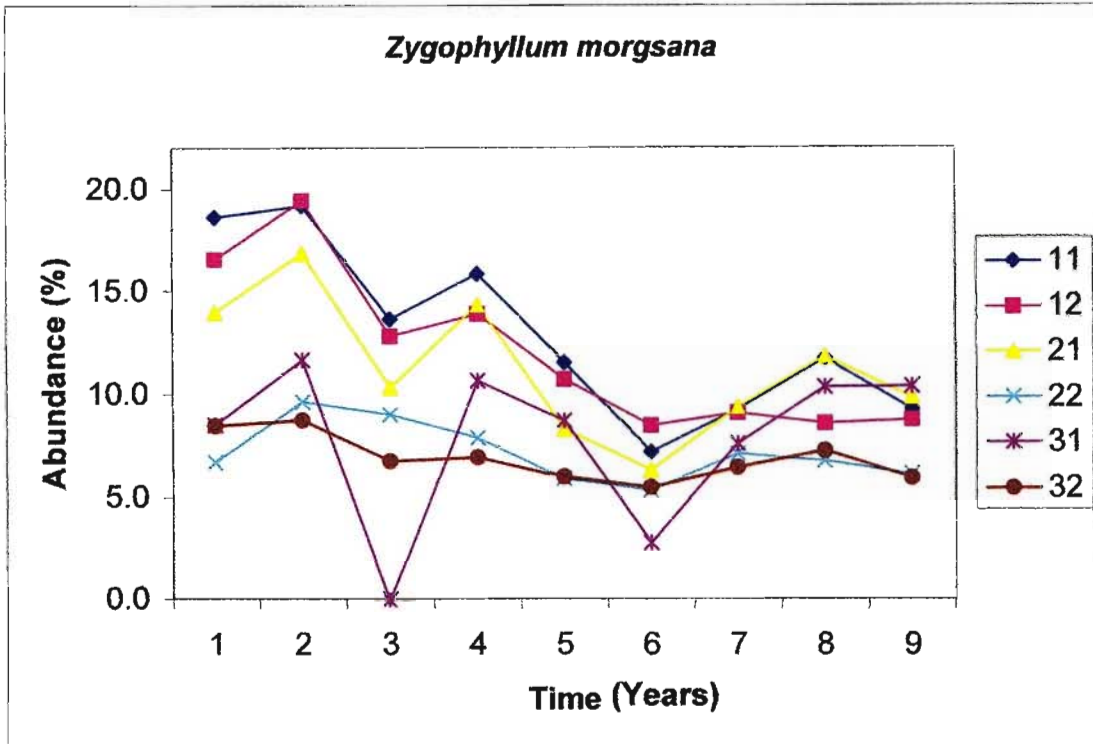


Figure 4.10a: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 73, *Zygophyllum morgsana* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

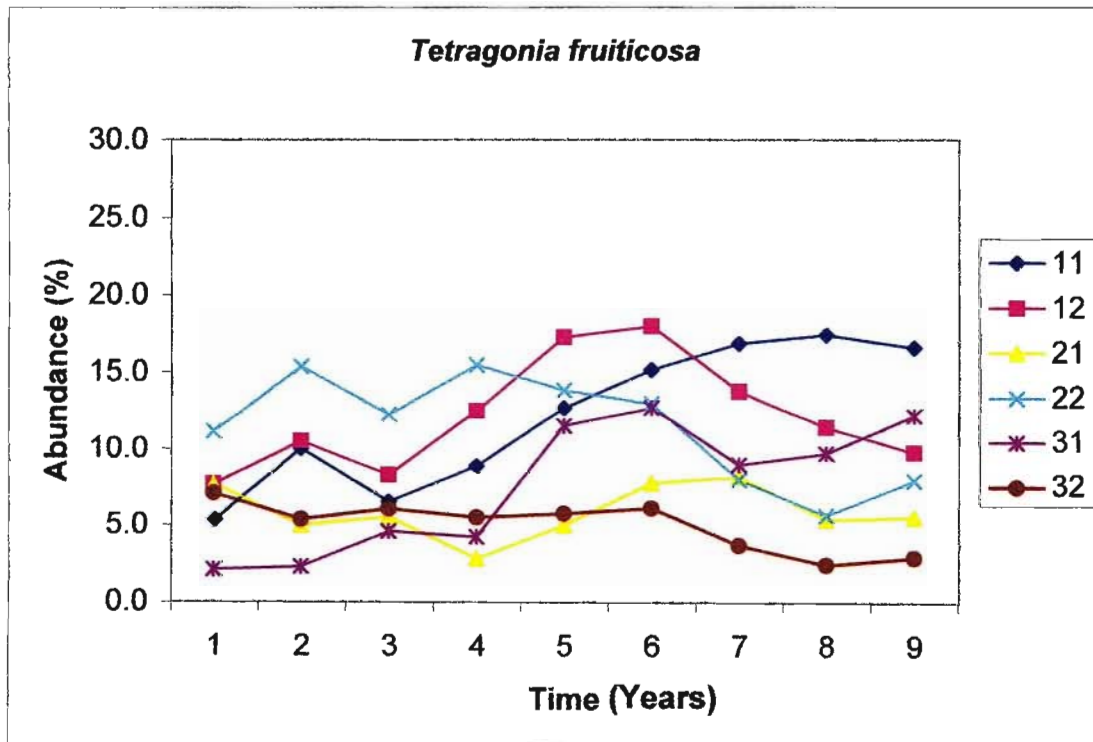


Figure 4.10b: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 44, *Tetragonia fruticosa* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

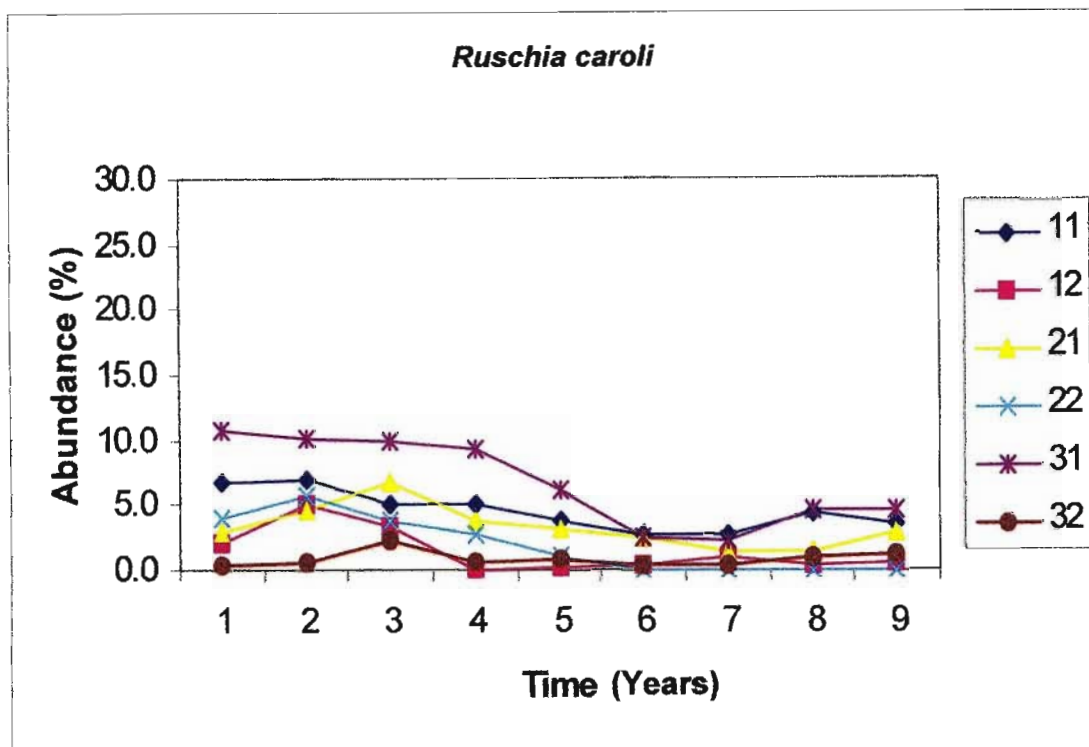


Figure 4.10c: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 65, *Ruschia caroli* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

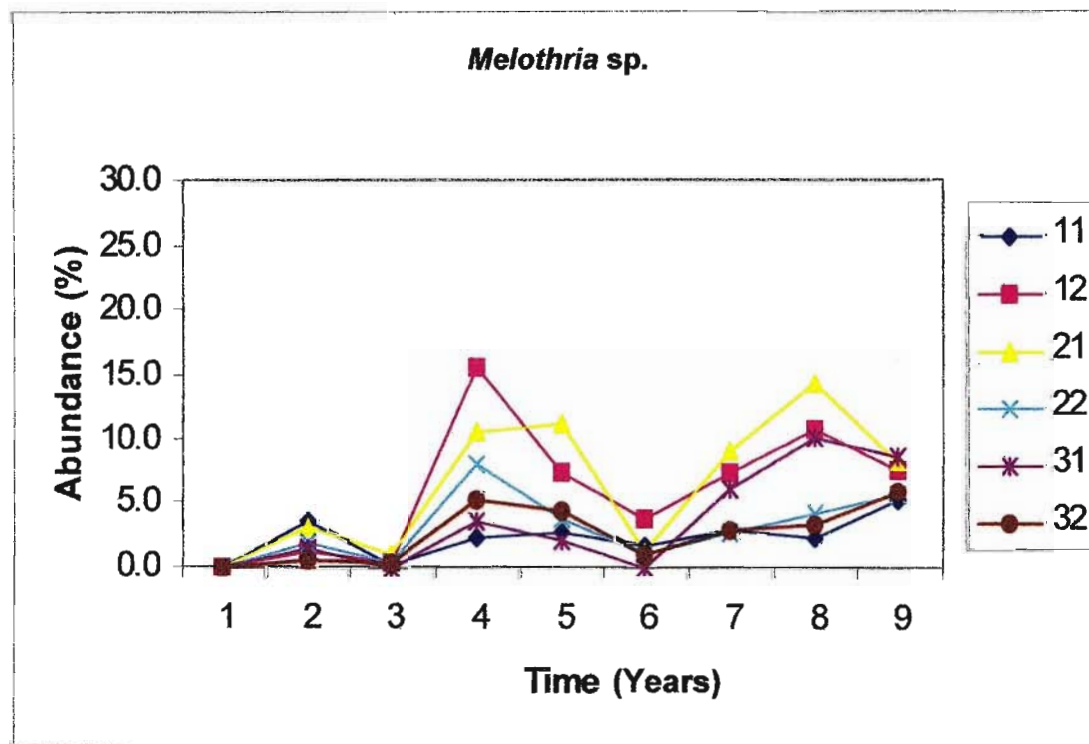


Figure 4.10d: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 61, *Melothria sp.* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

4.2.4 Partial Canonical Correspondence Analysis (Relative abundance-shrub/herb complex)

The removal of *Ehrharta calycina* (CCA-Rainfall (-74-9)) results in an increase in the amount of variation explained by the constrained ordination axis (axis 1 = 3.9%), when compared to CCA-Rainfall (-74) (axis 1 = 4.1%) (Table 4.2). This suggests that this species is not strongly related to the treatment variables. Furthermore, this finding confirms the results of the partial ordination analysis applied to the relative abundance matrix which showed *Ehrharta calycina* as having a low cumulative fit value along the grazing axis. While this conclusion can be made, it should be noted that the first four axes of this analysis only account for 7.2% of the species variance, a value shown to be non-significant by the Monte Carlo tests (Table 4.3). Nonetheless, the analysis of this data set provides valuable insight into the relation between various treatments and the veld resource and supports many of the findings revealed by the CCA applied to the absolute abundance matrix and ANOVA analyses.

Figure 4.11 illustrates the cumulative, directional nature of the species composition change over time experienced by the shrub/herb complex (CCA-Rainfall (-74-9)). This serves to highlight the influence of grazing on this veld component. This relation between grazing and the shrub/herb complex has developed in spite of the highly variable rainfall and coincides with Illius and O'Connor's (1999) key resource concept. The various treatment trajectories move in the same direction along axis 1 but different directions along axis 2. This suggests that grazing is having a similar influence on the trajectory of samples over time, the direction of which is determined by the season in which the grazing is applied. Plotting the explanatory variables along axis 1 and 2 (Figure 4.11m) confirms this notion. This trend is similar to that found in the partial ordination analyses applied to the full data set (Figure 4.6) which also showed axis 1 to be a grazing gradient with axis 2 corresponding with the influence of various grazing treatments over time. Species which show high cumulative fit along axis 1 include Species 61, *Melothria* sp. (Cumulative fit = 0.13), 65, *Ruschia caroli* (Cumulative fit = 0.13) and 73, *Zygophyllum morgsana* (Cumulative fit = 0.18) (Figure 4.12). Again the time*spring treatment variable best explained the variation along axis 1 (Canonical coefficient = -1.21; $t = -2.60$) with SR*time (Canonical coefficient = 3.09; $t = 2.25$), time*summer (Canonical coefficient = 1.82; $t = 2.31$) and time*autumn (Canonical coefficient = 2.90; $t = 2.26$) explaining the variation

along axis 2. The magnitude of the impact of grazing during spring is confirmed by the ANOVA, which revealed certain species as responding significantly to grazing during this season. Trajectories suggest that *Melothria* sp. increases in relative abundance with grazing while *Zygophyllum morgsana* and *Ruschia caroli* are sensitive to grazing and decrease in relative abundance in response of grazing. Examination of the species descriptions (Figure 4.13) for this and other analyses show consistency with these findings. Ordination trajectories (Figure 4.11) show that while grazing affected the relative abundance during the first few years of the trial the veld seemed to stabilize later on fluctuating around one point. This characteristic is also found in the trajectories obtained from the partial ordination (effects of rainfall removed) applied to the full data set, in which directional movement of samples is evident during the earlier years of the trial, stabilising with time. This decrease in directional movement over time is supported by the euclidean distance analyses (Figure 4.14) for both the relative abundance data and the shrub/herb complex stabilizes.

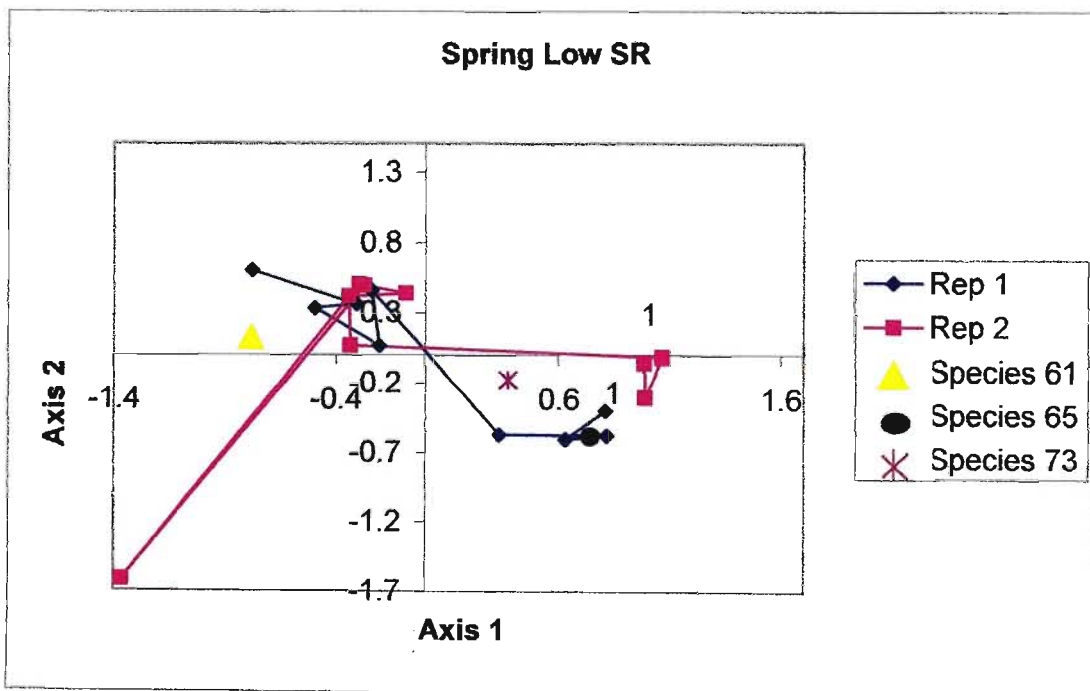


Figure 4.11a: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 1 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria* sp., 65, *Ruschia caroli* and 73, *Zygophyllum morgsana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1. Species positions depicted in Spring Low graph remain constant in all ordination plots (Figure 4.11b to 4.11f).

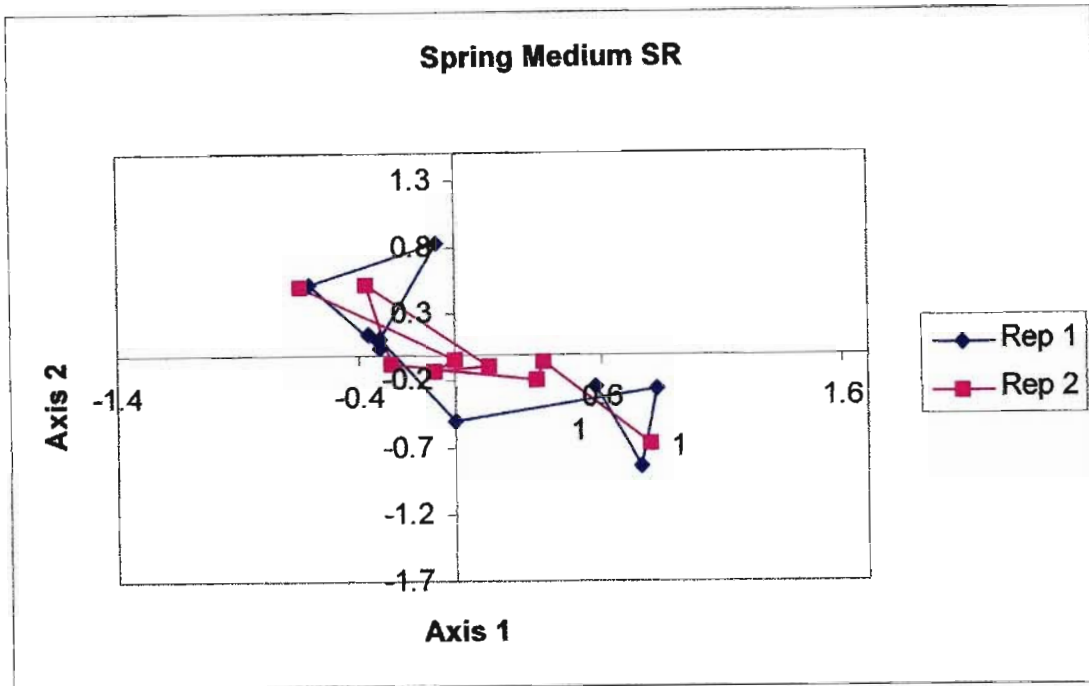


Figure 4.11b: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 2 using plot ID variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

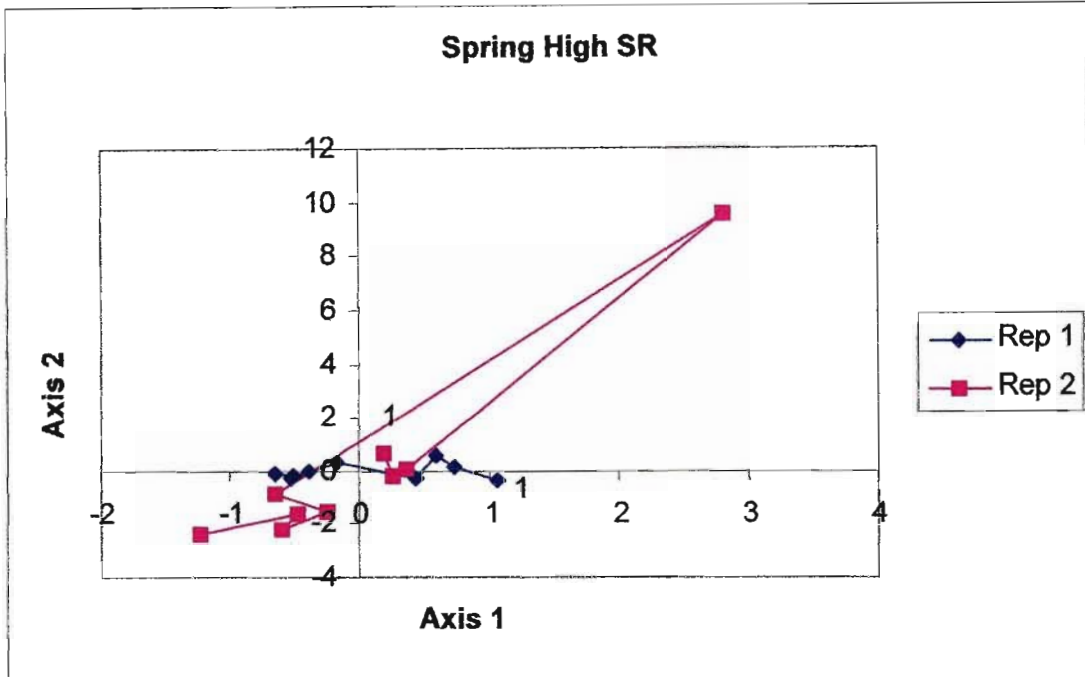


Figure 4.11c: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 3 using plot ID variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

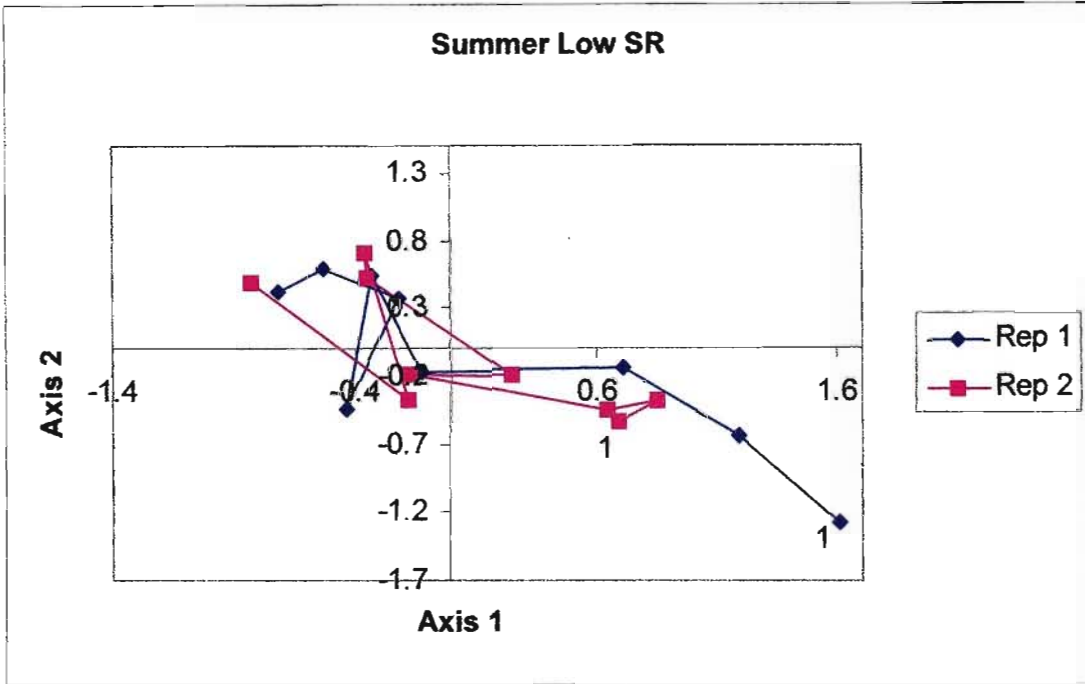


Figure 4.11d: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 4 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

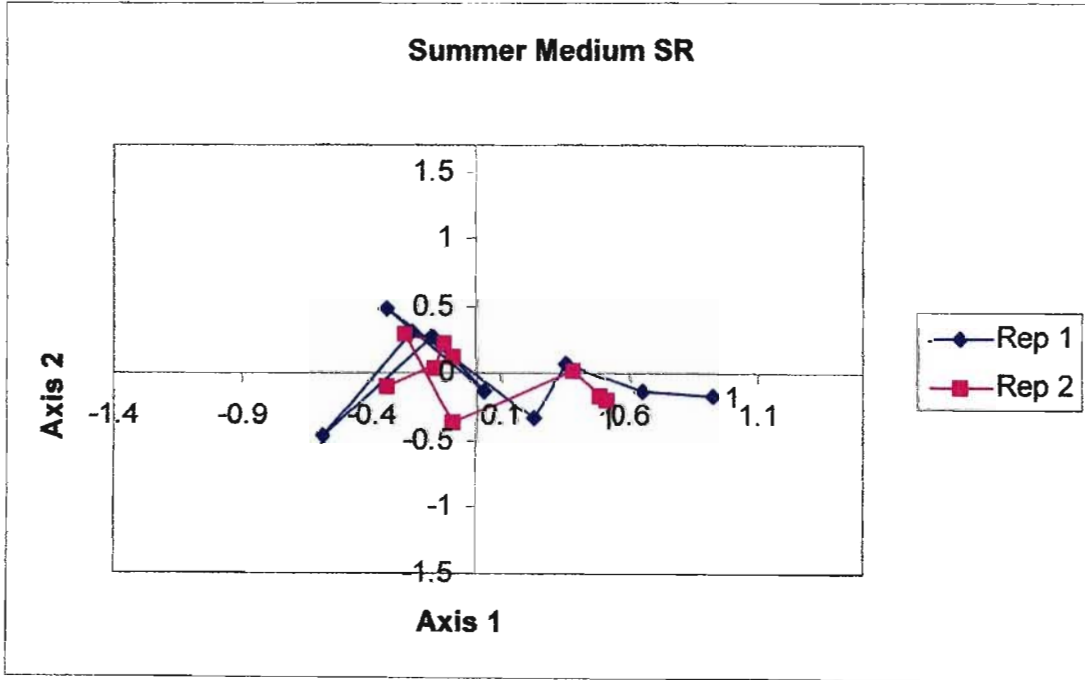


Figure 4.11e: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 5 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

