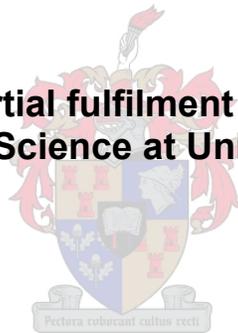


**Renosterveld Restoration:
The role of competition, herbivory and other disturbances**

By

Donald Midoko-Iponga

**This thesis presented in partial fulfilment of the requirements for the
degree of Master of Science at University of Stellenbosch.**



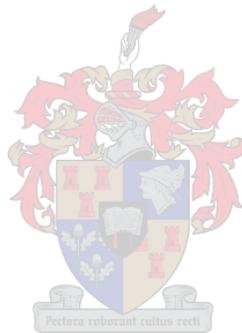
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December 2004

Declaration

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



Signature.....

Date.....

Abstract

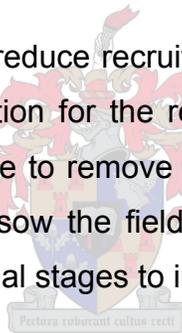
West Coast Renosterveld is one of the most threatened vegetation types in South Africa. Less than 5% of the original extent of this vegetation type remains, of which 80% is on private land. In addition to fragmentation, much of the vegetation has been ploughed for crop production and then abandoned and invaded by alien plants. Restoration of transformed areas may improve the conservation status of this vegetation type. Indigenous species do not return to abandoned agricultural fields for decades even if these are adjacent to natural areas since their return is limited either by seed dispersal or seedling establishment. The aim of this study was to examine the recovery of indigenous vegetation on abandoned fields.

Renosterveld, as we know it today, is an asteraceous shrubland, dominated mainly by renosterbos (*Eytropappus rhinocerotis*), but might have been a grassland or a grassland-shrubland mosaic. Historical records indicate that species of large game were common in the Western Cape when the early settlers arrived, but most of these have since disappeared. It is thus impossible to reconstruct exactly the ecological processes and functioning of Renosterveld.

The first part of the study was designed to examine the effects of grass competition, grazing by indigenous large herbivores, and interaction of these two factors on the establishment, growth and survival of transplanted Renosterveld seedlings on an abandoned agricultural field. Experimental transplanting of indigenous shrubs into an old field showed that most of the plants investigated competed for resources with lawn grasses on the field, and competition affected the seedlings throughout the experiment. Mortality was higher, and growth was reduced for seedlings exposed to grass competition. With the exception of wild olive (*Olea europaea spp.africana*), herbivory alone had no significant impact on the target species. Herbivory was at a low intensity (20 ha/large animal unit); higher grazing pressures might have given different results. No interaction between competition and herbivory was found for the species investigated; competition and grazing therefore seem to influence the seedlings independently.

The second part of this study was conducted to examine the effects of different management strategies, viz: brush cutting, burning and herbicide application on plant species recruitment and community composition and to ascertain their applicability by farmers for large scale restoration of Renosterveld. My comparison of the different strategies for controlling annual alien grasses indicated that these did not differ significantly in their effects on species richness. Burning reduced shrub cover and increased overall species richness and diversity. Burning also reduced grass biomass, and increased recruitment of indigenous seedlings. The use of herbicide resolved the problem of grass biomass invasion and increased shrub species richness. The herbicide application did not appear to have long-term negative effects on the soil quality. Brush cutting did not remove grass biomass on the old field. Experimental re-seeding with an indigenous grass and shrub species into treated plots resulted in low recruitment=

My conclusion is that grass can reduce recruitment and growth of many indigenous shrub species. My recommendation for the restoration of old fields in West Coast Renosterveld