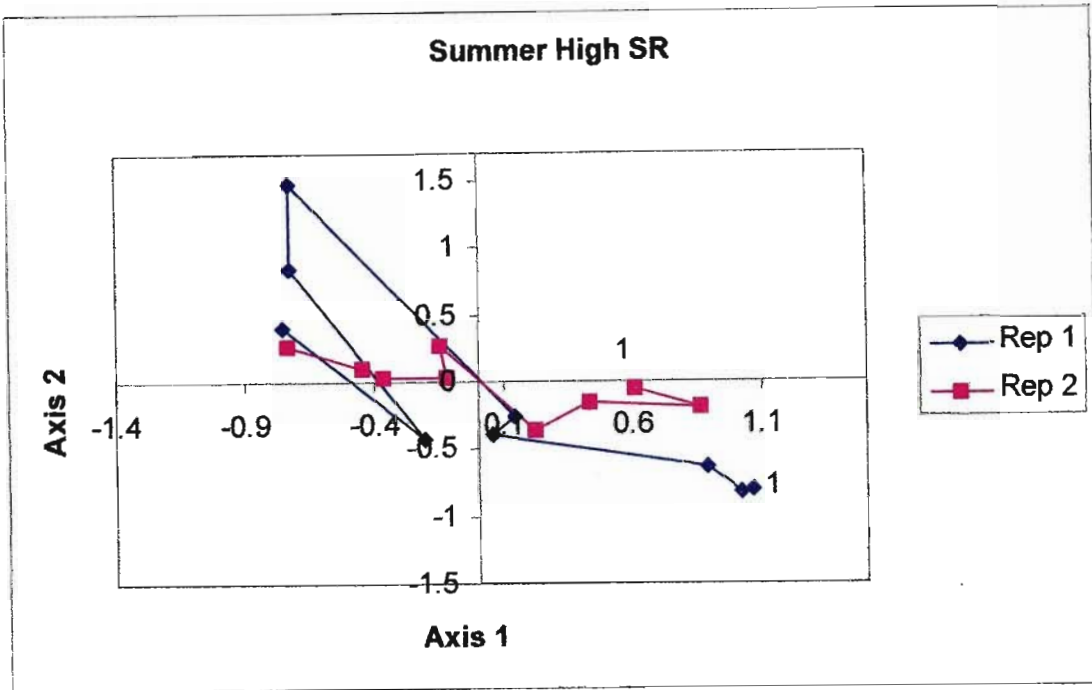


Figure 4.11f: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 6 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

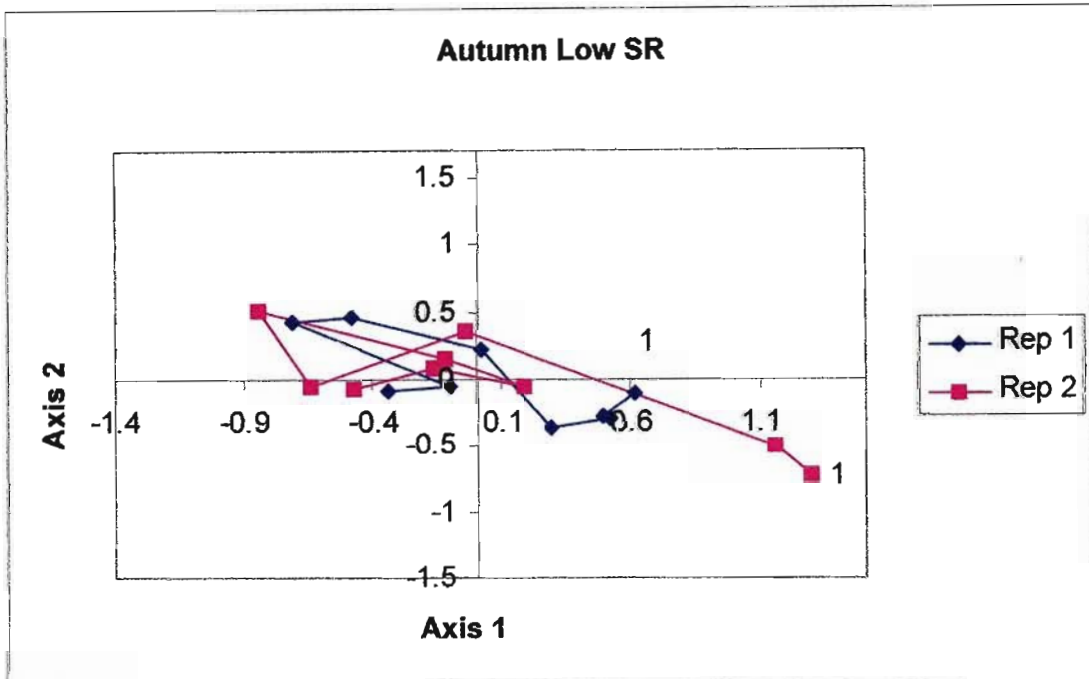


Figure 4.11g: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 7 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

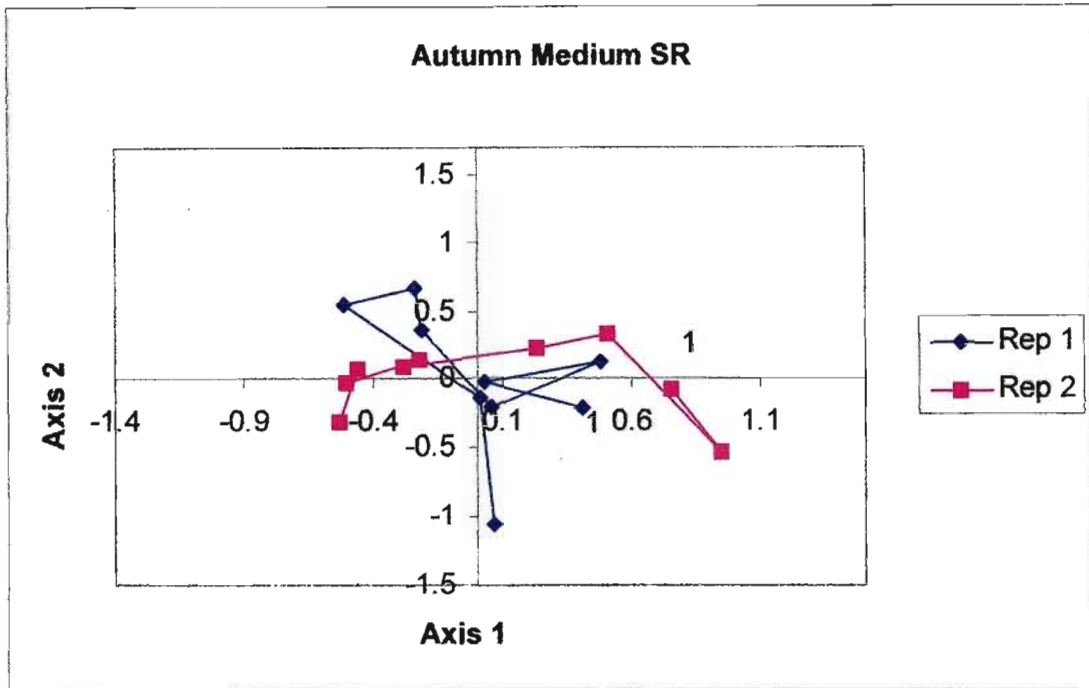


Figure 4.11h: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 8 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

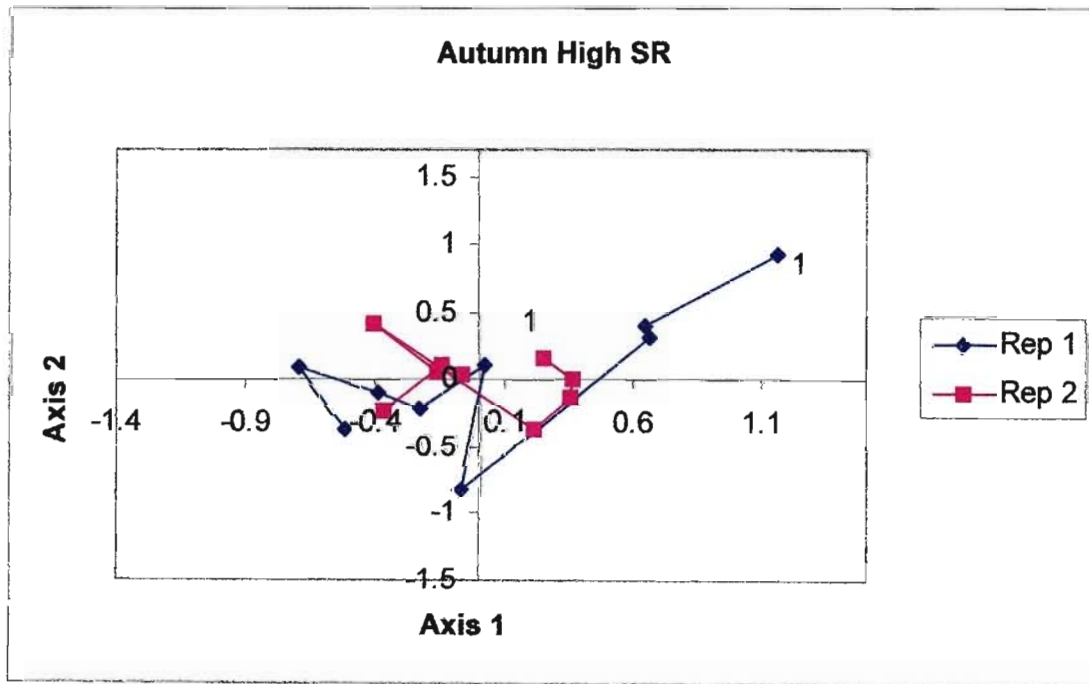


Figure 4.11i: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 9 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

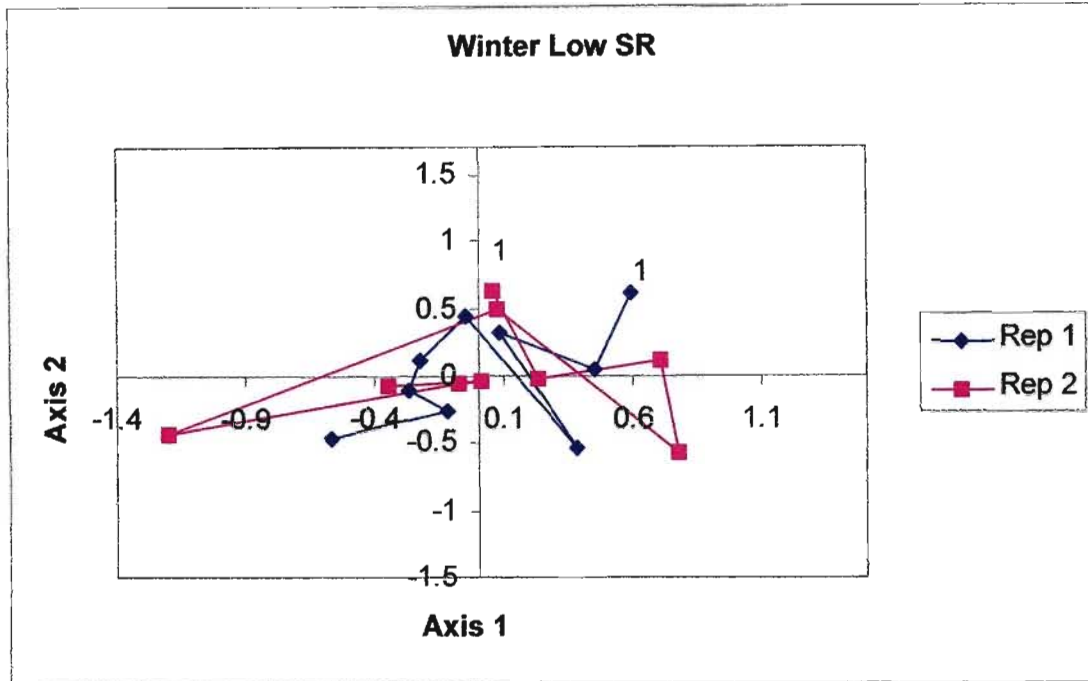


Figure 4.11j: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 10 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

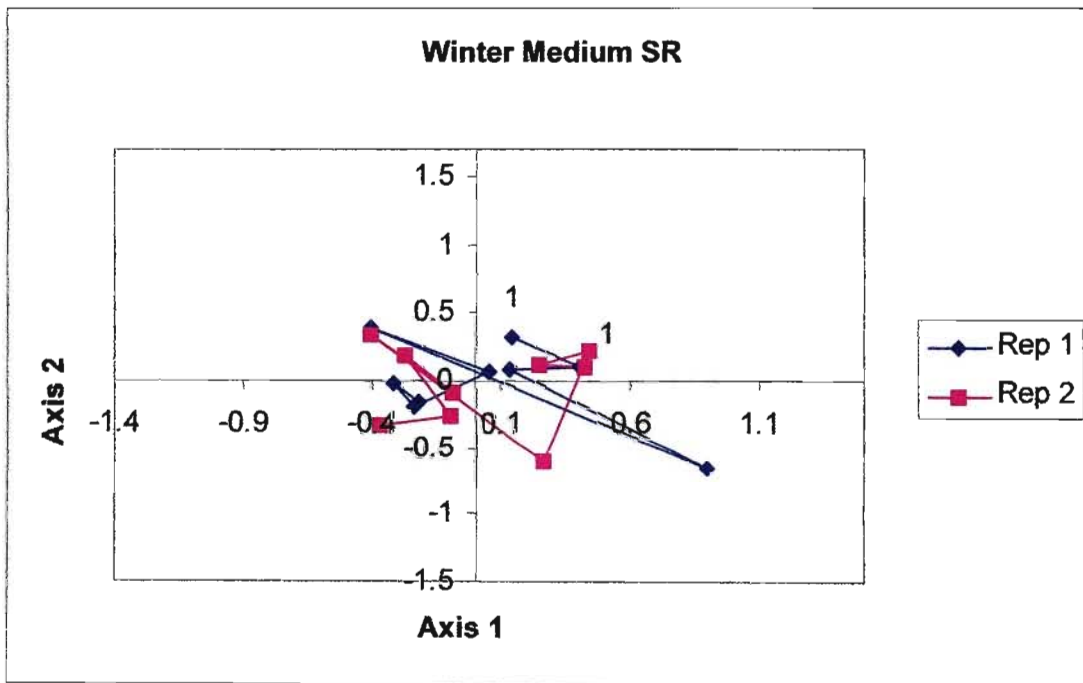


Figure 4.11k: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 11 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

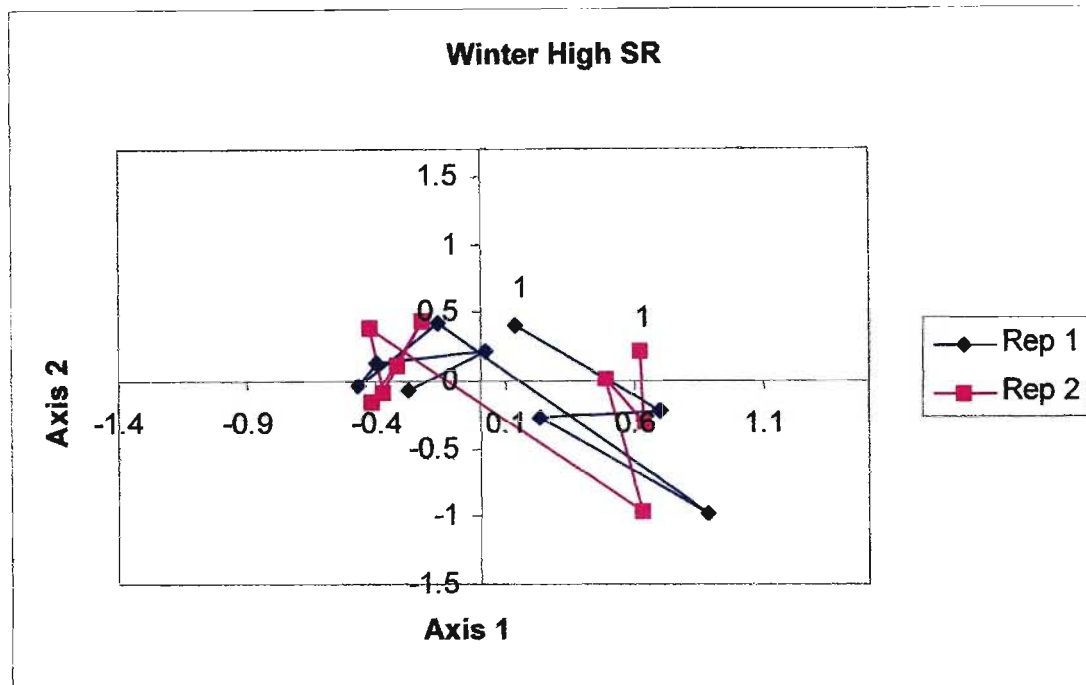


Figure 4.11l: Ordination trajectory obtained from Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed for treatment 12 using *plot ID* variables and rainfall variables as covariables. Species 61, *Melothria sp.*, 65, *Ruschia caroli* and 73, *Zygophyllum morganiana* show high cumulative fit values to axis 1. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60). 1= treatment in year 1.

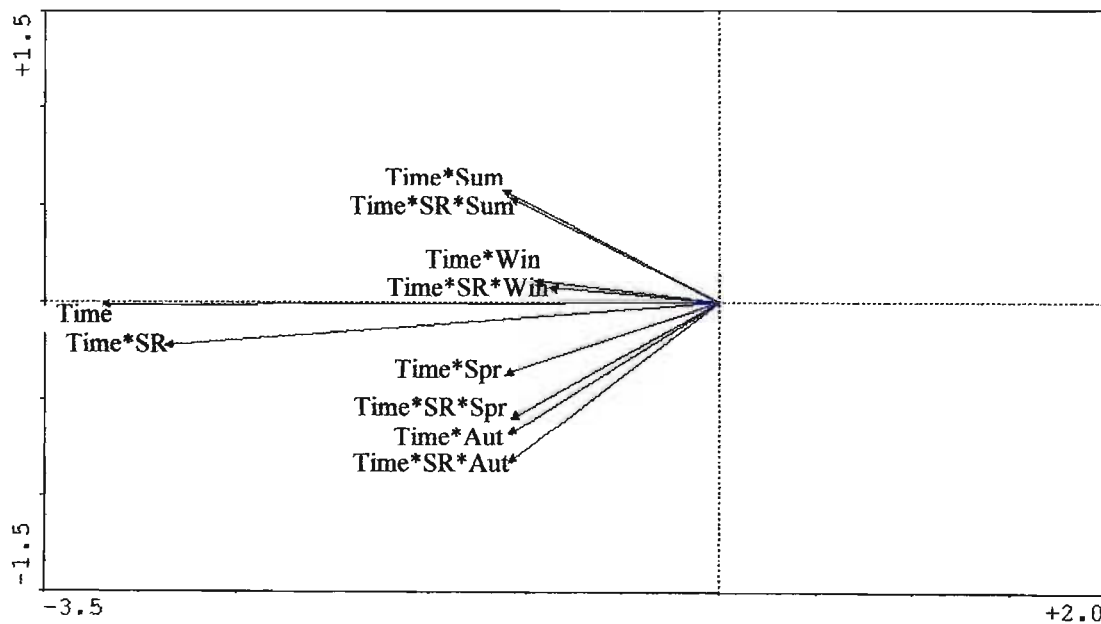


Figure 4.11m: Ordination scatter plot illustrating the direction of movement of plots under different treatments relative to one another for Canonical Correspondence Analysis applied to species matrix with 'bare ground' and *Ehrharta calycina* removed. Treatment spring*time explains the most variance along axis 1 with a canonical coefficient of -1.21 (t-value = -2.60).

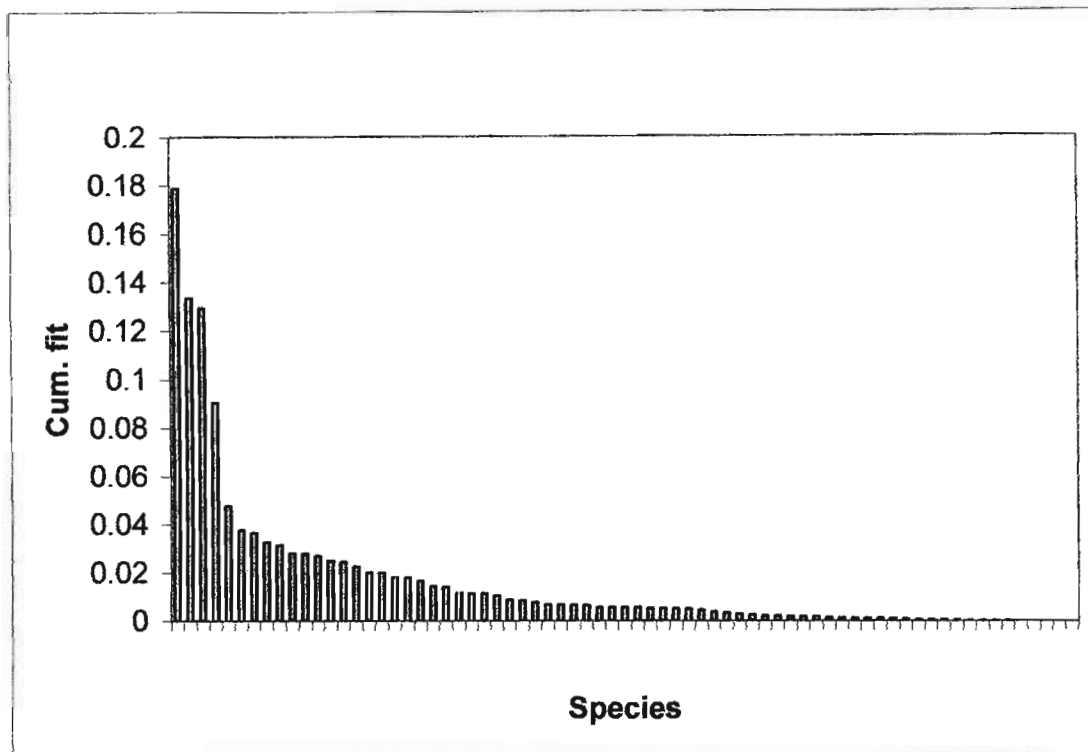


Figure 4.12: Cumulative fit along axis 1 for Canonical Correspondence Analysis applied to full data set with plot ID variables and rainfall variables used as covariables. Species 74 (bare ground) and species 9, *Ehrharta calycina* were removed from species matrix. The first 3 species are 73 = *Zygophyllum morskana* (0.18), 61 = *Melothria* sp (0.13), 65 = *Ruschia caroli* (0.13).

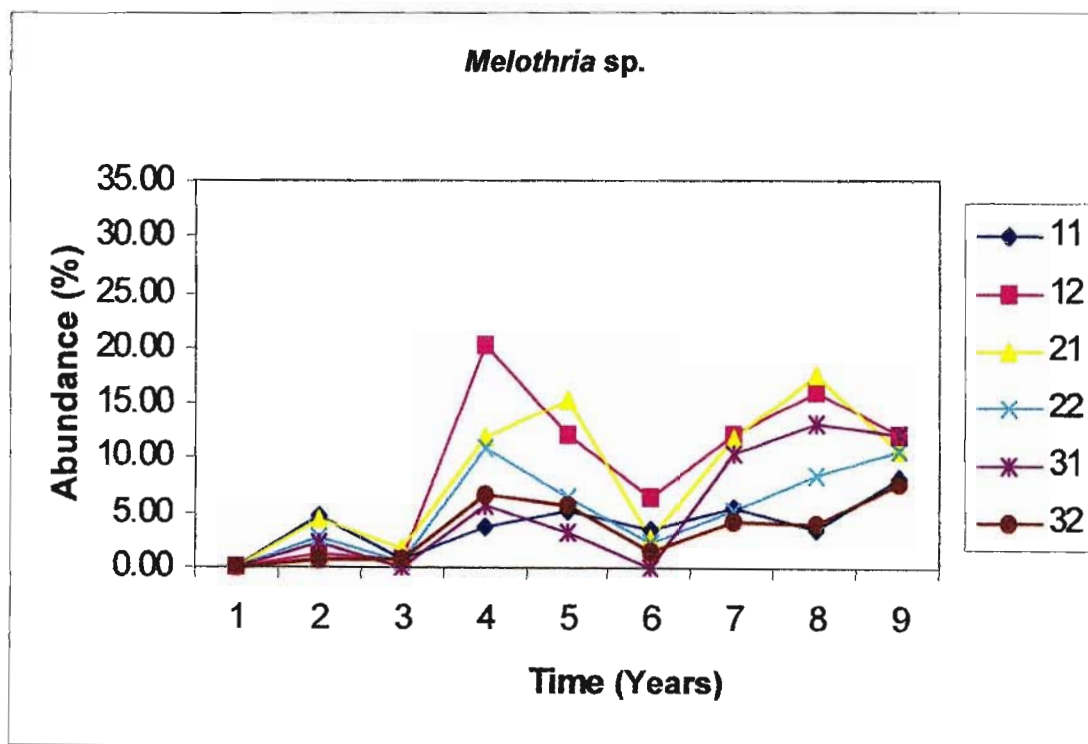


Figure 4.13a: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the full data set without sp.74 and 9 using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 61, *Melothria* sp. for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

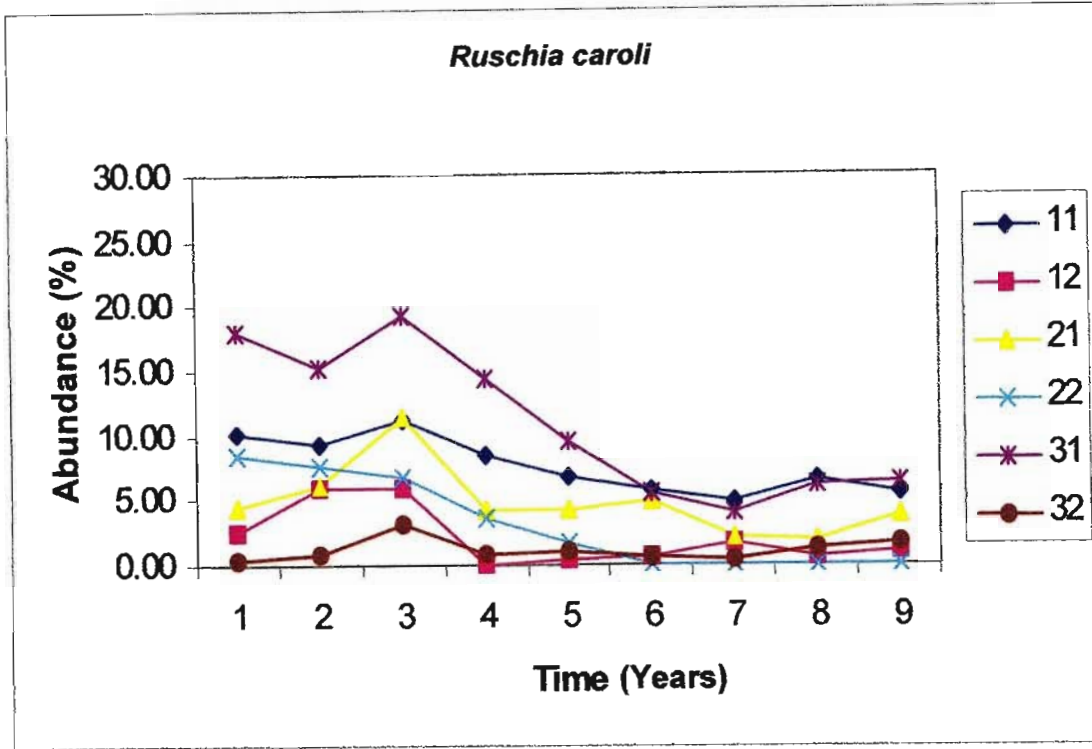


Figure 4.13b: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74 and 9** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 65, *Ruschia caroli* for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

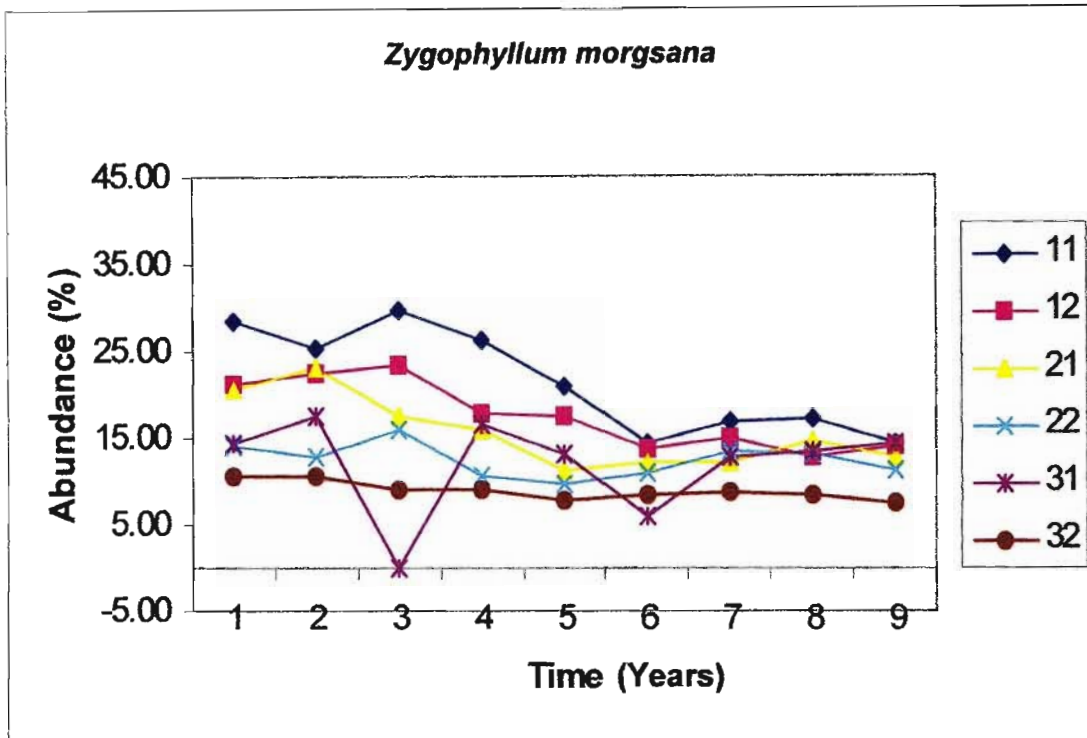


Figure 4.13c: Change in cover abundance in the spring grazing treatments of species with high cumulative fit for the Canonical Correspondence Analysis applied to the **full data set without sp.74 and 9** using 'Plot ID' variables and rainfall variables as covariables. Relative abundance of species 73, *Zygophyllum morgsana*. for treatments 1 (spring low SR), 2 (spring medium SR) and 3 (spring high SR) from year 1 to 9. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc.

4.2.5 Euclidean distance

Euclidean distance values were obtained for treatment sample years relative to year 1 from the full data set, the relative abundance data set and the relative abundance data set from which *Ehrharta calycina* had been removed. The significance of change in species composition over time is illustrated by the euclidean distance value of a sample, relative to that sample in year 1, rising above the upper confidence limit (UCL, see Chapter 3: Methodology).

The euclidean distance graphs for the absolute abundance data set (Figure 4.14.1) show samples changing dramatically from year to year in what appears to be a response to fluctuating rainfall (particularly PS rainfall – Figure 4.15.1). The significance of these fluctuations can be attributed to changes in cover of species such as *Ehrharta calycina* and ‘bare ground’ both of which were shown by the ordination analyses as responding significantly to rainfall. This assumption is further supported by comparison of the euclidean distance graphs with rainfall data (Figure 4.15). The peaks associated with the euclidean distances for the absolute abundance data set correspond to years of high PS rainfall during years 3 and 6 (Figure 4.15.1). From a significance perspective, it is during years of high rainfall that euclidean distances are highest above the UCL line emphasizing the overriding effect of rainfall on cover caused by fluctuations in *Ehrharta calycina* in particular. While this is the case, it is also apparent that very few treatment samples return to a species composition similar to that characterising the treatment in year 1. One would expect this to be the case if peaks and troughs in the euclidean distance graph were simply a consequence of eruptions and die offs of species responding to years of high and low rainfall. This suggests that perhaps an underlying directional trend, caused by the treatment variables, may be adding to the euclidean distance values experienced by samples relative to year 1. This deduction is confirmed by the results of the euclidean distance analysis applied to data sets from which species responding to rainfall have been removed.

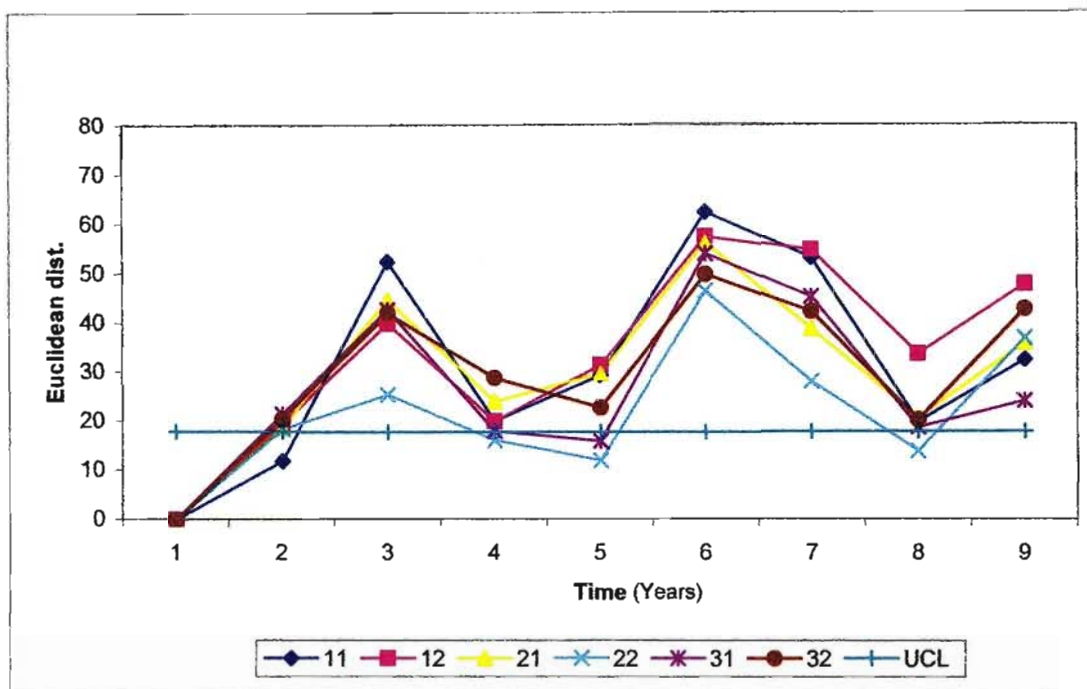


Figure 4.14.1a: Euclidean distance of treatment samples relative to year 1 for absolute abundance species matrix. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

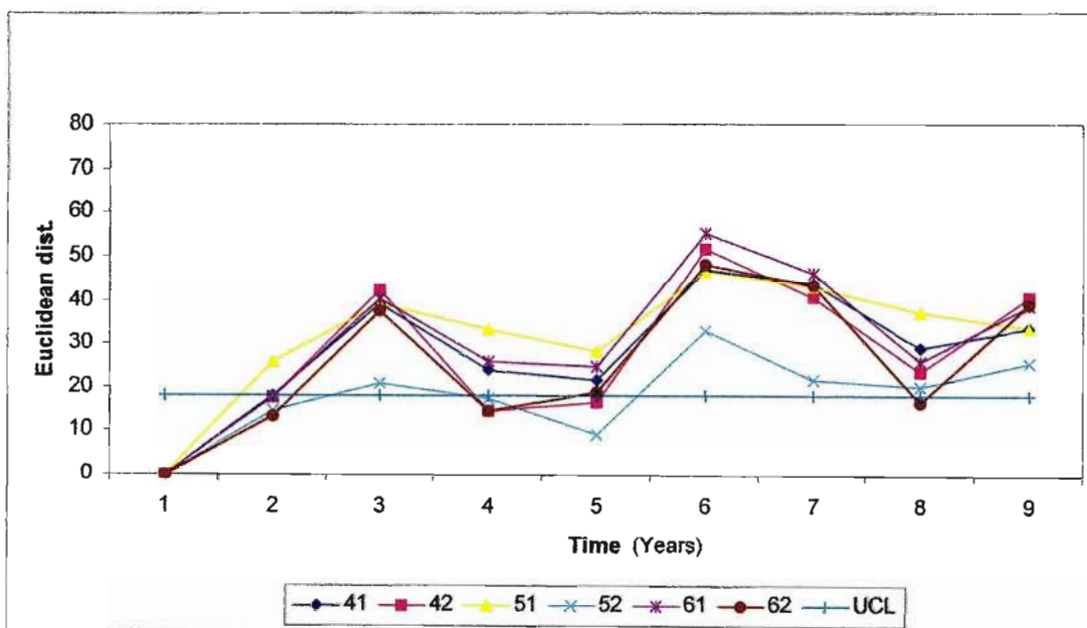


Figure 4.14.1b: Euclidean distance of treatment samples relative to year 1 for absolute abundance species matrix. 41 = Treatment 4, rep 1; 42 = Treatment 4, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

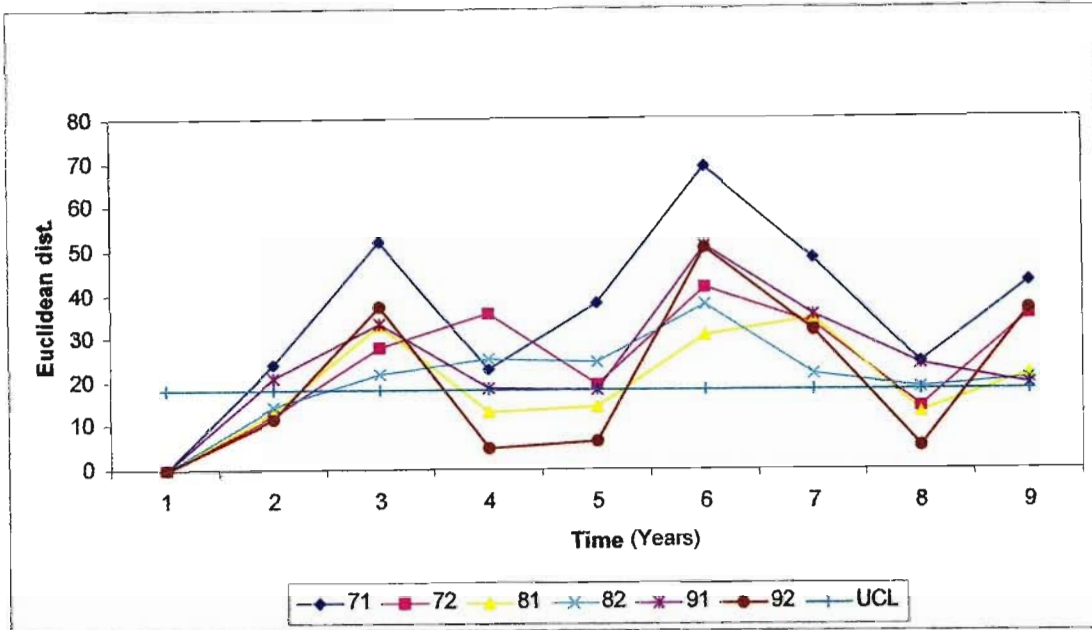


Figure 4.14.1c: Euclidean distance of treatment samples relative to year 1 for absolute abundance species matrix. 71 = Treatment 7, rep 1; 72 = Treatment 7, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

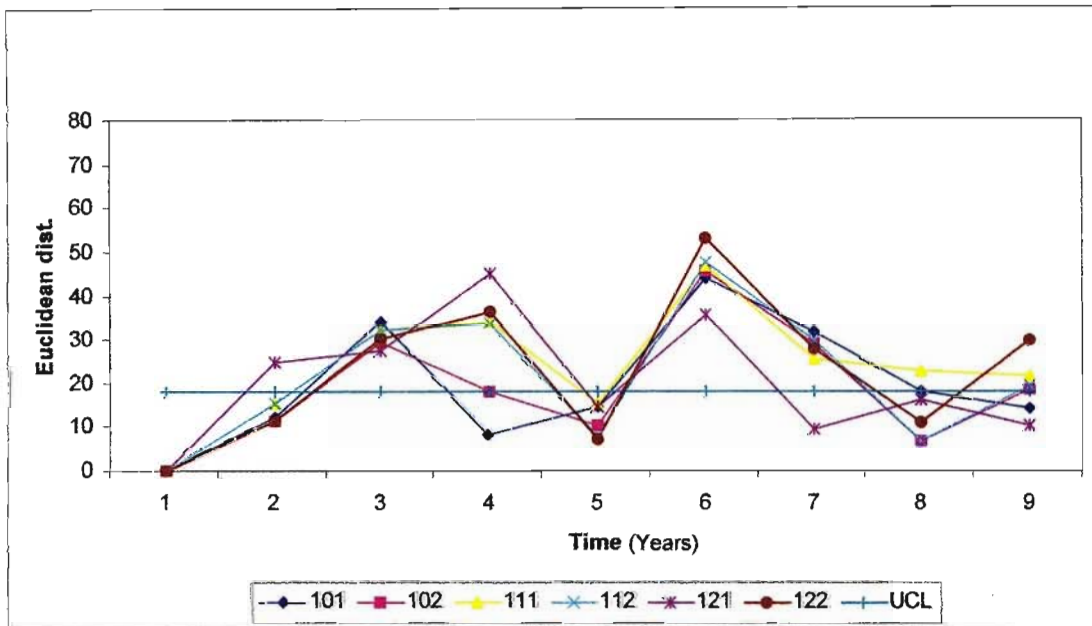


Figure 4.14.1d: Euclidean distance of treatment samples relative to year 1 for absolute abundance species matrix. 101 = Treatment 10, rep 1; 102 = Treatment 10, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

To remove the fluctuation in the euclidean distance measures caused by rainfall, the 'bare ground' variable was removed from the species matrix which was then relativised, creating a relative abundance matrix which provided the subject of the Euclidean distance analyses presented as Figure 4.14.2. The relative abundance species matrix (Figure 4.14.2) confirms the results of the relative abundance ordination analyses with the euclidean distances of samples increasing over time

relative to year 1. This occurs at a decreasing rate until a levelling off occurs, following which sporadic fluctuations are evident. A number of the samples change directionally to the extent that they can be considered significantly different post treatment application to what they were prior to the grazing trial. While a directional change is characteristic of all samples, not all change to an extent considered significant (i.e. above the UCL). This may be a consequence of the conversion of the data set from absolute abundance to relative abundance, a procedure which removed much of the variation from the ordination analyses. Even so, the distinct change in species composition over time, the directional nature of this change and the manner in which change levels off over time all suggest a response by the veld to the treatment variables.

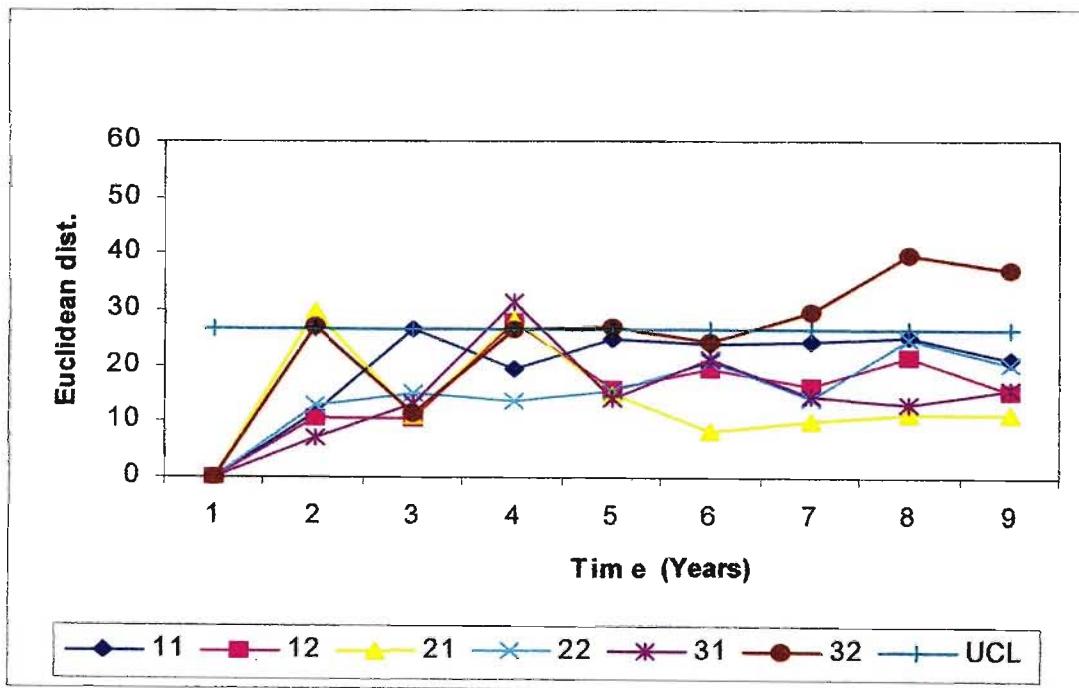


Figure 4.14.2a: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

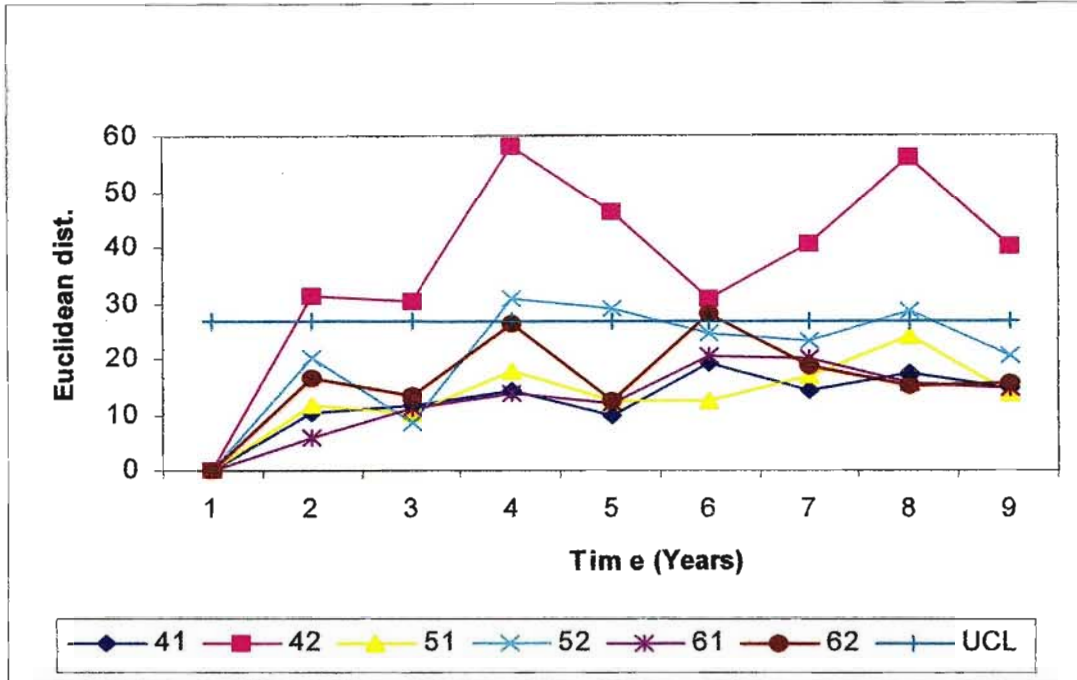


Figure 4.14.2b: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix. 41 = Treatment 4, rep 1; 42 = Treatment 4, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

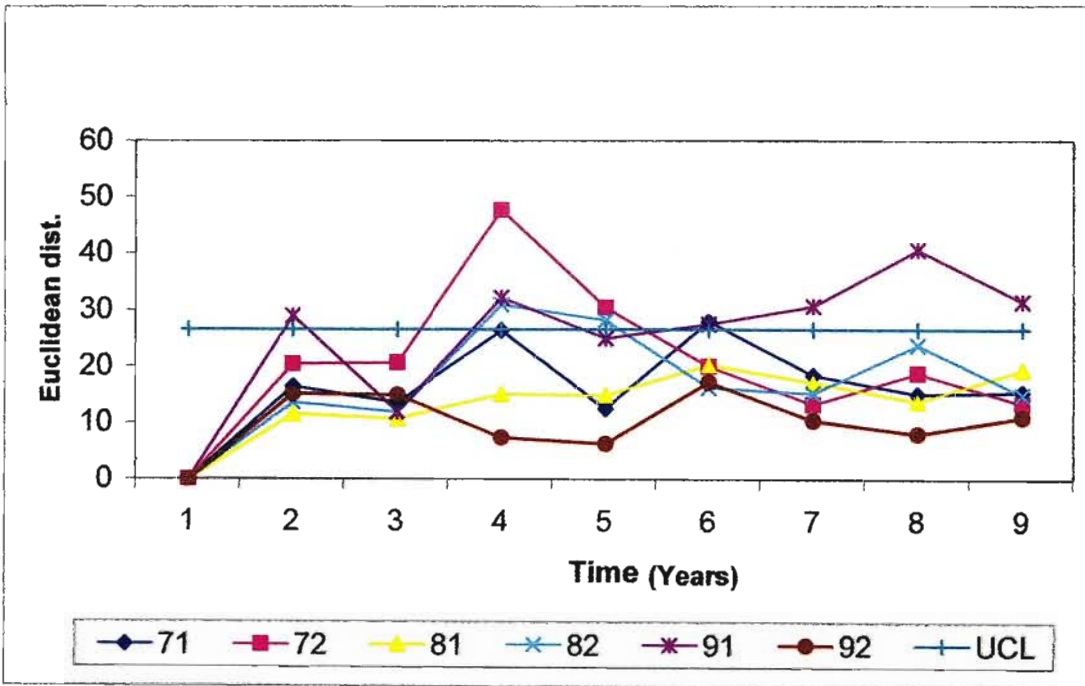


Figure 4.14.2c: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix. 71 = Treatment 7, rep 1; 72 = Treatment 7, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

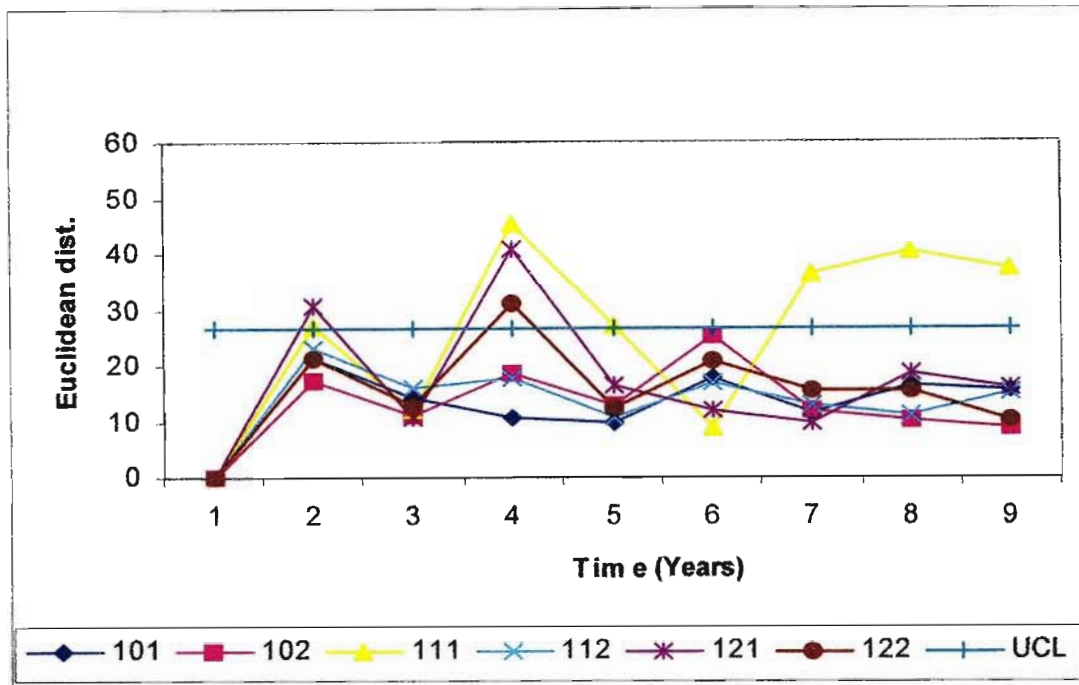


Figure 4.14.2d: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix. 101 = Treatment 10, rep 1; 102 = Treatment 10, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

The same trend exposed by the relative abundance euclidean distance tests is evident in the relative abundance matrix from which *Ehrharta calycina* has been removed (Figure 4.14.3). The removal of 'bare ground' and *Ehrharta calycina* serves to remove the two main variables fluctuating in response to rainfall. Most of the variation remaining in the data set is, as a result, a consequence of the various grazing treatments and any directional changes in euclidean distance can be attributed to the impact of grazing on the veld resource. As with the euclidean distance graphs for the relative abundance matrix, the changes in species composition in the shrub/herb complex appear to be directional in nature approaching the UCL and levelling off as the trial progresses. These characteristics suggest a relation between the various grazing treatments and the veld's dynamics.

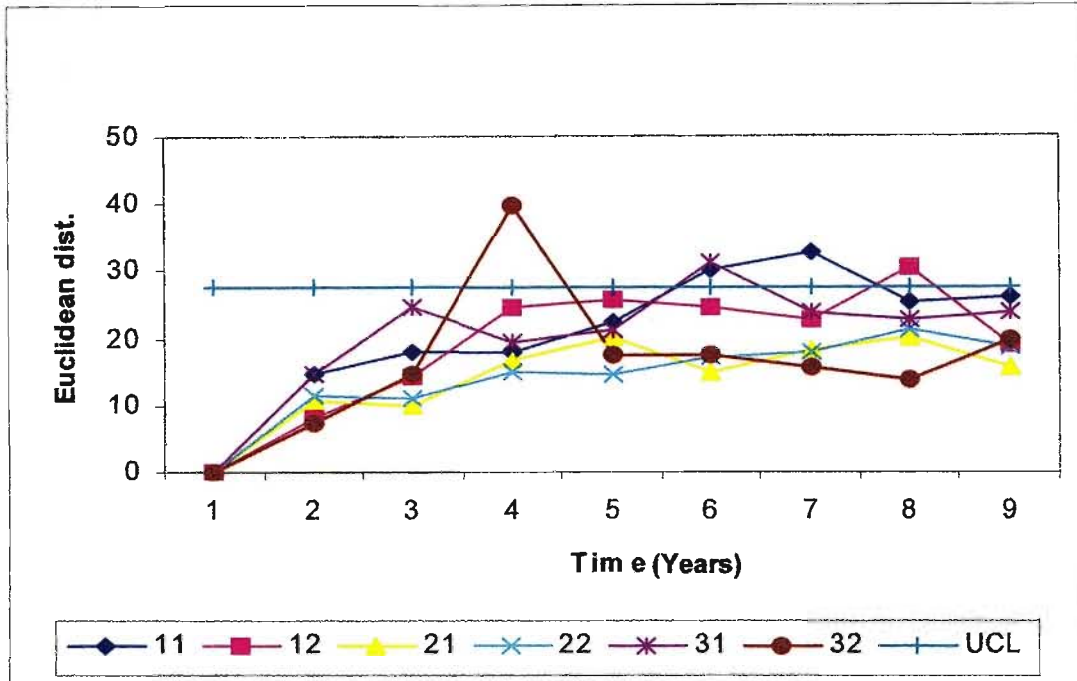


Figure 4.14.3a: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix with *Ehrharta calycina* removed. 11 = Treatment 1, rep 1; 12 = Treatment 1, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

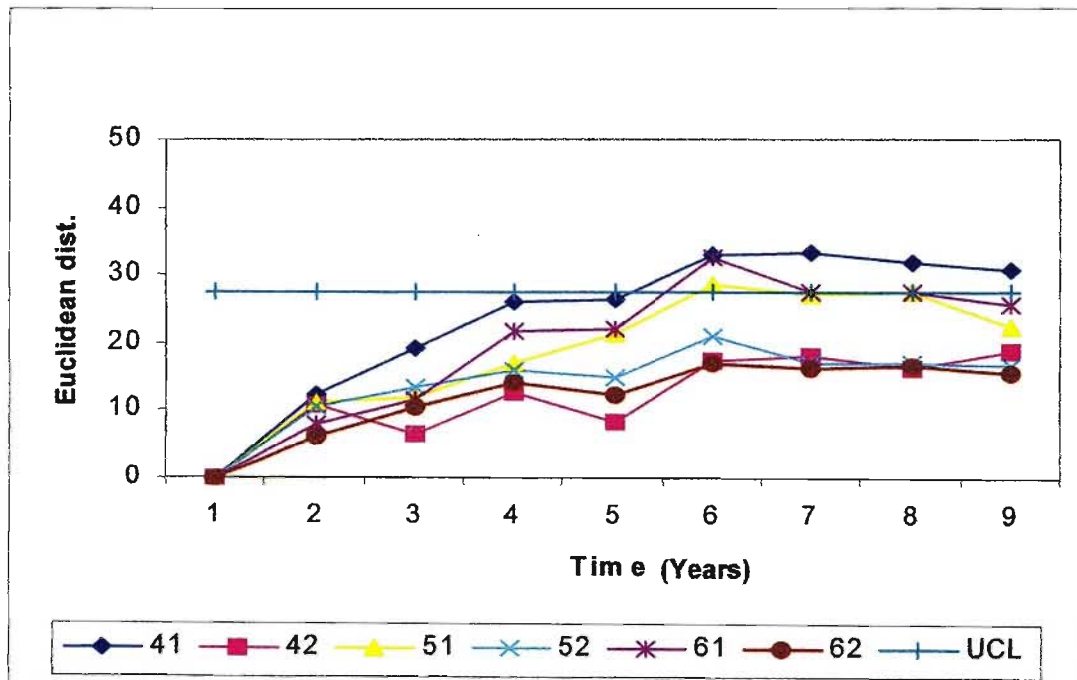


Figure 4.14.3b: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix with *Ehrharta calycina* removed. 41 = Treatment 4, rep 1; 42 = Treatment 4, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

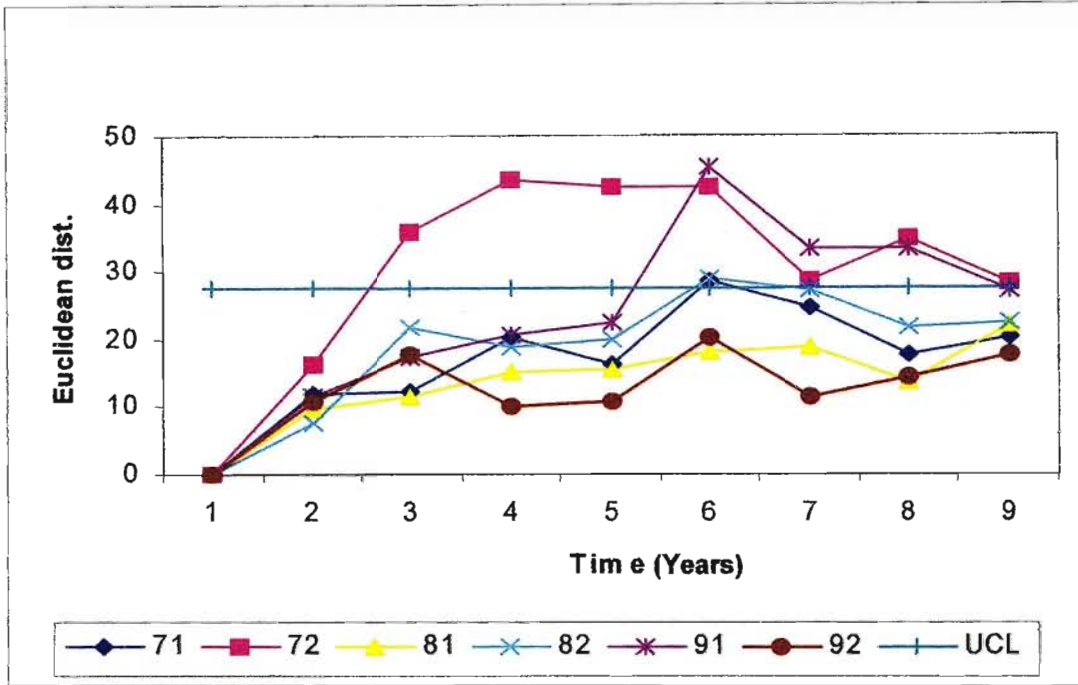


Figure 4.14.3c: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix with *Ehrharta calycina* removed. 71 = Treatment 1, rep 1; 72 = Treatment 7, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

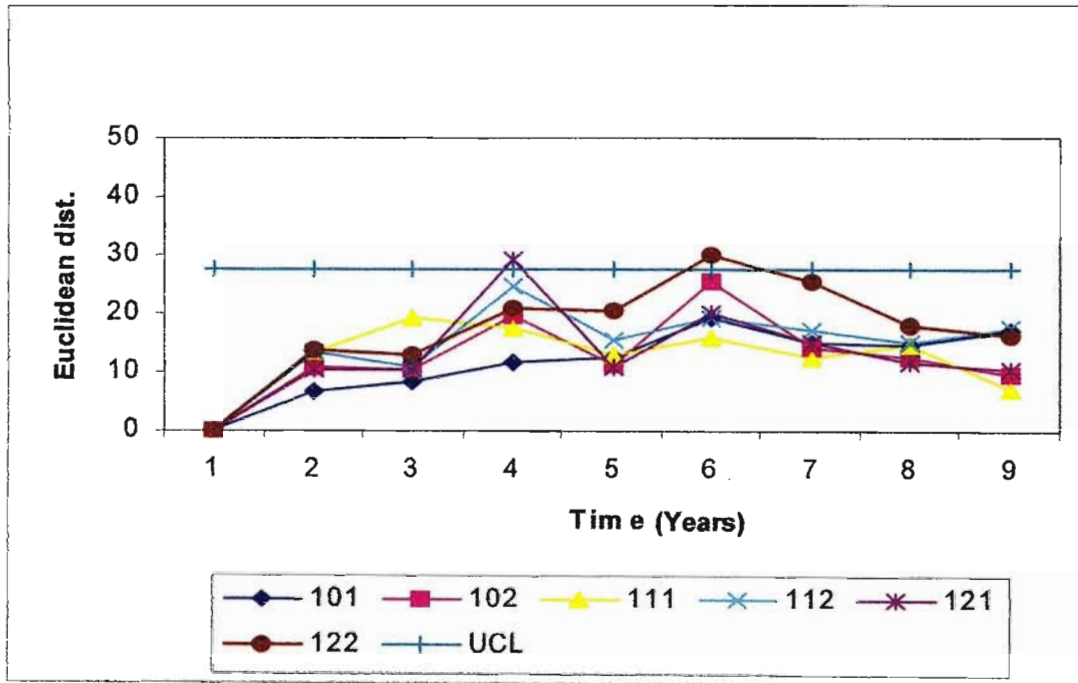


Figure 4.14.3d: Euclidean distance of treatment samples relative to year 1 for relative abundance species matrix with *Ehrharta calycina* removed. 101 = Treatment 10, rep 1; 102 = Treatment 10, rep 2 etc. UCL = Upper Confidence Limit ($p < 0.05$) which represents the level above which samples differ significantly from sample 1.

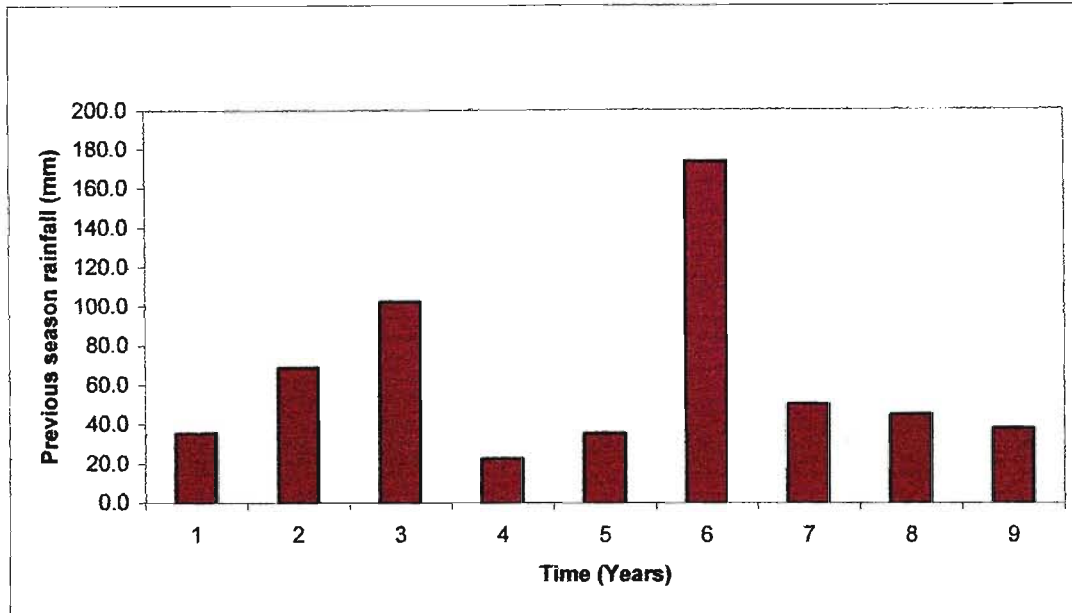


Figure 4.15.1: Previous Season rainfall (mm). Previous Season rainfall refers to rainfall which fell during the season prior to the season in which sampling took place. I.e. rainfall during autumn for samples taken during winter.

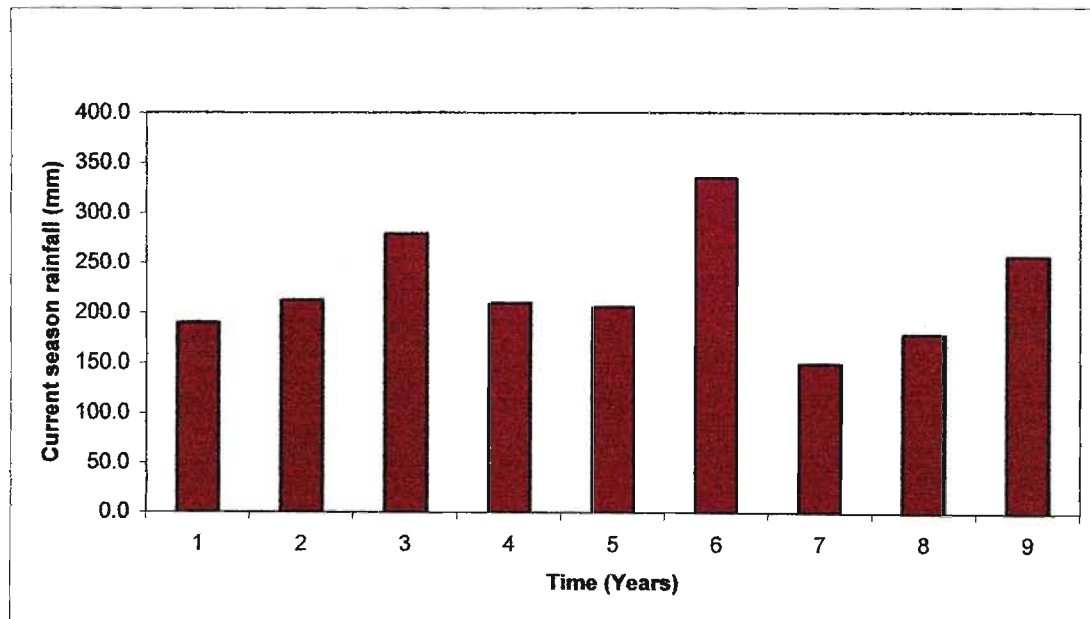


Figure 4.15.2: Year prior rainfall (mm). Includes rainfall from the three seasons prior to the season of sampling as well as the season in which sampling took place.

CHAPTER 5: RESULTS FROM ANALYSIS OF VARIANCE

5.1 Results of Analysis of Variance applied to absolute abundance data set

5.1.1 Plant categories (See Appendix 1 for ANOVA Summary)

5.1.1.1 Palatable species

The results of the ANOVA applied to the palatable category of the absolute abundance data set showed season ($p < 0.001$), time ($p < 0.001$), season*SR ($p = 0.005$) and season*time ($p = 0.008$) as significantly influencing the data. Examination of the tables of means for those treatments that showed significance reveals important information regarding the effect that the treatments have on this category. On average, the spring treatment has the highest abundance (60.1%) of palatable species followed by plots grazed during the summer (58.4%) and autumn months (57.4%) (Figure 5.1). The palatable plants category displayed a significantly higher absolute abundance in plots grazed during spring, summer and autumn compared to plots grazed during winter. Examination of the changes in palatable species which occur over time illustrates that, while different years do have significantly different abundances of palatable species (Figure 5.2), there is no consistent trend of increase or decrease but rather erratic changes which correspond largely to patterns in PS rainfall (Figure 4.15.1). This is because the palatable species category includes *Ehrharta calycina*, the abundance of which fluctuates according to PS rainfall. A better indication of the response of palatable plants to treatments is provided later. The season*SR interaction (Appendix 1) shows high palatable species absolute abundance means for spring (63.3%) and summer (64.5%) treatments at high and medium stocking rates respectively. The significance of the difference between the means of various season*SR treatments in the absolute abundance data set for this category indicates that grazing is having an influence on the palatable plant abundance in the Nortier rangeland. While the influence of grazing is shown by this analysis to be significant, the correlation between the mean abundances of the palatable category over time with PS rainfall data suggests that rainfall is having an overriding effect on the abundance of this category.

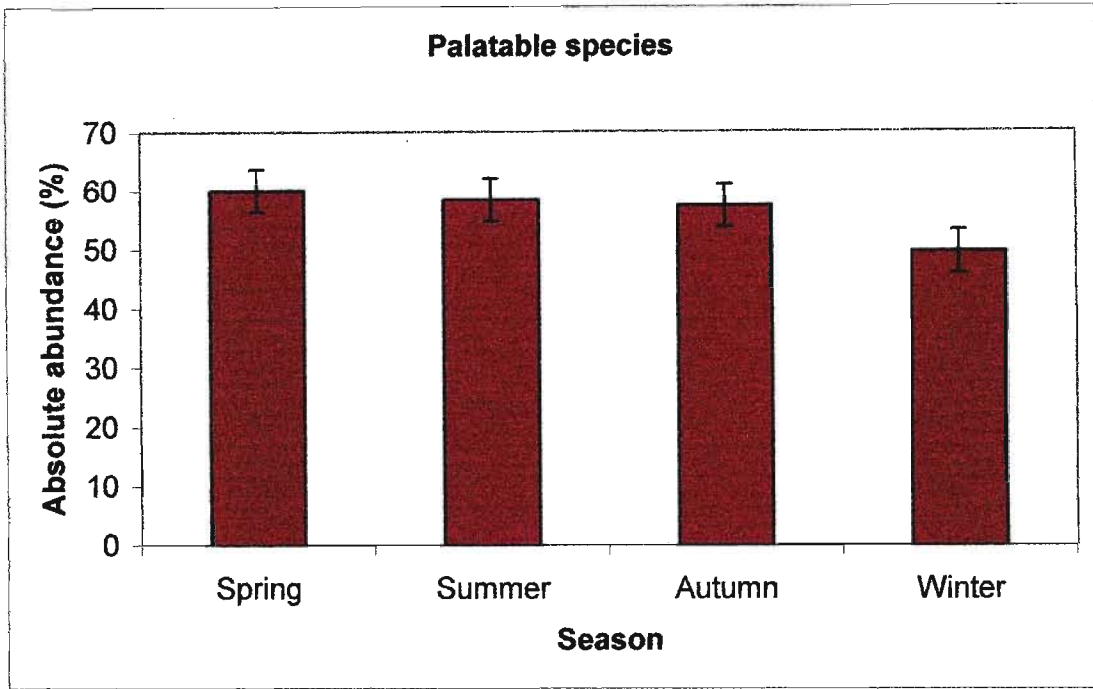


Figure 5.1: Mean absolute abundance of the palatable species category for plots under different season of grazing treatments. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

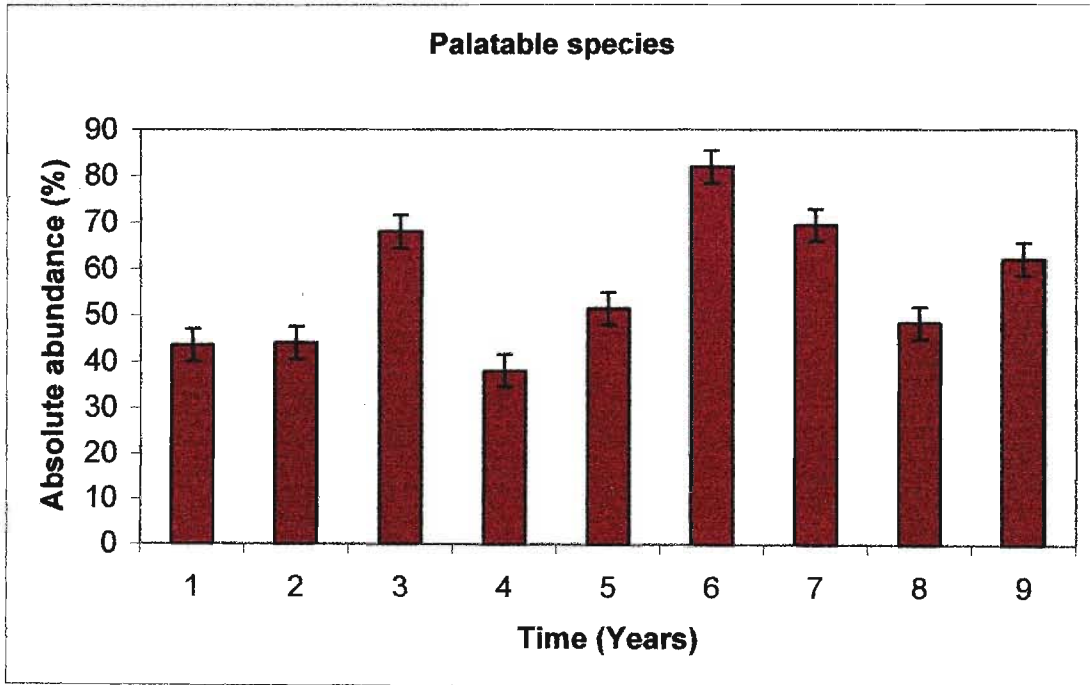


Figure 5.2: Mean absolute abundance of the palatable species category over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.1.2 Unpalatable species

Time ($p < 0.001$) (Figure 5.3), SR ($p = 0.016$) (Figure 5.4) and Season*SR ($p = 0.002$) significantly (at a 5% level of significance) affected the plots from an unpalatable species perspective. Unpalatable species have the highest absolute abundance in plots grazed at high SR during summer (24.8%) and low SR during winter (21.9%), with low SR generally having a significantly higher abundance of unpalatable species than those which are grazed at moderate to high SR. The significance of the difference in mean absolute abundance of plots grazed at different stocking rates, and at different stocking rates during different seasons, adds further support to the notion that grazing is having a significant impact on the Nortier rangeland.

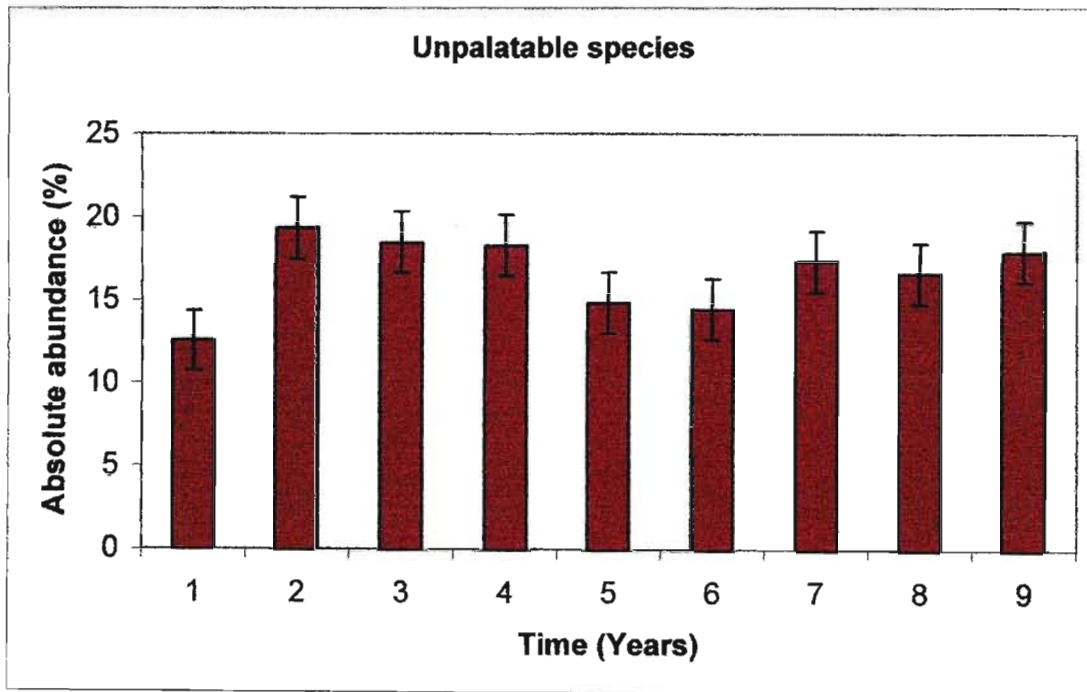


Figure 5.3: Mean absolute abundance of the unpalatable species category over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

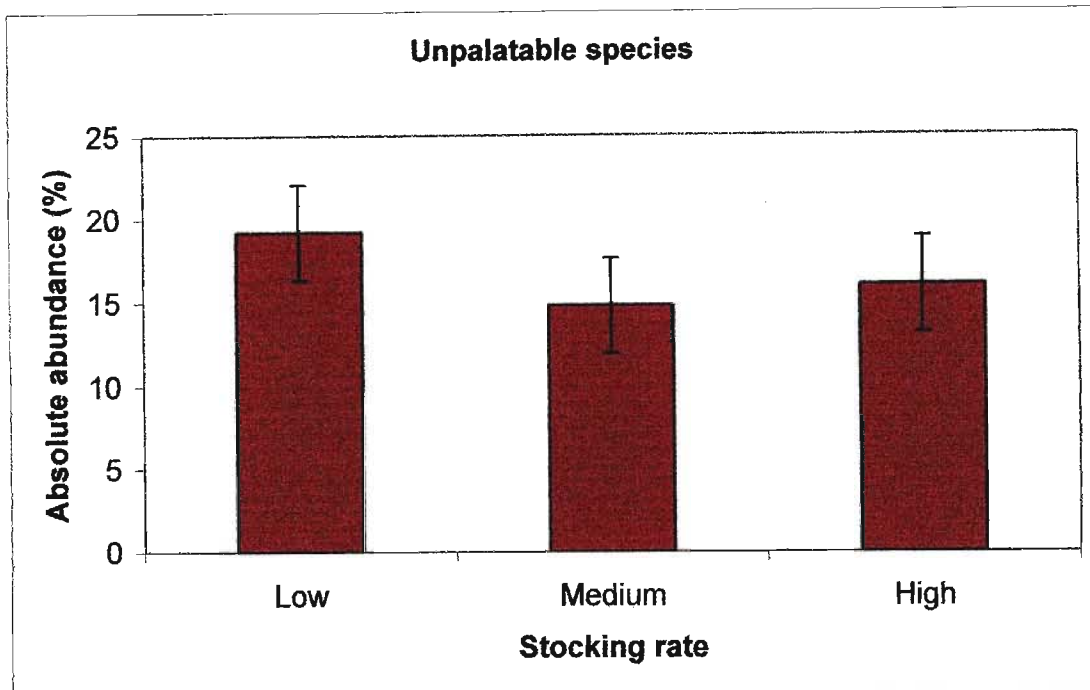


Figure 5.4: Mean absolute abundance of the unpalatable species category for plots under different stocking rate treatments. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.1.3 Shrub/herb complex

The shrub/herb complex in the absolute abundance data set showed a significant response to the time ($p < 0.001$) and time*season ($p = 0.003$) variables. Of particular importance is the change in the abundance of the shrub/herb complex over the entire trial period increasing from an abundance of 35.8% in year 1 to an abundance of 55.9% in year 9 (Figure 5.5). A straight line plotted through the mean yearly abundance of this category emphasizes the gradual increase in the cover of this resource over the trial period (trend line gradient = 1.67). While all the season of graze treatment plots experienced an increase in the absolute abundance of the shrub/herb complex the time*season interaction highlights the difference in the extent of this increase (Figure 5.6). Plots grazed during spring and summer show the greatest increase in the abundance of this resource, with increases of 63.6% and 86.3% respectively over the trial period. Autumn and winter plots experienced slightly smaller increases ending the trial with 50.2% and 27.4% increases respectively (Figure 5.6). The significance of the time*season interaction, constitutes an important finding and provides insight into how grazing has a significant influence on the shrub/herb complex from an absolute abundance perspective.

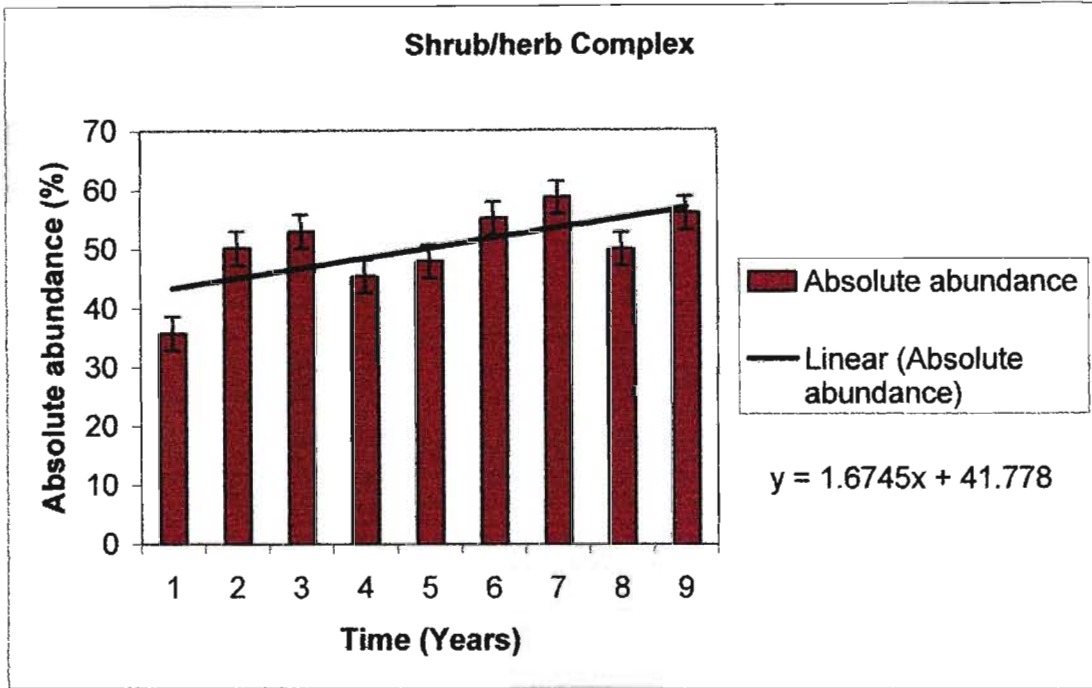


Figure 5.5: Mean absolute abundance of the shrub/herb complex category over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

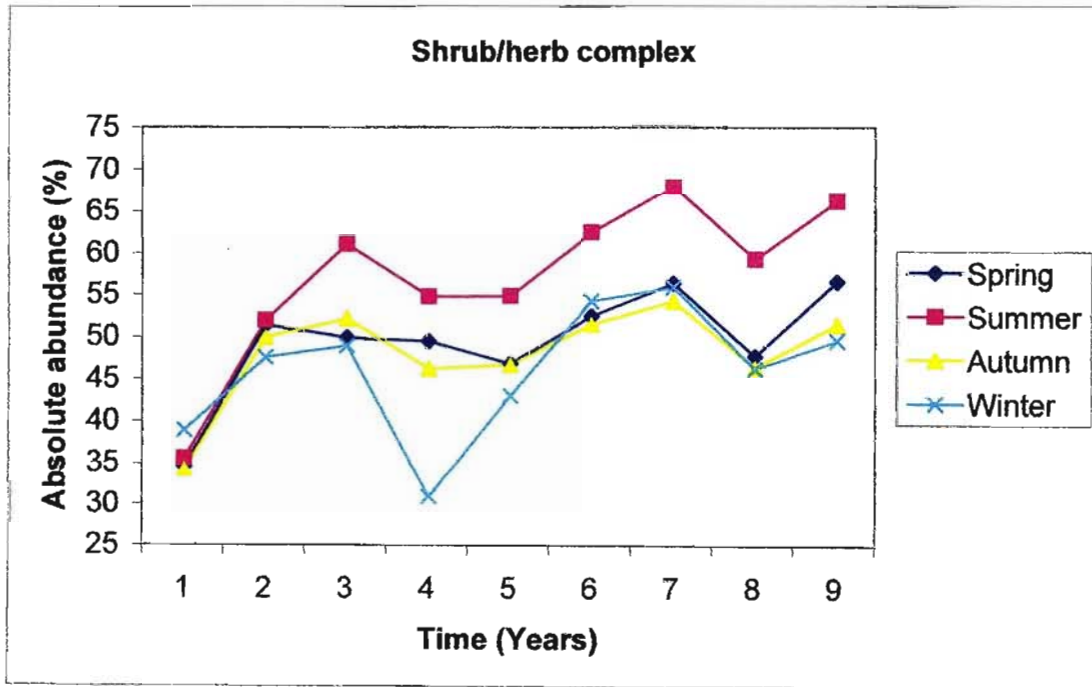


Figure 5.6: Mean absolute abundance of the shrub/herb complex category for plots under different season of grazing applications over the trial period. Obtained from analysis of variance applied to the absolute abundance data set.

5.1.1.4 Grasses

The grass category in the absolute abundance data set showed a significant response to time ($p < 0.001$). The year-to-year fluctuation in the absolute abundance of the grass category (Figure 5.7) correlates significantly with the PS rainfall variable highlighting the significance of the role played by rainfall in the Nortier rangeland.

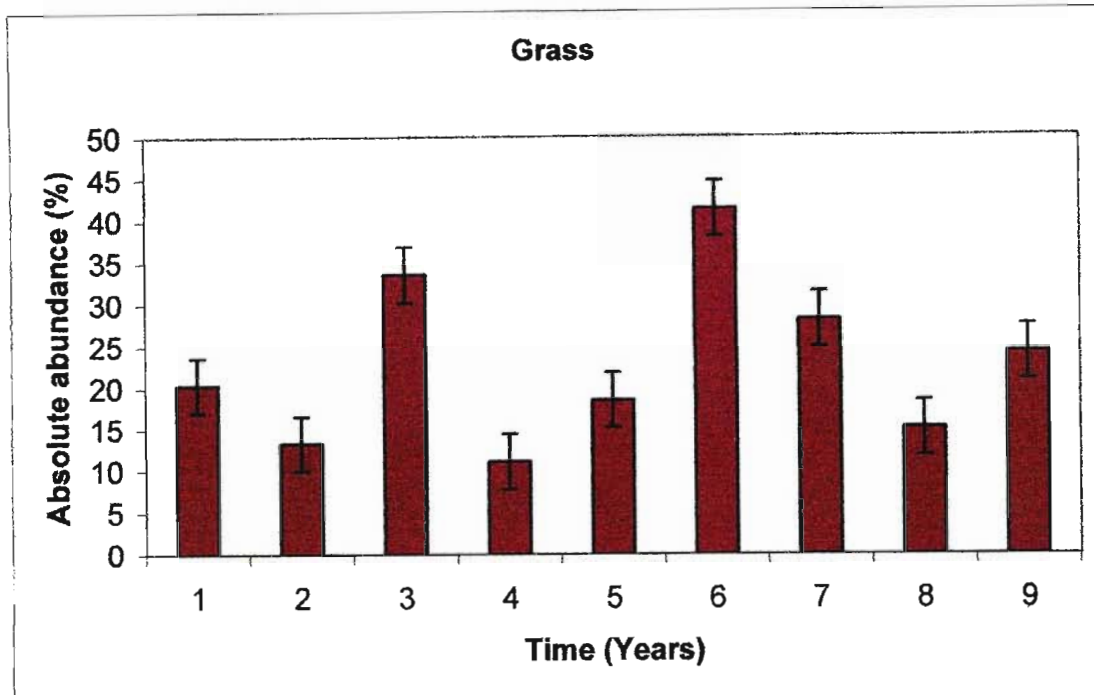


Figure 5.7: Mean absolute abundance of the grass category over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.1.5 Bare ground

The bare ground variable showed a significant response to time ($p < 0.001$), season ($p < 0.001$), SR ($p = 0.035$), season*SR ($p = 0.025$) and time*season ($p = 0.002$) variables. When averaged across all seasons, sample plots under low SR applications display the lowest measure of bare ground (25.0%) in comparison to plots grazed at moderate (27.2%) and high (28.7%) stocking rates (Figure 5.8). The high bare ground figures experience by plots grazed at high stocking rates is, however, largely a consequence of the adverse impact of intense grazing during the growing season (winter) and must not be taken as consistent across all seasons. The application of high stocking rates during spring (22.4%), for example, results in lower bare ground figures than at low and medium stocking rates. It is during the winter (39.6%) and autumn (29.3%) months that the application of high stocking is particularly detrimental to the veld from a bare ground perspective. Examination of the season

(Figure 5.9) and season*time means highlights the fact that grazing during spring (Year 9 abundance = 15.3%), summer (Year 9 abundance = 13.5%) and autumn (Year 9 abundance = 19.2%) has a significantly less detrimental effect, in terms of cover, than grazing during winter (Year 9 abundance = 31.6%). Examination of the 'bare ground' abundance averaged across treatments over the duration of the trial highlights the influence of rainfall on cover (Figure 5.10). Years experiencing high PS rainfall displayed low 'bare ground' abundance and *vice versa* for years experiencing low PS rainfall.

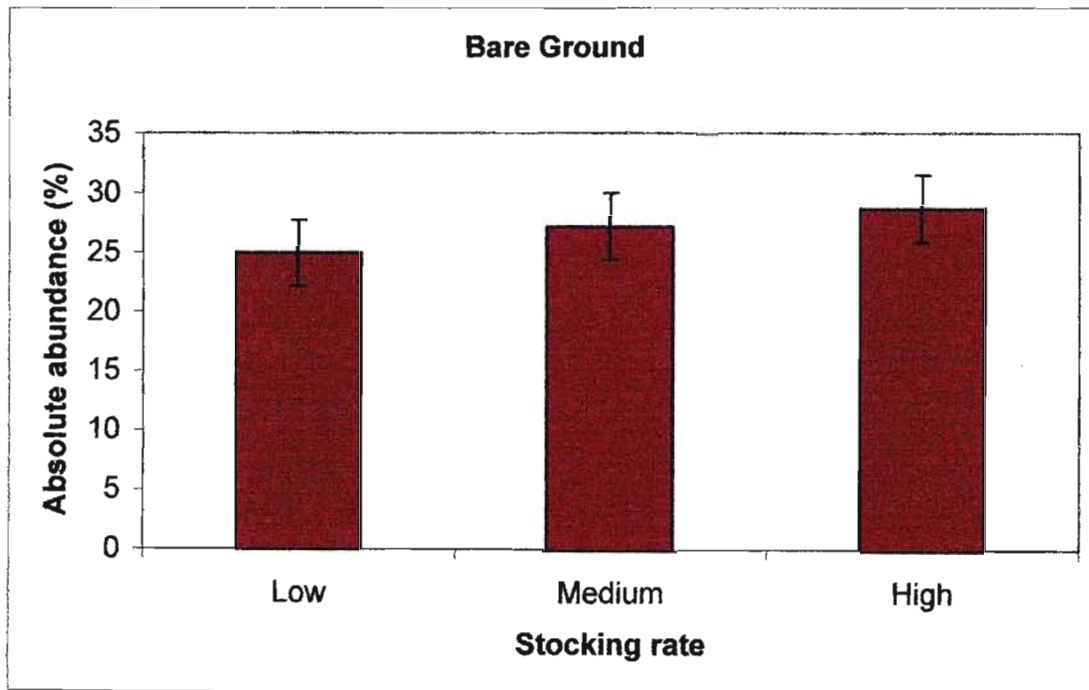


Figure 5.8: Mean absolute abundance of the bare ground category for plots under different stocking rate applications. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

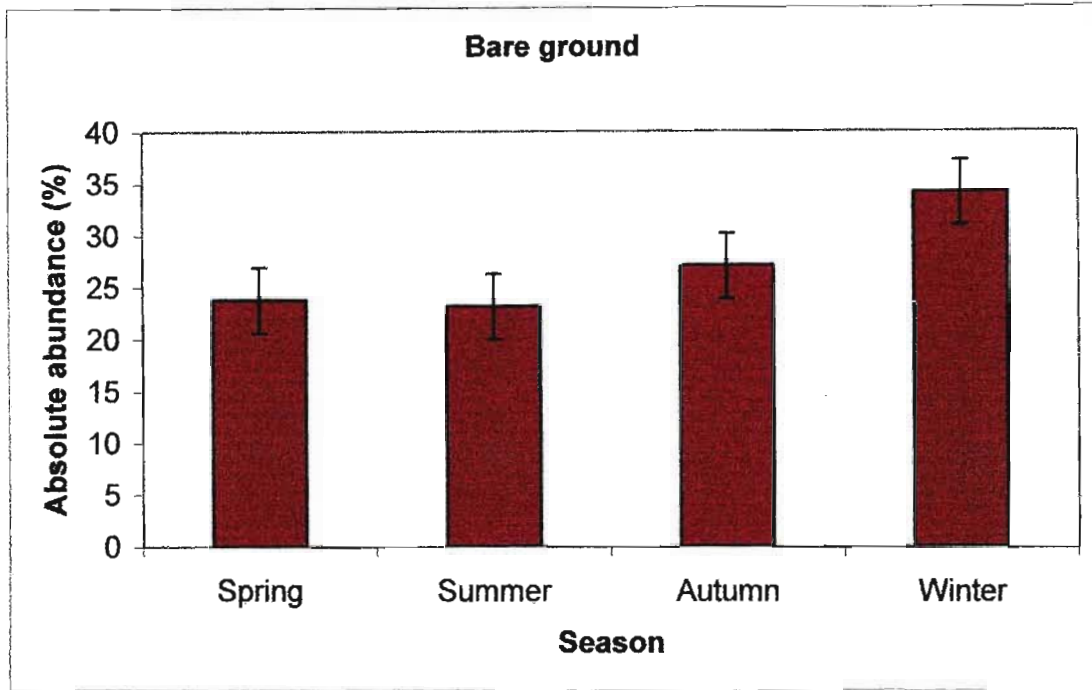


Figure 5.9: Mean absolute abundance of the bare ground category for plots under different season of grazing treatments. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

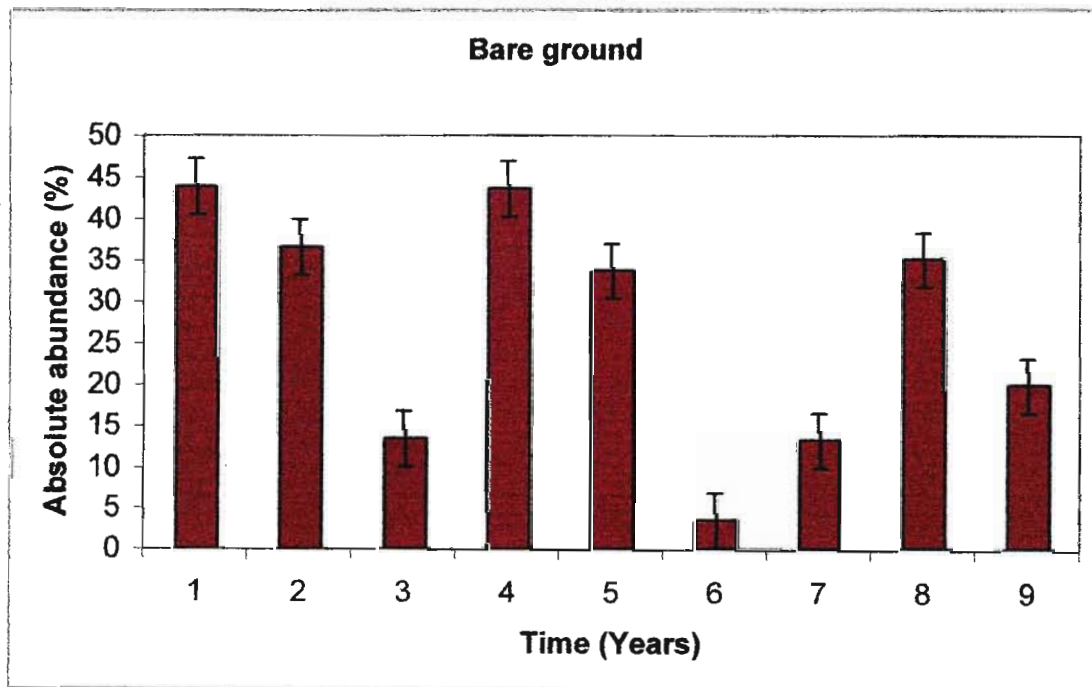


Figure 5.10: Mean absolute abundance of the bare ground category over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.2 Plant species (See Appendix 2 for ANOVA Summary)

5.1.2.1 *Hermannia scordifolia*

Species 20, *Hermannia scordifolia*, showed a significant response to time ($p < 0.001$) and time*season ($p < 0.001$). An overall increase in the absolute abundance of

H.scordifolia is evident when averaged across all treatments (trend line gradient = 0.31) (Figure 5.11). Of particular significance is the dramatic increase in the absolute abundance of *H.scordifolia* in plots grazed during summer (43.8% increase) (Figure 5.12 and 5.13). A less substantial but still notable increase in absolute abundance is also evident in plots grazed during spring (33.1% increase) and autumn (27.8% increase). The mean absolute abundance for *H.scordifolia* in the spring, summer and autumn plots at the end of the trial are all significantly different to the mean absolute abundance at the beginning of the trial (Appendix 2 – Species 20). This highlights the influence of grazing on this species. It is important to note that all plots did show an increase in the absolute abundance of this species though to varying extents.

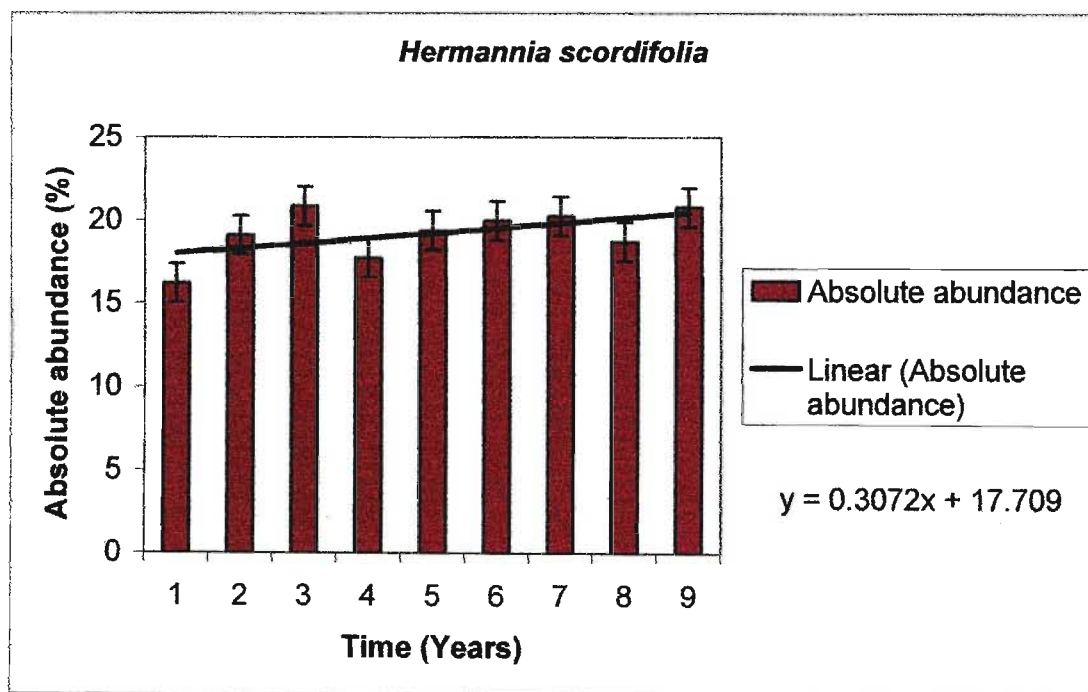


Figure 5.11: Mean absolute abundance of *Hermannia scordifolia* over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

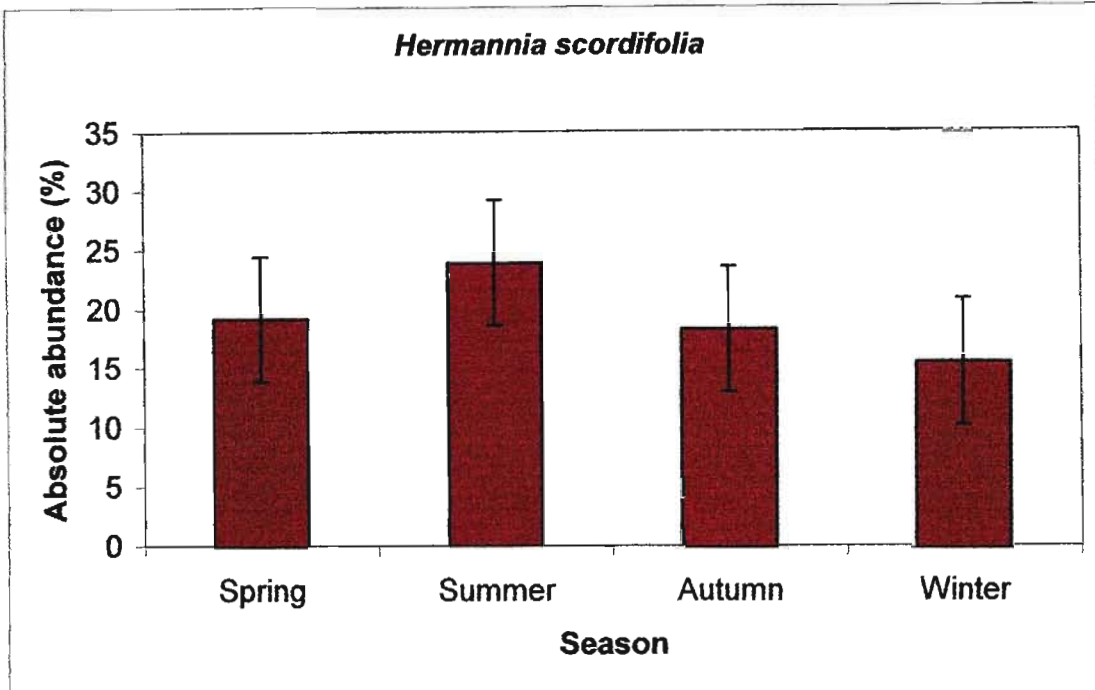


Figure 5.12: Mean absolute abundance of *Hermannia scordifolia* for plots under different season of grazing applications. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

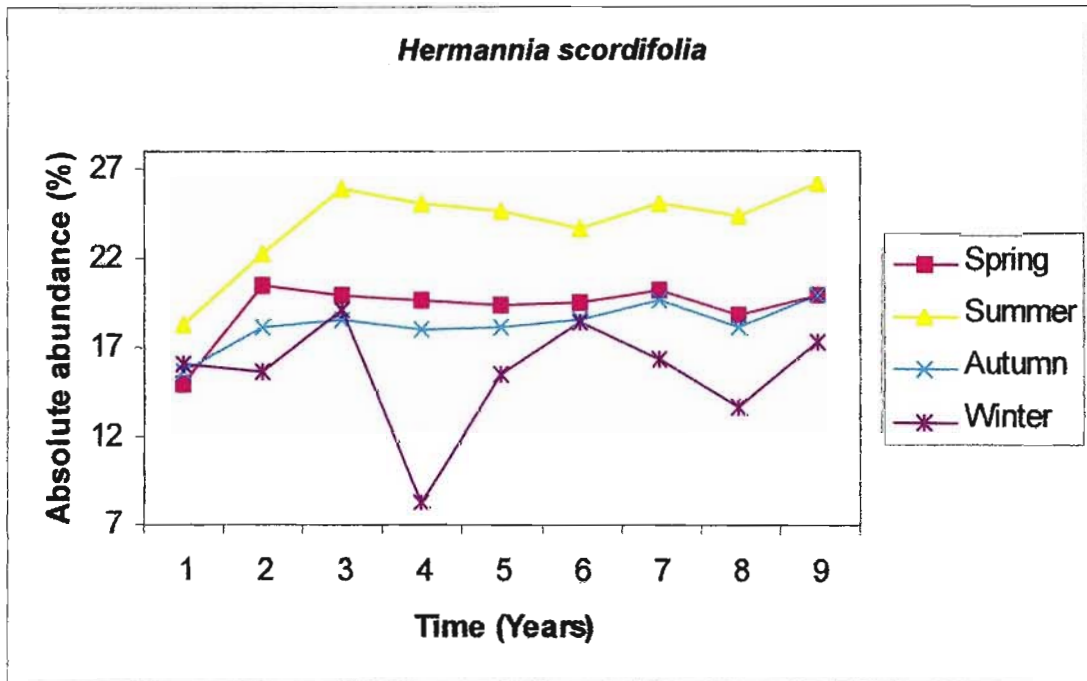


Figure 5.13: Mean absolute abundance of *Hermannia scordifolia* for plots under different season of grazing applications over the trial period. Obtained from analysis of variance applied to the absolute abundance data set.

5.1.2.2 *Tetragonia fruiticosa*

Species 44 (*Tetragonia fruiticosa*) responded significantly to time ($p < 0.001$). The bar graph generated from the mean absolute abundance of this species over each

treatment for the trial duration shows a strong relation with PS rainfall (Figure 5.14). This finding is consistent with the results of the CCA applied to the full data set which show *T.fruiticosa* to have a cumulative fit of 0.43 along axis 1 (Figure 5.5), shown to be a rainfall gradient. While the relation between *T.fruiticosa* and PS rainfall cannot be questioned it is worth noting that a trend line plotted through the bar graph depicting the change in its mean absolute abundance over time (Figure 5.14) does return a strongly positive gradient (trend line gradient = 0.79) suggesting an increase in abundance in response to grazing. This general increase in the abundance of this species is in agreement with the ordination analyses (Figure 4.4a) which indicate that it responds to both grazing and rainfall variables.

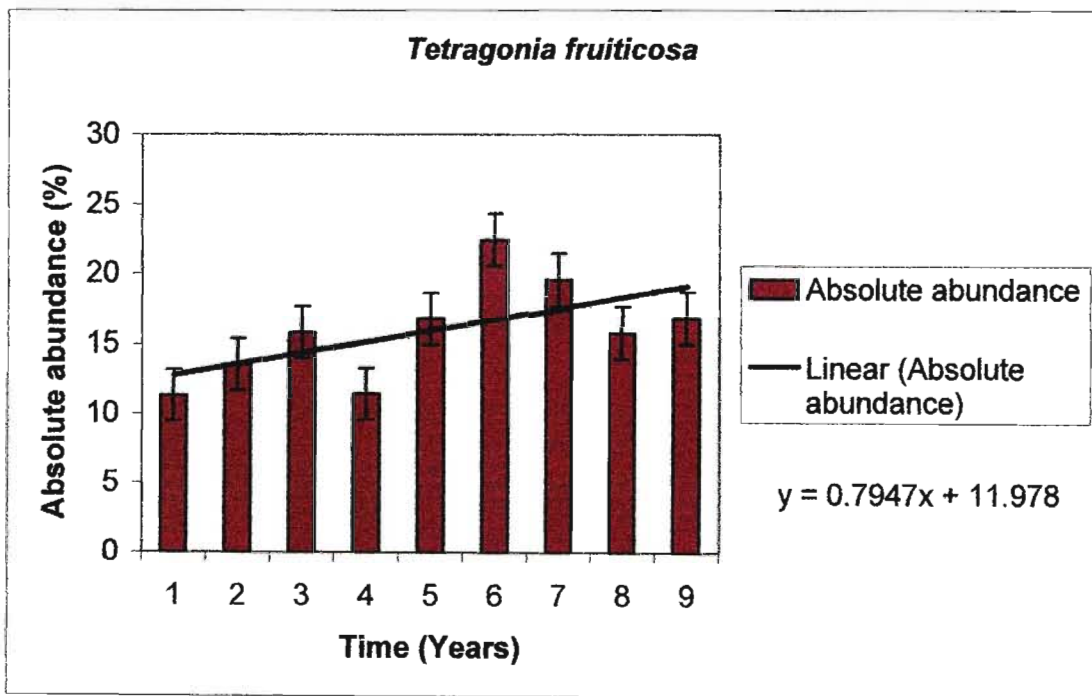


Figure 5.14: Mean absolute abundance of *Tetragonia fruiticosa* over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.2.3 *Melothria* sp.

Species 61 (*Melothria* sp.) shows significant response to time ($p < 0.001$) and time*season ($p = 0.006$). The effect of grazing on this species is made evident by the significance of the time*season interaction. Significant increases in the absolute abundance of *Melothria* sp. are noted for all season of grazing treatments and, in particular, plots grazed during spring and summer (Figure 5.15). The final year abundances for spring, summer and autumn treatments are all significantly higher than that of winter (Appendix 2 – Species 61). This is because the absolute abundance

of *Melothria* sp., while increasing for all season of grazing treatments, does so at different rates. The significance of the change in absolute abundance of this species over the trial period (Figure 5.16) serves to highlight the influence of grazing on certain components within the veld resource despite the highly variable rainfall.

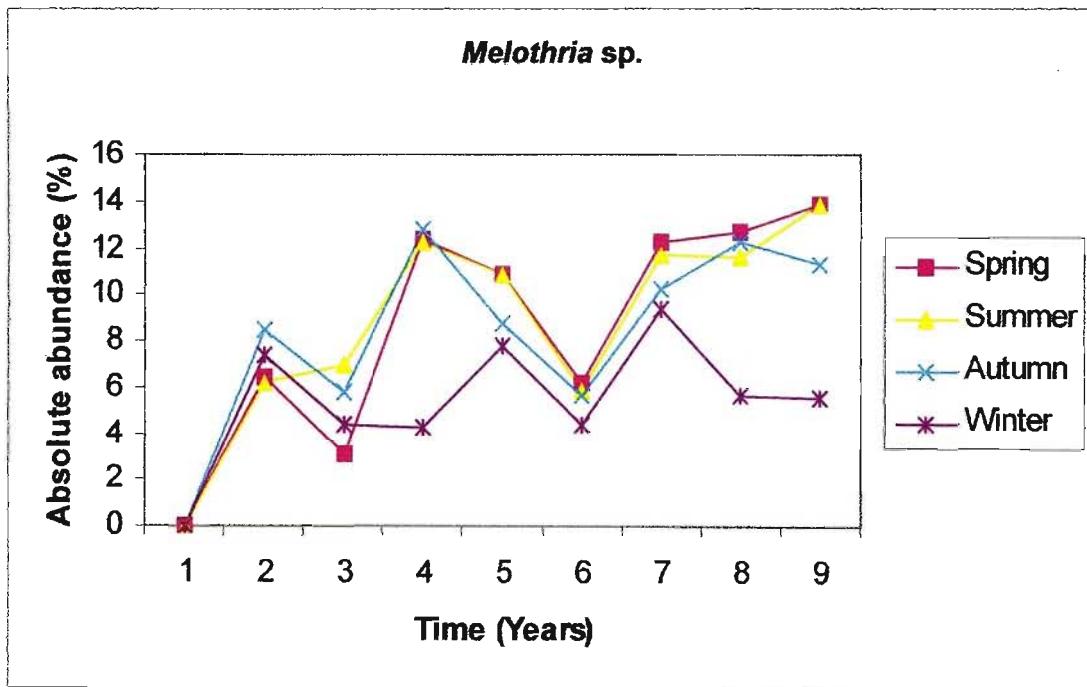


Figure 5.15: Mean absolute abundance of *Melothria* sp. for plots under different season of grazing applications over the trial period. Obtained from analysis of variance applied to the absolute abundance data set.

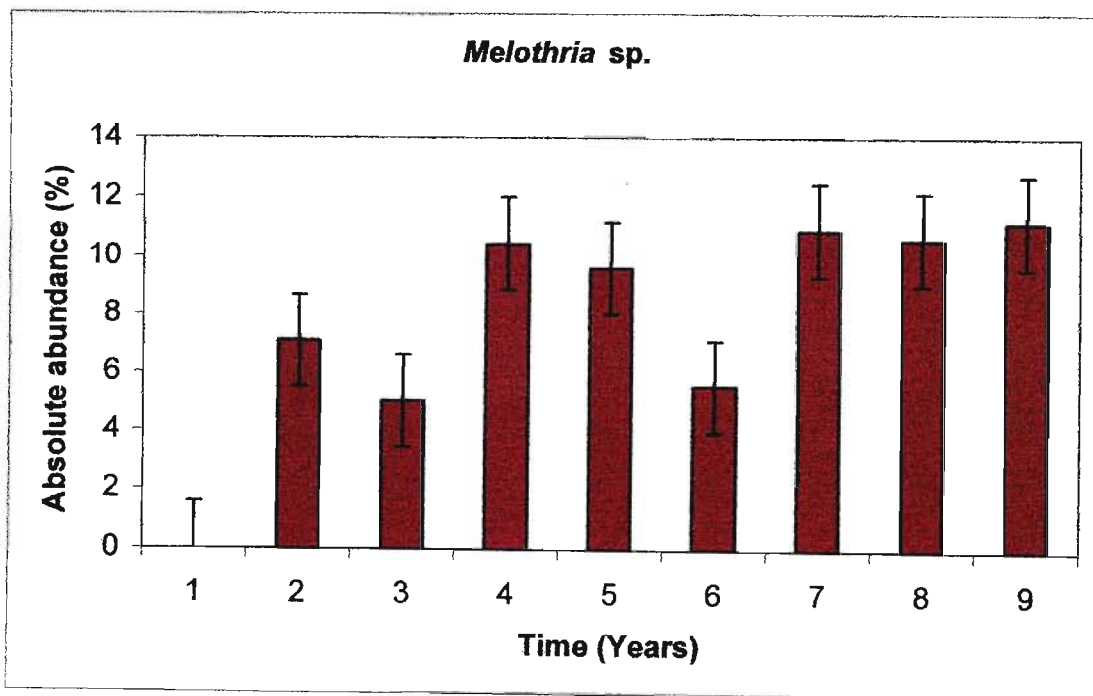


Figure 5.16: Mean absolute abundance of *Melothria* sp. over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.2.4 *Ruschia caroli*

Species 65 (*Ruschia caroli*) responds significantly to time ($p < 0.001$). Mean abundances over time show that, apart from an initial increase in absolute abundance, *R. caroli* experiences a decrease in absolute abundance, from 9.4% to 7.6% (19.0% decrease, trend line gradient = -0.56) (Figure 5.17). The significance of the difference between *R. caroli*'s absolute abundance in year 2 and year 9 and the steady directional nature of the decline suggests that the drop in abundance is a consequence of grazing rather than rainfall. The lack of differentiation between treatments further suggests that this species does not tolerate grazing at any level nor does it endure grazing better during certain seasons.

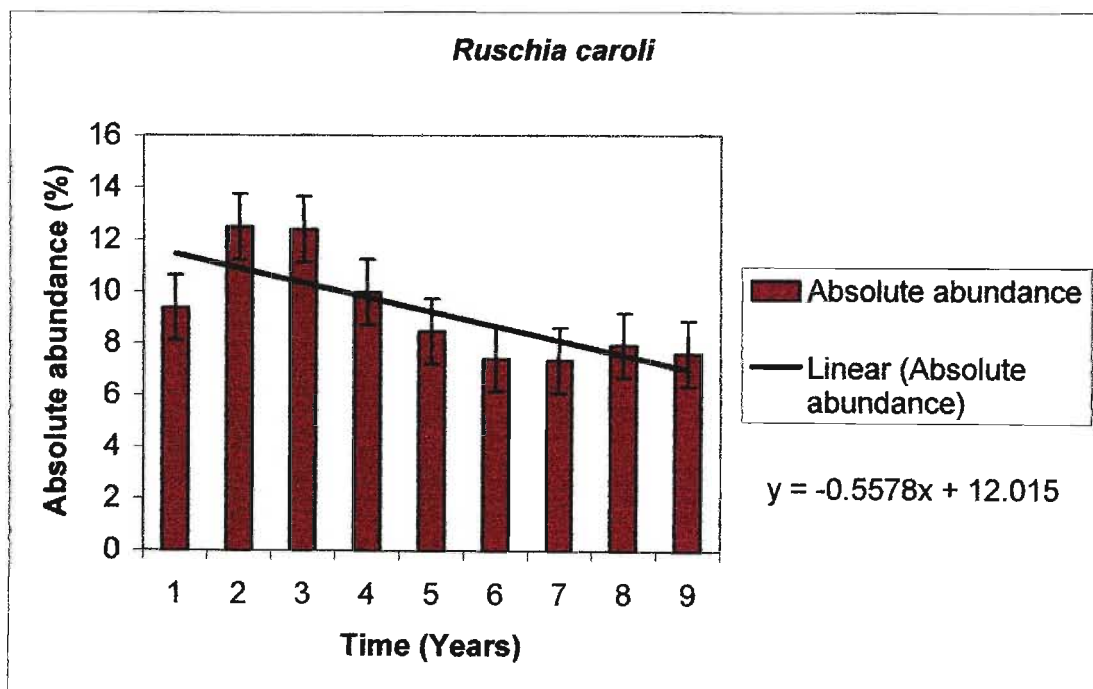


Figure 5.17: Mean absolute abundance of *Ruschia caroli* over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.1.2.5 *Zygophyllum morgsana*

Species 73 (*Zygophyllum morgsana*) shows significant responses to season of graze ($p = 0.016$), SR ($p = 0.052$) and time ($p = 0.023$). *Z. morgsana* appears to better tolerate grazing during summer and winter (Figure 5.18). This is confirmed by the species description graphs obtained from the relative abundance data set (Figure 4.10a) which shows *Z. morgsana* steadily decreasing in relative abundance over time under spring grazing. *Z. morgsana* also tolerates, on average, grazing at low SR's (Figure 5.19). This species does not change to the same degree as other species over the trial period

but does appear to respond negatively to the influence of grazing (trend line gradient = -0.12) (Figure 5.20).

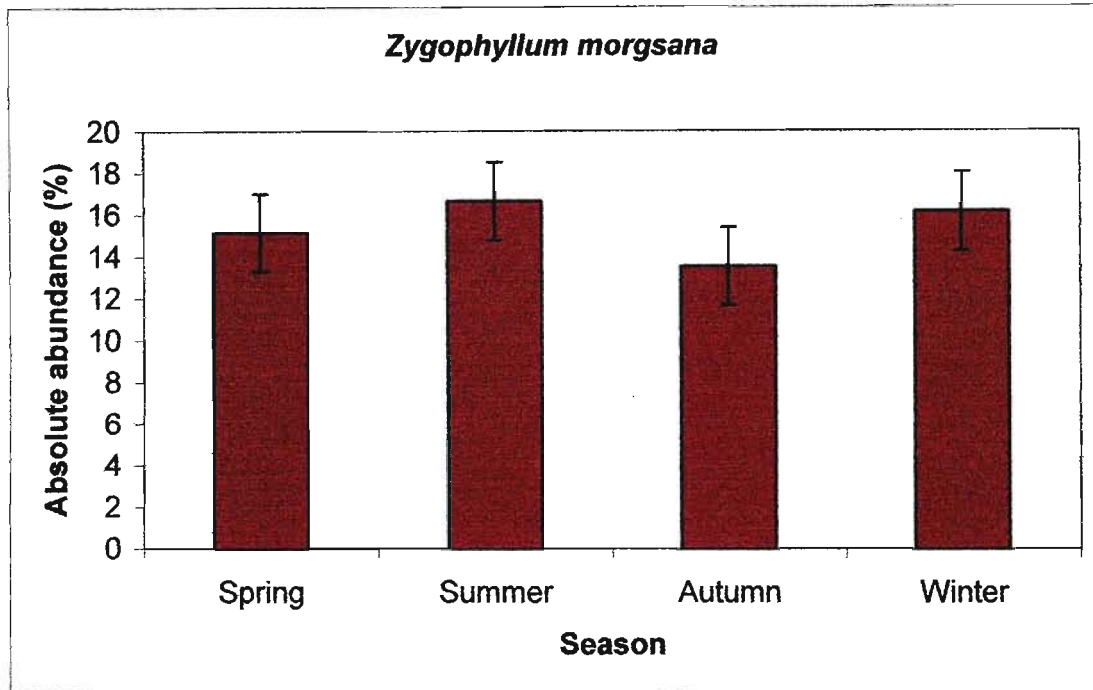


Figure 5.18: Mean absolute abundance of *Zygothyllum morgsana* for plots under different season of grazing applications. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

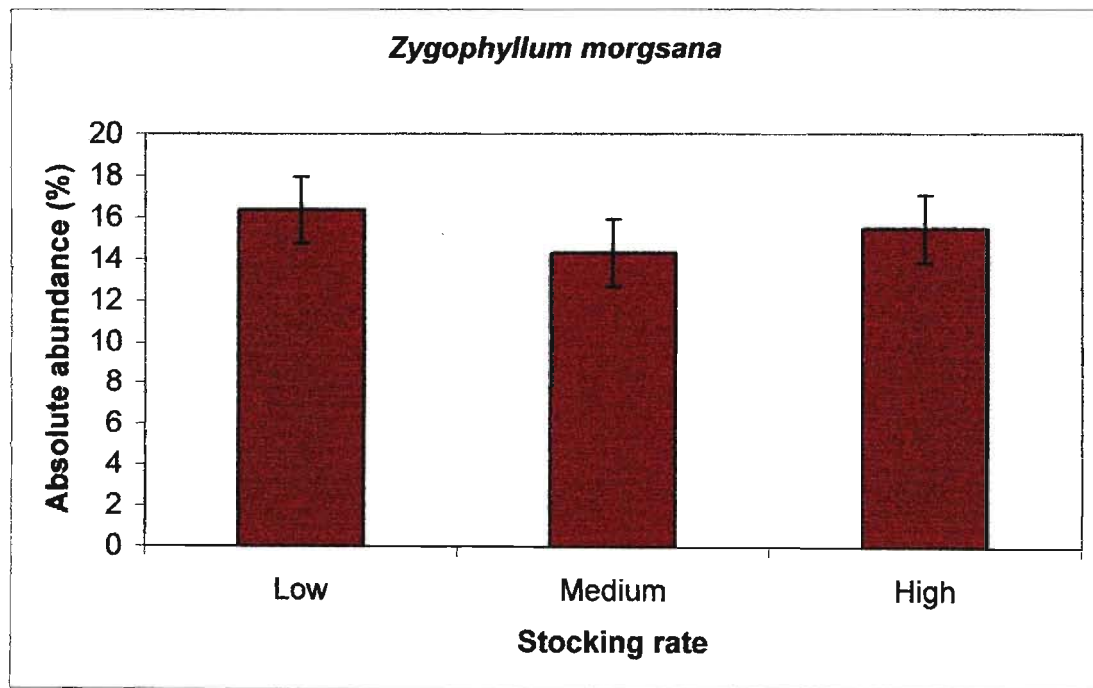


Figure 5.19: Mean absolute abundance of *Zygothyllum morgsana* for plots under different stocking rate applications. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

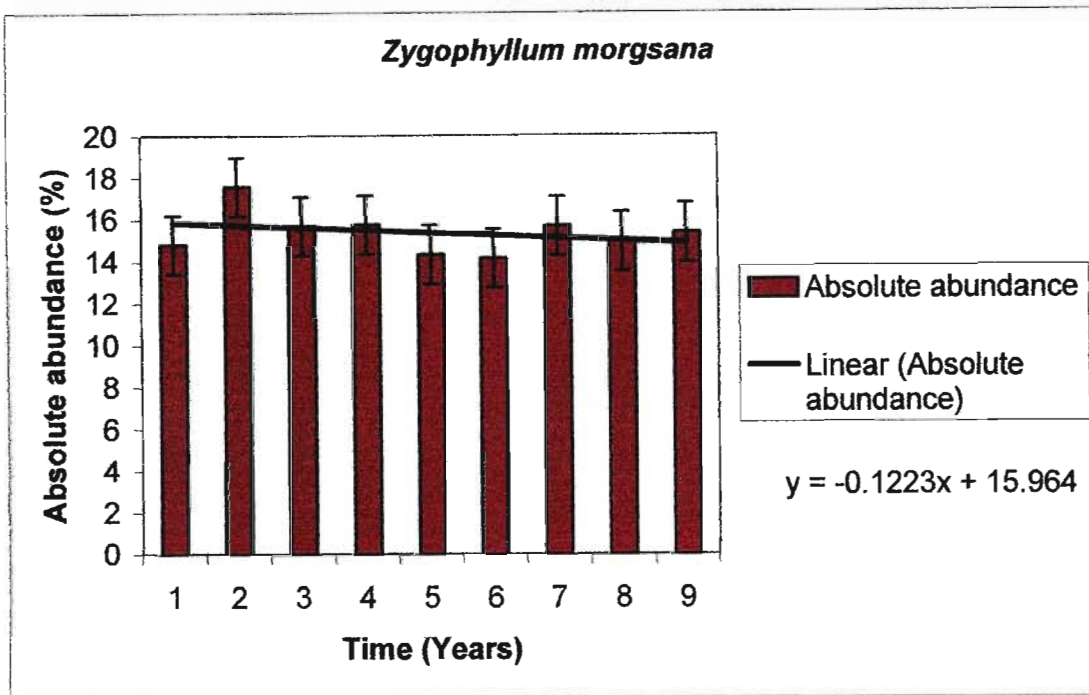


Figure 5.20: Mean absolute abundance of *Zygophyllum morgsana* over the trial period. Obtained from analysis of variance applied to the absolute abundance data set. Error bars are 95% confidence limits.

5.2 Results of Analysis of Variance applied to relative abundance shrub/herb complex

5.2.1 Plant categories (See Appendix 3 for ANOVA Summary)

5.2.1.1 Palatable/unpalatable

As discussed, the effect of grass on the absolute abundance matrix, as a result of its response to rainfall, confounds the interpretation of the extent to which palatable species are increasing or decreasing in the veld in response to the various treatments. This is because *Ehrharta calycina* is a palatable species and hence its fluctuations cause fluctuations in the palatable species category. As a result, a shrub/herb complex was created by removing *Ehrharta calycina* from the relative abundance matrix and re-relativising it. This enabled a more accurate assessment of the extent to which palatable/unpalatable categories are responding to the various treatments. The results of the ANOVA applied to this data set showed a significant response of palatable species to SR ($p = 0.004$), time ($p < 0.001$) and season*SR ($p = 0.003$). From a SR perspective (Figure 5.21), the palatable plants tolerate medium (70.0%) and high (67.6%) stocking rates, both of which display significantly higher relative palatable plant abundances than low stocking rates (61.6%). Palatable plants, in terms of

relative abundance, benefit from the application of high SR's during spring (72.2%) and autumn (77.6%) and medium SR's during summer (75.5%) and winter (71.9%).

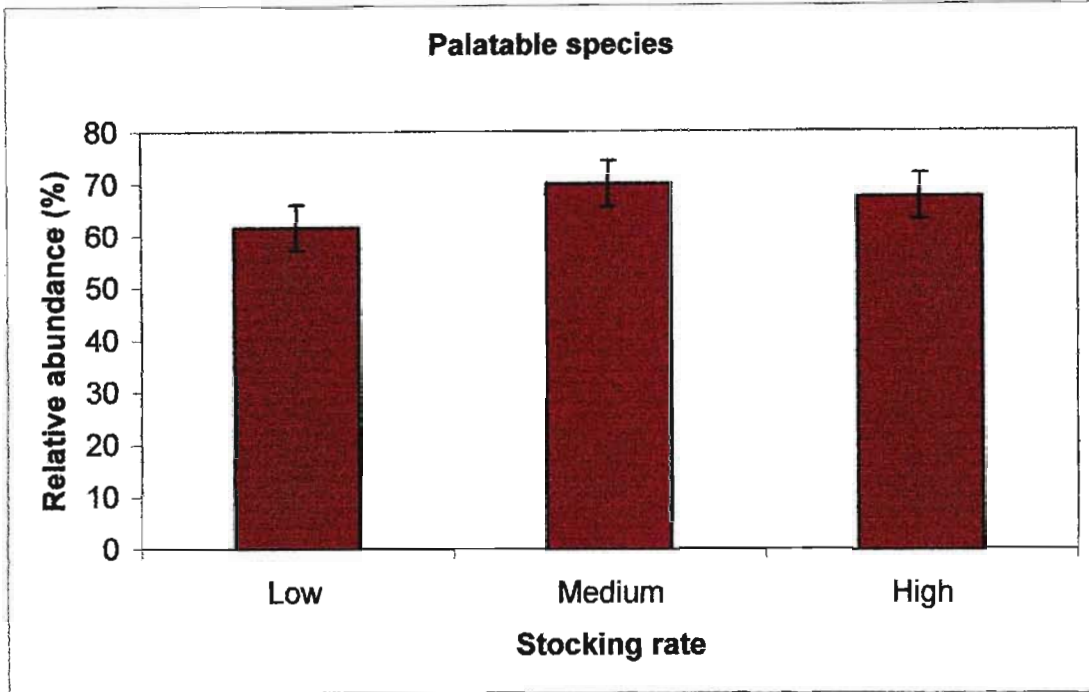


Figure 5.21: Mean relative abundance of the palatable plant species category, excluding *Ehrharta calycina*, for plots under different stocking rate applications. Obtained from analysis of variance applied to the shrub/herb complex. Error bars are 95% confidence limits.

To ascertain which plots/treatments result in the highest absolute abundance of palatable plants one multiplies the absolute abundance values for the shrub/herb complex under the various season*SR treatment combinations by the relative percentage of the palatable plant category within the shrub/herb complex for the corresponding treatments. The above calculations yield the following matrix (Table 5.1).

Table 5.1: Absolute abundance of the palatable plant category of the shrub/herb complex for different season of grazing and stocking rate treatment combinations.

	0.22 SSU/ha	0.32 SSU/ha	0.42 SSU/ha
Spring	27.37	34.07	37.96
Summer	38.29	37.07	39.64
Autumn	27.98	34.75	33.72
Winter	33.02	31.79	22.99

Medium and heavy stocking rates during the spring, summer and autumn months result in the highest percentage abundance of palatable plants, with high stocking rates during winter having a detrimental effect on this group. Low stocking rates yield the highest abundance of palatable species in plots grazed during winter.

A trend line plotted through the mean relative abundance of palatable plants within the shrub/herb complex across all treatments over the duration of the trial returns a gradient of 0.97 illustrating the general increase in the mean relative abundance of this category in response to grazing (Figure 5.22).

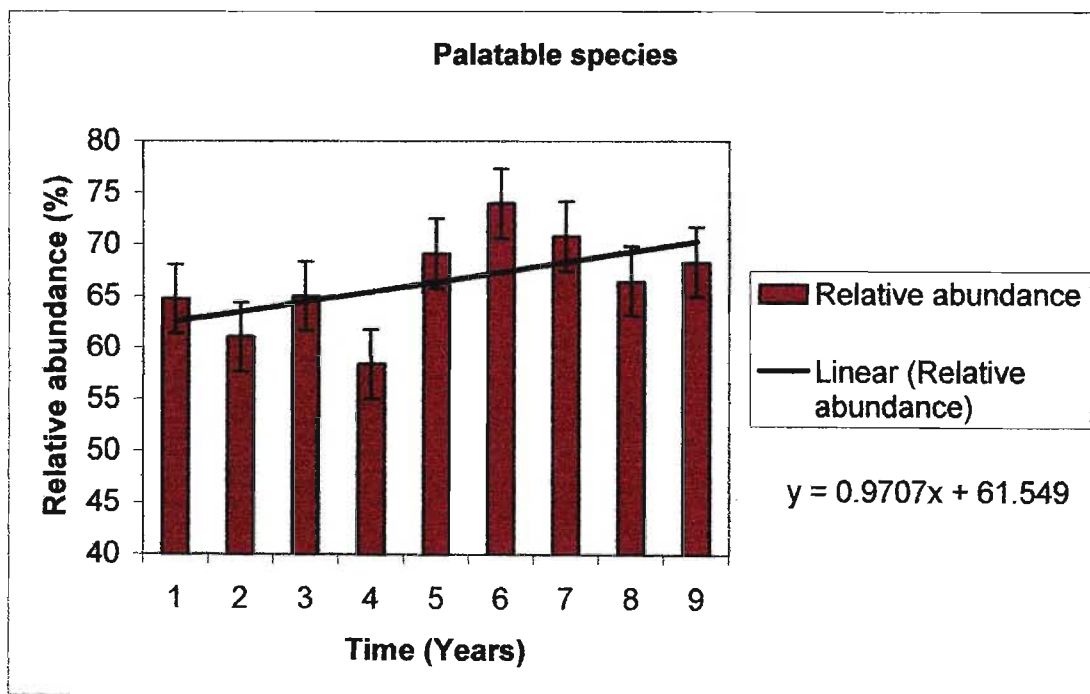


Figure 5.22: Mean relative abundance of palatable plant species category, excluding *Ehrharta calycina*, over the trial period. Obtained from analysis of variance applied to the shrub/herb complex. Error bars are 95% confidence limits.

The results of the ANOVA applied to the unpalatable category yields the same information as found for the palatable category. This is because the two categories are complementary.

The ANOVA applied to the various plant categories (palatable/unpalatable, shrub/herb complex etc.) and individual plant species serve to confirm the results of the ordination analyses applied to the data set. The significance of the relationship between the grass component, and in particular *Ehrharta calycina*, and PS rainfall, an

important finding of the ordination analyses, was confirmed by the ANOVA analyses which emphasized the predominance of non-equilibrial type relations within the Nortier system. While highlighting the prevalence of non-equilibrial relations, the ANOVA facilitated the detailed inspection of individual species and plant categories suggested, by the ordination, to be responding to the influence of grazing and in particular the season of grazing variable. It was found that a number of the plant categories and individual plant species showed a significant response to the various treatments to which they were subjected, confirming the presence of equilibrial type relations between certain veld components and herbivores. The overriding influence of rainfall and underlying impact of grazing on the veld resource at the Nortier Experimental Farm and the implications of these for the contemporary equilibrium/non-equilibrium debate are discussed in the following chapter.

CHAPTER 6: DISCUSSION

6.1 Equilibrium/Non-equilibrium Theory

Much of the recent work undertaken in the ecological, and more specifically the rangeland discipline has yielded results which have led to the questioning and re-examination of the classical Clementsian succession based range model which historically has provided the basis for understanding vegetation dynamics in South Africa's rangelands. Contention regarding the conformity of ecosystem response to either equilibrium or non-equilibrium principles has culminated in the re-assessment of the applicability of popular ecosystem models by many authors (Ellis and Swift 1988; Fernandez-Gimenez and Allen-Diaz 1999; Illius and O'Connor 1999; Fynn and O'Connor 2000; Briske *et al.* 2003) who emphasize the need for clarity on the issue because of its importance in terms of veld management.

It was in 1988 with the influential work of Ellis and Swift, that the concept of non-equilibrium system dynamics were introduced to range science. Prior to this, it was generally accepted that the range succession model effectively explained the dynamics in rangeland ecosystems and as a result management regimes were developed according to its principles. Only recently however are rangeland scientists beginning to understand the role played by both equilibrium and non-equilibrium forces in rangeland systems and the relative importance of each in different environments. The results obtained from the grazing trial undertaken at the Nortier Experimental Farm, which has a mean annual rainfall of 221mm/annum and a high inter annual rainfall variability, provided an ideal opportunity to observe and interpret the effects of variable rainfall and various grazing treatments on the veld dynamics in an arid environment. As a result, much of this discussion involves the interpretation of the results of the various statistical procedures applied to the data set in the context of the equilibrium/non-equilibrium debate. The conclusions drawn in terms of the rangeland debate as well as the findings of the various statistical procedures applied to the data set have certain implications from a management perspective, the details of which are also discussed.

The Nortier data set, comprising data from plots subject to various stocking rate by season of grazing treatments, the influence of which was monitored over time, was

examined initially using reductionist methods such as ordination. Once the enormity of the data set had been dealt with using such tools as correspondence analysis, and an idea obtained of which variables were responsible for the major variation within the data set, more detailed analysis in the form of analysis of variance followed. Consequently, the results will be discussed in this order.

The examination of the results obtained from the indirect correspondence analysis and the direct canonical ordination applied to the full data set illustrated the importance of rainfall, and in the case of the Nortier Experimental Farm, variable PS rainfall on the plant species dynamics taking place in the veld. The fluctuation of axis one sample scores in the unconstrained correspondence analysis showed high correlations with PS rainfall patterns supporting to a strong degree the principles of a non-equilibrium system. Added to this, the euclidean distance (Figure 4.14) of individual samples relative to year 1 rose high above the upper confidence limit ($p = 0.05\%$) during years of high rainfall and in graph form mirrored the graphs produced for PS rainfall (Figure 4.15.1). The effect of rainfall on veld dynamics was also strongly supported by the t-values for the canonical co-efficients obtained for the PS rainfall variable, which were highly significant along axis 1 in both the CA and the CCA applied to the full data set. Notably, the effects of treatment were not shown to significantly explain the main variation in the data set (i.e. variation along axis 1) in both the constrained and unconstrained analyses applied to the full data set. The significance of the t-values along axis 2 for each of the treatments over time (in the CCA applied to the full data set) however, does suggest that while rainfall is having the dominant effect on the absolute abundance species composition, grazing too is having a significant impact although to a lesser extent. This notion is further supported by the ordination diagrams plotted for the CCA applied to the full data set which indicate a progressive, directional movement in species composition (along axis 2) beneath the dramatic inter annual fluctuations in response to rainfall (along axis 1) (particularly evident in plots grazed during spring and summer – Figure 4.4a-f). The significance of both equilibrium and non-equilibrium variables in explaining variation within the species composition data displayed by the CCA (applied to the full data set), although highly disproportionate, provides the first support for the applicability of an equilibrium/non-equilibrium continuum in the Nortier rangeland.

In response to the findings of the CA and CCA applied to the full data set, further analyses, which attempted to remove the variation associated with rainfall, were applied to the data set to examine the relation between the various treatments and species composition. The results obtained from the subsequent analyses applied to the absolute abundance data set (CCA-Rainfall), the relative abundance data set (CCA-Rainfall(-74)) and the shrub/herb complex (CCA-Rainfall(-74-9)) with the effects of rainfall removed showed that, while less of the variation was being accounted for by each of the analyses, certain treatments were being shown to significantly affect the species composition of the veld. The ordinations applied to the shrub/herb complex displayed a distinct directional trend in species composition change in response to grazing similar to that exposed by the partial CCA applied to the full data set. The directional change in species composition in response to grazing highlights the influence of internal forces on the Nortier rangeland. This is further supported by the euclidean distance graphs derived from the relative abundance matrix and the shrub/herb complex both of which show significant change initially with levelling off occurring over time. This levelling off coincides with the ordinations, where directional change is apparent in the first few years of the trial following which a reduction in yearly directional change occurs and what appear to be fluctuations around a central point are evident. Plotting the treatment variables in multivariate space for the analysis applied to the shrub/herb complex highlights the manner in which the various grazing treatments are moving in the same direction over time. This suggests an overall system response to grazing (following the removal a variation attributable to rainfall) with less substantial variations being attributable to the different treatments (Figure 4.11m).

Essentially the ordination and euclidean distance analyses highlight how different components of the veld respond to varying extents to rainfall and grazing. Prior to the removal of 'bare ground' and *Ehrharta calycina* the main vegetation dynamics were driven by rainfall and hence were largely in agreement with the principles of non-equilibrium theory. The vegetation which remained following removal of *Ehrharta calycina* and bare ground (variables both highly responsive to rainfall), the shrub/herb complex, responded far less to rainfall fluctuations in both the ordination and euclidean distance analyses. Furthermore, the discontinuation of trajectory movement (Figure 4.11a to Figure 4.11i) and levelling off of the euclidean distance values

(Figure 4.14.2 and 4.14.3) suggests that the veld, or rather certain components of the veld (i.e. the shrub/herb complex), can tend towards an equilibrium with the grazing influence, around which fluctuations take place according to rainfall.

These findings hold special relevance to the equilibrium/non-equilibrium debate for a number of reasons. Briske *et al.* (2003) challenge the perception that equilibrium and non-equilibrium paradigms are mutually exclusive. Rather they argue that systems can display both equilibrial and non-equilibrial traits with grazing influencing the long term trajectory of a system upon which are exerted short-term fluctuations associated with variable climate (Figure 2.3). This theory is in line with Heady's (1973 (cited by Holechek *et al.* 1989)) depiction of succession (Figure 2.2), which illustrates the development of a community towards equilibrium and the impact of various environmental cycles. The relative influence of rainfall and grazing on the veld dynamics at the Nortier Experimental Farm, shown by the ordination and euclidean distance analyses, supports the idea of an equilibrium/non-equilibrium continuum. It also provides evidence for the notion that a relation can develop between internal factors such as grazing and certain elements of the rangeland resource in systems subject to highly variable rainfall.

One of the issues at the centre of the equilibrium/non-equilibrium debate is the role played by scale and time aspects of data collection and analysis. The time aspect has been of particular importance and is a possible cause for contention and ambiguity in the understanding of system dynamics over the years (Fuhlendorf *et al.* 2001). Fuhlendorf and Smeins (1997) went so far as to state the spatio-temporal scale at which their conclusions apply in the knowledge that an assessment of the same system at a different spatio-temporal scale may yield different results and conclusions. O'Connor and Roux (1995) too, emphasize the importance of time and in particular ensuring that data collection is initiated immediately following the implementation of grazing treatments. O'Connor and Roux (1995) found little evidence of grazing affecting vegetation dynamics but only began data collection 8 years after the implementation of the grazing trial. By that stage, and as had occurred at the Nortier trial, the effects of grazing may have already manifested themselves and any further changes in species composition were becoming less as a result of grazing and more a response to fluctuating rainfall. The importance of trials having a minimum time

period is emphasized further by the Nortier ordination analyses, the diagrams of which show that the effects of grazing after a single year of treatment application are not as substantial as after four or five years. Furthermore, in slowly changing systems the effects of rainfall can mask the effects of grazing treatment (Westoby *et al.* 1989). This is due to the fact that over short time periods the impact of grazing may be considered by statistical analyses to be insignificant, particularly in comparison to the effects of variable rainfall. Even in a trial of nine years, and when the system or the shrub/herb complex appeared to be approaching an equilibrium with grazing, the ordinations (CA and CCA) applied to the full data set placed more emphasis on the influence of rainfall, with treatment associated impacts only being brought to the fore through careful examination and specialised partialling techniques.

The results of the analysis of variance served to corroborate the findings of broader ordination methods and euclidean distance analyses. The gradual, directional change in the abundance of certain plant species over time both up and down confirm that grazing is having an effect on certain species in the Nortier rangeland. Furthermore, the fluctuations attributable to rainfall were non-significant when compared to that of the grass category. Examples of species shown to respond to grazing are *Hermannia scordifolia* (Figure 5.13) and *Melothria* sp. (Figure 5.15) both of which increase under the influence of grazing and *Ruschia caroli* (Figure 5.17) which decreases with grazing. An interesting observation is that certain species (e.g. *Ruschia caroli*) were not affected by the different combinations of SR and season of grazing, made evident by the lack of significant response to these variables in the ANOVA output summary, but were responsive to grazing on a whole. Other species such as *Melothria* sp. and *H. scordifolia* responded to different season of grazing treatments to different extents, an occurrence which has certain management implications. It must also be noted that although certain individual species and plant categories did respond differently to the various season of grazing treatments over time, the difference in response was more the extent to which their abundances increased/decreased rather than changes in abundance in opposite directions. This result is consistent with the ordination scatter plot presented as Figure 4.11m which shows similar directional movement of samples along axis 1 with differentiation along axis 2 being as a result of the extent to which individual species are responding to the different season of grazing and SR treatments.

Examination of grass fluctuations, through ANOVA, show none of the treatments having any significant effect on grass abundance both in the absolute and relative abundance data set. Instead, the crests and troughs in grass abundance over the trial period correspond strongly with the PS rainfall variable. This confirms indications by ordination and the literature that the dynamics of the grass component of the Karoo veld is almost entirely rainfall driven. The dramatic fluctuations of this component, and *Ehrharta calycina* in particular, in response to rainfall preclude the development of a relation between the grass component and the grazing treatments.

In systems where the predominant fluctuations of plants or plant components are linked to external disturbances there exist suites of species which have adapted to these disturbances to the extent that they do not fluctuate to the same degree as others (Illius and O'Connor 1999). The results of the ANOVA applied to various forms of (absolute and relative abundance) and categories within (shrub/herb complex, grasses, individual species etc) the Nortier data set reveals the existence of plant species which fluctuate less dramatically to variable inter annual rainfall. The absolute abundance of numerous plant species and the shrub/herb complex as a whole showed consistent, cumulative trends which resulted in significant changes in the abundance of certain species over the duration of the trial. These species are comparable to what Illius and O'Connor (1999) refer to as the key resource, defined as 'those components of the vegetation with which the animal population is in equilibrium'. The shrub/herb complex, as a consequence of its relative inter annual consistency in terms of absolute abundance and the directional trends displayed by its constituents in response to grazing (e.g. *Hermannia scordifolia*), constitutes the key resource at the Nortier Experimental Farm.

In summary, the rangeland at the Nortier Research Station displays quite distinctly characteristics of both equilibrium and non-equilibrium systems. To classify the system into one of these categories would be impossible and would provide a basis for management which was misleading. Classification hence, must adopt an approach similar to that contemplated by Fuhlendorf *et al.* (2001) and Briske *et al.* (2003), which considers the two paradigms, not as being mutually exclusive, but rather as representing the poles of a continuum upon which different ecosystems can be placed

according to the relative influence of both internal and external forces on the system. Indeed the Nortier rangeland is best described according to an equilibrium/non-equilibrium continuum and would, as a result of the overriding impact of rainfall, be positioned near the continuum's non-equilibrium pole.

6.2 The Range Succession Model and the State and Transition Model

The conformance of various components within the Nortier rangeland to internal and external components presents a problem when it comes to modeling system dynamics. Indeed the application of models based on either equilibrium or non-equilibrium principles will have shortcomings in an environment where dynamics characteristic of both these paradigms exist. For example, the range succession model, in explaining eco-system dynamics, relies on the existence of negative feedback relations which result in continuous and reversible vegetation dynamics (Briske *et al.* 2003). For this reason, the applicability of the range succession model, an equilibrium model, in predicting plant dynamics in non-equilibrium environments, where the development of negative feedback relations are hindered by the influence of external forces, is questionable.

The range succession model's shortcomings in systems where external forces have a significant influence on species dynamics is evident in the results of the statistical procedures applied to the Nortier rangeland. The analyses applied to the Nortier data set revealed different plant components responding to different variables (internal and external). Therefore, to adequately organize the information and explain the dynamics within the Nortier Rangeland, particularly for management purposes, one requires a model with the ability and flexibility to incorporate both equilibrial and non-equilibrial system dynamics.

The state and transition model was designed for application in rangelands where event-driven dynamics were not adequately explained by the range succession model (Briske *et al.* 2003). The state and transition model was not designed with the intention of replacing the range succession model but rather has the capacity to incorporate transitions explained by the range succession model as well as the event driven dynamics characteristic of many arid and semi-arid rangelands. In terms of the state and transition model, the direct ordination analysis applied to the full absolute

abundance data set exposed two dominant transitions (equilibrial and non-equilibrial) within the Nortier rangeland (Figure 4.4). The most prominent transition involves the non-equilibrial relation between variable inter annual rainfall and *Ehrharta calycina* with a significant positive correlation existing between these two variables (Figure 5.7). The grass category, and *Ehrharta calycina* in particular, constitutes that component of the vegetation which displays non-equilibrial characteristics and is not adequately explained by the range succession model.

The second, less dramatic transition in the Nortier rangeland is that experienced by the shrub/herb complex. Westoby *et al.* (1989) outlines how, according to the range succession model, grazing pressure opposes the successional tendency pushing vegetation away from the climatic climax. Furthermore, they state that the grazing pressure can be made 'equal but opposite to the successional tendency, producing an equilibrium in the vegetation at a set stocking rate' (Westoby *et al.* 1989) referred to by Clements (1916) as a proclimax state. Thus, one expects two outcomes on the introduction of various grazing treatments to climax vegetation;

1. The plant community will adjust in terms of species composition in response to the grazing influence with yearly adjustments becoming smaller and smaller until an equilibrium between the plant community and the grazing influence is reached; and,
2. Vegetation which has reached equilibrium with a given stocking rate (or grazing regime) will differ in species composition to vegetation which has reached equilibrium with a different stocking rate (or grazing regime).

Both of these predictions are consistent with the results of the Nortier Trial, which in the first instance experiences a change in the species composition of the shrub/herb complex over time in response to the influence of grazing eventually reaching an equilibrium (Figure 4.11 and 4.14). Secondly, the results show that the magnitude of change, which in most cases occurs in the same direction (Figure 4.11m), differs under various stocking rate and season of grazing treatment applications resulting in proclimax communities characterized by different species compositions. The change in the species composition over time of the shrub/herb complex in response to the influence of grazing and the various proclimax states associated with the different treatment combinations is consistent with the principles of the range succession

model and constitutes the second significant transition in the Nortier vegetation. This transition in the shrub/herb complex is characterized by an increase in the absolute abundance of species such as *Hermannia scordifolia* (Figure 5.11 and 5.13) and *Melothria* sp. (Figure 5.15) and a decrease in the absolute abundance of *Ruschia caroli* (Figure 5.17). The Analysis of Variance and ordination analyses illustrate how, although various treatments had similar influences on the floristic composition of the veld, the extent to which each treatment influenced the communities differed resulting in different proclimax states. Each of these proclimax communities differ in terms of the abundances of plant species within the shrub/herb complex which are influenced by grazing (e.g. *Hermannia scordifolia*, *Melothria* sp. and *Ruschia caroli*). The cumulative, directional nature of the change displayed by the shrub/herb complex in response to grazing constitutes a transition, which is consistent with the range succession model.

The state and transition model, through its ability to incorporate both equilibrium and non-equilibrium dynamics, provides a useful means of 'organizing information for management' (Westoby *et al.* 1989). As a model it effectively incorporates both the equilibrium and non-equilibrium dynamics within the Nortier rangeland and should be used as a means of organizing botanical information for management.

6.3 Management implications

The relative effect of forces influencing rangeland dynamics has been subject to much consideration and deliberation over the past few decades (Illius and O'Connor 1999). It is argued that environmental variability in semi-arid systems results in the development of non-equilibrium dynamics to the extent that the development of a relation between the veld component and herbivores is severely inhibited (Ellis and Swift 1988). Numerous papers have been published detailing the impact of various grazing treatments on the veld in systems typically considered non-equilibrium in nature. The statistical analyses employed in this project were designed primarily to extract information pertaining to the influence of internal and external forces on the dynamics of the Nortier rangeland. In achieving this objective much of the information gathered was found to have important implications in terms of the management of this type of vegetation. Possibly the most important outcome of this investigation from a management perspective has been showing that grazing does

have an influence on the floristic composition in the veld resource. Therefore, further experimentation assessing the influence of various rotational grazing and resting regimes at the Nortier Experimental Farm would be a worthwhile undertaking, something which may have been questionable prior to the findings of this thesis. Because little formal research has been published on veld management in the Strandveld Vegetation Type itself, the recommendations which are made are limited and based largely on trials undertaken in similar Karoo vegetation and the findings of the statistical analyses of the Nortier Trial. For further insight into how to manage veld in the Strandveld Vegetation Type to achieve maximum production whilst maintaining the condition of the veld, trials investigating the impact of various rotational grazing and resting regimes need to be carried out.

The conformation of various components in the Nortier rangeland, situated in the Strandveld Vegetation Type, to different explanatory variables has certain veld management implications which must be addressed in order to generate an effective grazing management plan. For management of any livestock, farmers attempt to achieve two goals both of which are crucial in realizing the overall objective of sustainable livestock production. The first goal involves maximizing usage of the resource in terms of animal production. The second goal, sustainability of resource, involves applying grazing strategies which at worst maintain veld condition, ensuring the well being of the food resource for livestock over time. As a result, interpretation of the results from both the ordination and ANOVA applied to the Nortier data set and incorporation of information provided by the literature, in the generation of a grazing strategy, must be undertaken with these two objectives in mind.

The extent to which the grass component within the Nortier system fluctuates in response to rainfall has led to the development of a relation between the more stable shrub/herb complex and the livestock utilising the veld resource. Because the available forage provided by the grass component of the veld cannot be forecast from year to year the development of a grazing strategy revolves largely around the more stable and predictable shrub/herb complex.

Both in the literature and in the Nortier grazing trial, the impact of grazing has varied between different seasons. The results of du Toit (1998) illustrate how, as grazing

approached the growing season (spring and summer) so the shrub component of the veld became more dominant with grasses tolerating grazing during the dormant season. Furthermore, du Toit (1998) showed how continuous grazing promoted the herbaceous component over the shrub component of the veld. The findings of du Toit (1998) serve to highlight how grazing during different seasons and different grazing strategies (e.g. continuous versus rotational) can influence the species composition and structure of Karoo veld. The impact of grazing during different seasons is certainly apparent in the Strandveld rangeland however appears slightly different to that experienced at the Grootfontein Research Station in the False Upper Karoo (du Toit 1998). In addition to receiving less rainfall than the Grootfontein Research Station, the majority of rainfall at the Nortier Experimental Farm falls during the winter months resulting in the active growing period falling between March/April and late August/early September (Vorster 1999). The results of the statistical analyses applied to the Nortier data set show that the shrub/herb complex benefited in terms of absolute abundance from grazing during the summer and spring months, effectively the dormant season. Because the abundance of the grass component does not respond significantly to grazing, precluding the development of a relation between the two, the principles employed in the generation of the grazing management plan for the Strandveld Vegetation Type must aim to maximise and maintain the quality of the shrub/herb complex which constitutes the main source of forage for grazing animals. In this respect, the positive influence of grazing during the dormant period in terms of the cover of the shrub/herb complex must be considered.

Examination of the shrub/herb complexes response to grazing during the different seasons at the Nortier Experimental Farm shows absolute abundance increasing for all seasons, but most substantially in plots grazed during summer and spring (the dormant season). Furthermore, the statistical analyses show that while the application of medium and high stocking rates are beneficial in terms of palatable plant abundance in plots grazed in spring, summer and autumn, intense grazing leads to the degradation of veld when applied during winter. To minimise veld degradation both Vorster (1999) and Roux (1968) state that in the arid winter rainfall areas of the Karoo, paddocks should be afforded a 'growing season rest' once every three years, in addition to rotational grazing, to maintain veld condition. In addition to this, Vorster (1999) recommends that paddocks which are grazed during the growing season,

winter in the Strandveld, should be done so on a rotational basis with periods of occupation not exceeding two months. The combination of the findings of the Nortier grazing trial and recommendations made by Vorster (1999) and Roux (1968) suggest that in the arid winter rainfall areas of the Karoo, veld should be rested rotationally as depicted in Table 2.1 and that paddocks grazed during the growing season are done so at a reduced stocking rate.

Another valuable finding of the Nortier trial was the decrease in bare ground associated with grazing (Figure 4.4) with the lowest level of bare ground being observed in plots which were grazed in summer at low stocking rates and spring at high stocking rates. The least bare ground was observed in plots grazed during spring, summer and autumn with a significantly higher amount of bare ground evident in plots grazed during winter. Because changes in grass cover correspond mainly to rainfall, the difference in bare ground observed in plots grazed during the active (winter) and dormant (spring, summer and autumn) months can be attributed to the changes in the shrub/herb complex. The negative influence of grazing during the active growing season on this component of the veld, particularly at medium to high stocking rates, further illustrates the need for rotational resting and reduced stocking rates over the winter months.

While the absolute abundance of the shrub/herb complex does increase over the trial period, it is promising from a livestock production perspective only if the palatable plant component is increasing at a rate equal to or higher than the unpalatable plants. To ascertain the extent to which this was happening, analysis of variance was applied to palatable and unpalatable plant categories obtained from a re-relativised shrub/herb complex. When averaged across all seasons, the mean relative abundance of palatable plants within the shrub/herb complex does appear to be increasing over the trial period. The results of the ANOVA applied to this category also showed that palatable species were high from a relative perspective in plots grazed during spring and autumn at high stocking rates as well as those grazed during winter and summer at medium stocking rates. On average, medium and high stocking rates resulted in the greatest relative abundance of palatable species. The positive influence of moderate to high, infrequent defoliation is a common theme throughout the literature dealing with the impact of grazing on veld condition in Karoo systems and one which is in line

with the findings of the Nortier grazing trial. From an absolute abundance perspective, plots grazed during spring, summer and autumn at medium to high stocking rates all resulted in higher palatable species abundances than plots grazed at a low stocking rate (apart from summer where all stocking rates resulted in high palatable plant abundances). Notably, the reverse is true for plots grazed during winter where palatable plants were more abundant under low to moderate grazing intensity. Intensive grazing during the winter season (Figure 5.1 and Table 5.1) appears to have a significant negative impact on the palatable plant component of the Strandveld Vegetation Type.

An important consideration is that the trial at the Nortier Experimental Farm comprised plots grazed for one season (three months) and rested for the remainder of the year. In addition to the positive influence of infrequent defoliation on the palatable component of the shrub/herb complex displayed by the statistical analyses, numerous authors (Vorster 1982, Vorster *et al.* 1983, Hoffman 1988 and du Toit 1998) advocate the positive influence of infrequent defoliation on Karoo shrubs. Because shrubs constitute the majority of species incorporated by the shrub/herb complex infrequent defoliation by means of rotational grazing strategies is crucial to maintaining the absolute abundance of this forage resource. Should continuous grazing be unavoidable however, Roux (1975 (cited by Vorster *et al.* 1983)) states that stocking rates should be maintained at or below the carrying capacity of the veld.

The dynamics of the grass component and in particular, *Ehrharta calycina*, conforms almost entirely to external factors, specifically rainfall. As a result, any grazing management plan in the Strandveld Vegetation Type should be adaptive in nature with the flexibility to deal with high inter-annual rainfall variability. The implementation of Roux's (1968) during and post-drought recommendations will ensure that stress on livestock during drought is minimised.

Both the Nortier data set and the literature dealing with the Karoo, and specifically the arid winter rainfall regions of the Karoo, point in the direction of a grazing system which employs the principles of rotational grazing and resting. Contributing factors to this recommendation include the following:

- Both the literature and the results of the Nortier grazing trial indicate the positive influence of moderate to intense, infrequent defoliation on botanical composition;
- Roux (1966b (cited by Vorster 1999), Skinner (1996) and Roux (1968) all advocate the need for extended rest periods of up to 12 months, particularly for veld in poor condition. Furthermore, Vorster (1999) states that to ensure sustainable production, veld should be rested during the growing season every three years. This is because of the variability of the periods of active growth, flowering and fruiting among the different plants (Roux 1966b (cited by Vorster 1999));
- The application of moderate to high stocking rates in homogenous paddocks reduces selective grazing and the corresponding veld degradation; and
- Rotational grazing systems provide flexibility in terms of altering stocking rates during droughts.

In arid environments subject to highly variable rainfall, grazing regimes should promote the abundance of those species that constitute the key resource. In the Strandveld Vegetation Type, the key resource comprises the shrub/herb complex which displays a limited response to rainfall and provides a relatively stable source of forage for grazing animals. It is therefore in the interest of any livestock farmer in the Karoo that the grazing regime promotes this component of the veld. Based on this, the results of the statistical analysis applied to the data set and the aforementioned advantages associated with rotational grazing regimes, a three paddock rotational grazing system should be applied to the Strandveld Vegetation Type. From a maintenance of veld condition perspective, paddocks should not be grazed for the same season consecutively and should be afforded a full years rest on a rotational basis (Table 2.1) (Roux 1968). Stocking rate should be reduced significantly during the winter months to a rate of approximately 0.216 SSU/ha (this may require the addition of a further paddock i.e. a fourth paddock, or the introduction of supplementary feed). For the remainder of the year, stocking rates of between 0.316 and 0.416 SSU/ha should be applied. Paddocks within the system must be configured, as far as possible, to incorporate homogenous units of vegetation to minimise selective feeding and the associated veld degradation. Management plans designed

according to these principles will serve to ensure the sustainable utilisation of the Strandveld veld resource.

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APPENDICES

Appendix 1: Results of the ANOVA's applied to the Palatable, Unpalatable, Bare ground, Grasses and Shrub/Herb Complex categories obtained from the absolute abundance data set.

***** Analysis of variance *****

Variate: Palatable

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	3517.41	1172.47	15.68	<.001
SR	2	300.22	150.11	2.01	0.177
Season.SR	6	2631.17	438.53	5.86	0.005
Residual	12	897.52	74.79	2.04	
[1].Time stratum					
d.f. correction factor 0.4796					
Time	8	41628.79	5203.60	141.81	<.001
Time.Season	24	2392.13	99.67	2.72	0.008
Time.SR	16	617.92	38.62	1.05	0.411
Time.Season.SR	48	1684.85	35.10	0.96	0.532
Residual	96	3522.60	36.69		
Total	215	57192.61			

***** Tables of means *****

Variate: Palatable

Grand mean 56.35

Time	1	2	3	4	5	6	7
	43.58	44.05	68.05	38.10	51.45	82.01	69.39
Time	8	9					
	48.35	62.14					

L.S.D: 3.52

Season	1	2	3	4
	60.07	58.38	57.37	49.56

L.S.D: 3.63

Time	Season	1	2	3	4
1		40.78	43.13	46.12	44.28
2		49.23	45.98	46.38	34.62
3		69.82	67.50	69.84	65.04
4		47.78	45.79	38.00	20.83
5		56.77	52.27	51.14	45.60
6		83.30	81.57	81.90	81.28
7		73.60	71.93	70.69	61.35
8		53.26	51.55	47.93	40.65
9		66.14	65.71	64.30	52.40

L.S.D: 7.39

***** Analysis of variance *****

Variate: Unpalatable

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	250.912	83.637	1.34	0.308
SR	2	751.474	375.737	6.01	0.016
Season.SR	6	2790.527	465.088	7.45	0.002
Residual	12	749.616	62.468	6.36	

[1].Time stratum

d.f. correction factor 0.4576

Time	8	971.165	121.396	12.36	<.001
Time.Season	24	155.998	6.500	0.66	0.766
Time.SR	16	98.672	6.167	0.63	0.737
Time.Season.SR	48	329.629	6.867	0.70	0.816
Residual	96	943.110	9.824		

Total 215 7041.102

***** Tables of means *****

Variate: Unpalatable

Grand mean 16.67

Time	1	2	3	4	5	6	7
	12.55	19.37	18.51	18.32	14.87	14.48	17.34
Time	8	9					
	16.61	17.95					

L.S.D: 1.82

SR	0.22	0.32	0.42
	19.20	14.78	16.02

L.S.D: 2.87

Season	SR	0.22	0.32	0.42
1		18.60	15.51	14.31
2		18.86	11.79	24.75
3		17.44	19.63	9.83
4		21.92	12.17	15.18

L.S.D: 5.74

L.S.D (When comparing means with the same SR): 3.16

***** Stratum standard errors and coefficients of variation *****

Variate: Unpalatable

Stratum	d.f.	s.e.	cv%
[1]	12	2.635	15.8
[1].Time	96	3.134	18.8

L.S.D (When comparing means with the same levels of season): 7.04

Season	SR	0.22	0.32	0.42
1		55.98	60.93	63.32
2		59.20	64.48	51.47
3		56.78	54.43	60.89
4		51.32	52.08	45.28

L.S.D: 6.28

L.S.D (When comparing means with the same levels of SR): 6.10

***** Stratum standard errors and coefficients of variation *****

Variate: Palatable

Stratum	d.f.	s.e.	cv%
[1]	12	2.883	5.1
[1].Time	96	6.058	10.8

***** Analysis of variance *****

Variate: shrub/herb complex

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	3735.81	1245.27	2.39	0.120
SR	2	133.52	66.76	0.13	0.881
Season.SR	6	6171.70	1028.62	1.97	0.149
Residual	12	6263.92	521.99	21.90	

[1].Time stratum

d.f. correction factor 0.3520

Time	8	8905.31	1113.16	46.71	<.001
Time.Season	24	2163.09	90.13	3.78	0.003
Time.SR	16	207.80	12.99	0.54	0.760
Time.Season.SR	48	892.80	18.60	0.78	0.701
Residual	96	2287.73	23.83		

Total 215 30761.69

***** Tables of means *****

Variate: shrub/herb complex

Grand mean 50.15

Time	1	2	3	4	5	6	7
	35.79	50.15	52.95	45.30	47.80	55.07	58.55

Time	8	9
	49.85	55.89

L.S.D: 2.87

Time	Season	1	2	3	4
1		34.54	35.49	34.25	38.86
2		51.34	51.90	49.87	47.49
3		49.83	61.01	52.07	48.89
4		49.42	54.73	46.16	30.89
5		46.74	54.83	46.63	42.99
6		52.38	62.34	51.41	54.16
7		56.28	67.91	54.16	55.84
8		47.69	59.19	46.34	46.19
9		56.51	66.10	51.43	49.52

L.S.D: 10.673

L.S.D (When comparing means with the same level of season): 5.73

***** Stratum standard errors and coefficients of variation *****

Variate: shrub/herb complex

Stratum	d.f.	s.e.	cv%
[1]	12	7.616	15.2
[1].Time	96	4.882	9.7

***** Analysis of variance *****

Variate: Grass

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	2063.56	687.85	1.98	0.171
SR	2	249.01	124.50	0.36	0.706
Season.SR	6	3046.85	507.81	1.46	0.271
Residual	12	4167.82	347.32	10.79	
[1].Time stratum					
d.f. correction factor 0.3842					
Time	8	19321.17	2415.15	75.01	<.001
Time.Season	24	1319.13	54.96	1.71	0.121
Time.SR	16	631.03	39.44	1.22	0.316
Time.Season.SR	48	1296.88	27.02	0.84	0.648
Residual	96	3090.80	32.20		
Total	215	35186.25			

***** Tables of means *****

Variate: Grass

Grand mean 22.86

Time	1	2	3	4	5	6	7
	20.35	13.27	33.61	11.12	18.52	41.42	28.18
Time	8	9					
	15.10	24.20					

L.S.D: 3.32

***** Stratum standard errors and coefficients of variation *****

Variate:Grass

Stratum	d.f.	s.e.	cv%
[1]	12	6.212	27.2
[1].Time	96	5.674	24.8

***** Analysis of variance *****

Variate: Bare ground

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	4018.89	1339.63	23.13	<.001
SR	2	518.61	259.31	4.48	0.035
Season.SR	6	1297.83	216.31	3.74	0.025
Residual	12	694.94	57.91	1.71	

[1].Time stratum

d.f. correction factor 0.3766

Time	8	41636.73	5204.59	153.26	<.001
Time.Season	24	3123.14	130.13	3.83	0.002
Time.SR	16	551.18	34.45	1.01	0.432
Time.Season.SR	48	1455.00	30.31	0.89	0.591
Residual	96	3260.11	33.96		

Total 215 56556.44

***** Tables of means *****

Variate: Bare ground

Grand mean 26.99

Time	1	2	3	4	5	6	7
	43.87	36.57	13.44	43.58	33.68	3.51	13.27
Time	8	9					
	35.05	19.91					

L.S.D: 3.41

Season	1	2	3	4
	23.78	23.15	27.00	34.02

L.S.D: 3.19

SR	0.22	0.32	0.42
	24.97	27.24	28.74

L.S.D: 2.76

Time	Season	1	2	3	4
1		47.61	43.43	42.75	41.69
2		32.92	33.14	34.70	45.53
3		13.20	10.97	13.31	16.29
4		33.50	34.29	43.06	63.49
5		28.62	31.32	34.95	39.85
6		2.33	2.50	4.86	4.36
7		9.67	8.67	13.77	20.97
8		30.88	30.51	36.41	42.39
9		15.34	13.51	19.18	31.61

L.S.D: 7.029

L.S.D (When comparing means with the same levels of season): 6.82

Season	SR	0.22	0.32	0.42
1		25.42	23.56	22.37
2		21.93	23.74	23.78
3		25.78	25.94	29.28
4		26.77	35.74	39.55

L.S.D: 5.53

L.S.D (When comparing means with the same SR): 5.91

***** Stratum standard errors and coefficients of variation *****

Variate: Bare ground

Stratum	d.f.	s.e.	cv%
[1]	12	2.537	9.4
[1].Time	96	5.827	21.6

Appendix 2: Results of the Analysis of Variance (ANOVA) applied to the species in the absolute data set which displayed prominence along grazing gradients in the CCA applied to the Nortier data set. Species 20 was included because it appeared in more than 5% of the samples and had a mean overall abundance above 5%.

***** Analysis of variance *****

Variate: species 20 (*Hermannia scordifolia*)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	1965.952	655.317	4.13	0.032
SR	2	747.642	373.821	2.35	0.137
Season.SR	6	1325.874	220.979	1.39	0.294
Residual	12	1905.753	158.813	40.30	
[1].Time stratum					
d.f. correction factor 0.3652					
Time	8	449.333	56.167	14.25	<.001
Time.Season	24	522.053	21.752	5.52	<.001
Time.SR	16	40.831	2.552	0.65	0.688
Time.Season.SR	48	192.527	4.011	1.02	0.465
Residual	96	378.322	3.941		
Total	215	7528.287			

***** Tables of means *****

Variate: species 20 (*Hermannia scordifolia*)

Grand mean 19.24

Time	1	2	3	4	5	6	7
	16.19	19.13	20.88	17.74	19.41	20.00	20.29
Time	8	9					
	18.74	20.82					

L.S.D: 1.16

Season	1	2	3	4
	19.20	23.93	18.29	15.56

L.S.D: 5.28

Time	Season	1	2	3	4
1		14.94	18.22	15.60	16.00
2		20.49	22.27	18.19	15.59
3		19.97	25.93	18.51	19.11
4		19.59	25.08	17.93	8.34
5		19.41	24.63	18.18	15.43
6		19.51	23.62	18.53	18.34
7		20.19	25.02	19.59	16.35
8		18.79	24.36	18.18	13.63
9		19.88	26.20	19.93	17.25

L.S.D: 5.60

L.S.D (When comparing means with the same season): 2.33

Variate: species 20 (*Hermannia scordifolia*)

Stratum	d.f.	s.e.	cv%
[1]	12	4.201	21.8
[1].Time	96	1.985	10.3

***** Analysis of variance *****

Variate: Species 44 (*Tetragonia fruiticosa*)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	108.400	36.133	0.74	0.547
SR	2	85.760	42.880	0.88	0.440
Season.SR	6	349.742	58.290	1.20	0.371
Residual	12	584.104	48.675	5.11	
[1].Time stratum					
d.f. correction factor 0.2008					
Time	8	2527.371	315.921	33.15	<.001
Time.Season	24	183.217	7.634	0.80	0.559
Time.SR	16	61.740	3.859	0.40	0.764
Time.Season.SR	48	208.067	4.335	0.45	0.895
Residual	96	914.879	9.530		
Total	215	5023.280			

***** Tables of means *****

Variate: Species 44 (*Tetragonia fruiticosa*)

Grand mean 15.95

Time	1	2	3	4	5	6	7
	11.31	13.52	15.80	11.43	16.76	22.47	19.62
Time	8	9					
	15.80	16.85					

L.S.D: 1.86

***** Stratum standard errors and coefficients of variation *****

Variate: 44

Stratum	d.f.	s.e.	cv%
[1]	12	2.326	14.6
[1].Time	96	3.087	19.4

***** Analysis of variance *****

Variate: Species 61 (*Melothria* sp.)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	417.718	139.239	2.45	0.114
SR	2	251.326	125.663	2.21	0.152
Season.SR	6	202.707	33.784	0.60	0.729
Residual	12	681.139	56.762	7.73	
[1].Time stratum					
d.f. correction factor	0.4449				
Time	8	2706.820	338.353	46.06	<.001
Time.Season	24	517.405	21.559	2.93	0.006
Time.SR	16	179.746	11.234	1.53	0.182
Time.Season.SR	48	424.025	8.834	1.20	0.296
Residual	96	705.226	7.346		
Total	215	6086.113			

***** Tables of means *****

Variate: Species 61 (*Melothria* sp.)

Grand mean 7.81

Time	1	2	3	4	5	6	7
	0.00	7.08	5.03	10.43	9.59	5.52	10.89
Time	8	9					
	10.58	11.14					

L.S.D: 1.58

Time	Season	1	2	3	4
1		0.00	0.00	0.00	0.00
2		6.39	6.15	8.39	7.37
3		3.07	6.90	5.80	4.33
4		12.37	12.28	12.80	4.27
5		10.89	10.93	8.78	7.74
6		6.15	5.82	5.70	4.41
7		12.25	11.70	10.21	9.40
8		12.65	11.68	12.31	5.69
9		13.85	13.85	11.36	5.50

L.S.D: 4.19

L.S.D (When comparing means with the same level of season): 3.16

***** Stratum standard errors and coefficients of variation *****

Variate: 61

Stratum	d.f.	s.e.	cv%
[1]	12	2.511	32.2
[1].Time	96	2.710	34.7

***** Analysis of variance *****

Variate: Species 65 (*Ruschia caroli*)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	371.021	123.674	0.84	0.496
SR	2	81.452	40.726	0.28	0.762
Season.SR	6	2108.293	351.382	2.40	0.093
Residual	12	1757.931	146.494	31.15	

[1].Time stratum

d.f. correction factor 0.4380

Time	8	791.606	98.951	21.04	<.001
Time.Season	24	148.064	6.169	1.31	0.254
Time.SR	16	42.181	2.636	0.56	0.784
Time.Season.SR	48	247.743	5.161	1.10	0.387
Residual	96	451.497	4.703		

Total 215 5999.788

***** Tables of means *****

Variate: Species 65 (*Ruschia caroli*)

Grand mean 9.22

Time	1	2	3	4	5	6	7
	9.39	12.49	12.40	9.98	8.47	7.41	7.35
Time	8	9					
	7.93	7.61					

L.S.D: 1.26

***** Stratum standard errors and coefficients of variation *****

Variate: 65

Stratum	d.f.	s.e.	cv%
[1]	12	4.034	43.7
[1].Time	96	2.169	23.5

***** Analysis of variance *****

Variate: Species 73 (*Zygophyllum morganiana*)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	306.914	102.305	5.12	0.016
SR	2	152.716	76.358	3.82	0.052
Season.SR	6	321.059	53.510	2.68	0.069
Residual	12	239.659	19.972	3.62	

[1].Time stratum

d.f. correction factor 0.2423

Time	8	199.768	24.971	4.52	0.023
Time.Season	24	161.528	6.730	1.22	0.332
Time.SR	16	25.358	1.585	0.29	0.878
Time.Season.SR	48	232.956	4.853	0.88	0.576
Residual	96	530.144	5.522		

Total 215 2170.101

***** Tables of means *****

Variate: Species 73 (*Zygophyllum morganiana*)

Grand mean 15.35

Time	1	2	3	4	5	6	7
	14.81	17.56	15.67	15.74	14.32	14.11	15.68
Time	8	9					
	14.93	15.35					

L.S.D: 1.40

Season	1	2	3	4
	15.13	16.63	13.51	16.15

L.S.D: 1.87

SR	0.22	0.32	0.42
	16.33	14.28	15.45

L.S.D: 1.62

***** Stratum standard errors and coefficients of variation *****

Variate: Species 73 (*Zygophyllum morganiana*)

Stratum	d.f.	s.e.	cv%
[1]	12	1.490	9.7
[1].Time	96	2.350	15.3

Appendix 3: Result of the Analysis of Variance (ANOVA) applied to the palatable and unpalatable categories in the shrub/herb complex.

***** Analysis of variance *****

Variate: Palatable

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
[1] stratum					
Season	3	581.89	193.96	1.34	0.308
SR	2	2667.19	1333.59	9.20	0.004
Season.SR	6	5613.03	935.50	6.46	0.003
Residual	12	1739.04	144.92	4.36	
[1].Time stratum					
d.f. correction factor 0.3672					
Time	8	4482.71	560.34	16.86	<.001
Time.Season	24	898.93	37.46	1.13	0.370
Time.SR	16	365.60	22.85	0.69	0.658
Time.Season.SR	48	946.91	19.73	0.59	0.878
Residual	96	3191.26	33.24		
Total	215	20486.55			

***** Tables of means *****

Variate: Palatable

Grand mean 66.40

Time	1	2	3	4	5	6	7
	64.66	61.00	64.96	58.35	69.12	73.98	70.79
Time	8	9					
	66.45	68.31					

L.S.D: 3.38

Season	SR	0.22	0.32	0.42
1		59.03	69.16	72.18
2		66.71	75.49	61.32
3		61.03	63.46	77.56
4		59.80	71.93	59.17

L.S.D: 8.74

L.S.D (When comparing means with the same level of SR): 5.85

SR	0.22	0.32	0.42
	61.64	70.01	67.56

L.S.D: 4.37

***** Stratum standard errors and coefficients of variation *****

Variate: Palatable

Stratum	d.f.	s.e.	cv%
[1]	12	4.013	6.0
[1].Time	96	5.766	8.7

Appendix 4: Species list.

1. *Antholiza plicata*
2. *Aspalanthus cuspidate*
3. *Aspalanthus divaricata*
4. *Cassine crocea*
5. *Chaetobromus schraderi*
6. *Chrysanthemoides monilifera*
7. *Cissampelos capensis*
8. *Cladoraphis cyperoides*
9. *Ehrharta calycina*
10. *Ehrharta villosa*
11. *Eriocephalus racemosus*
12. *Euphorbia karroica*
13. *Exomis microphylla*
14. *Felicia dregei*
15. *Hebenstretia robusta*
16. *Heliophylla variabilis*
17. *Heliophylla elata*
18. *Helichrysum hebelepis*
19. *Helichrysum marmarolepis*
20. *Hermannia scordifolia*
21. *Hermannia heterophylla*
22. *Hermannia trifurca*
23. *Lebeckia multiflora*
24. *Lessertia* sp.
25. *Lightfootia namaquana*
26. *Limeum africanum*
27. *Lycium arenicolum*
28. *Lycium austrimum*
29. *Manulea altissima*
30. *Manulea laxa*
31. *Microloma sagittatum*
32. *Manochlamys albicans*
33. *Melolobium adenosa*

34. *Pelargonium gibbosum*
35. *Pelargobium tintoe*
36. *Pteronia divaricata*
37. *Pteronia incana*
38. *Pteronia onobromoides*
39. *Pteronia ovalifolia*
40. *Putterlickia pyracantha*
41. *Rhus glauca*
42. *Restio* sp.
43. *Salvia lanceolata*
44. *Tetragonia fruiticosa*
45. *Wilborgia sericea*
46. *Wildenowia incurvata*
47. *Zygophyllum pygmaeum*
48. *Asparagus africanus*
49. *Asparagus capensis*
50. *Ballota africana*
51. *Cynanchum ellipticum*
52. *Cysticapnos africana*
53. *Cephalophyllum aroe-rubrum*
54. *Cryophytum crystalinum*
55. *Euclea racemosa*
56. *Euphorbia burmannii*
57. *Euphorbia tuberculata*
58. *Euphorbia mauritanica*
59. *Galenia africana*
60. *Galium tomentosum*
61. *Melothria* sp.
62. *Melianthus minor*
63. *Myrsiphyllum multituberosum*
64. *Othonna floribunda*
65. *Ruschia caroli*
66. *Ruschia cymosa*
67. *Ruschia* (langblaar)

68. *Sanderia hispida*
69. *Senecio corymbiferus*
70. *Senecio perfoliata*
71. *Solanum guineense*
72. *Tylecodon wallichii*
73. *Zygophyllum morgsana*
74. Bare ground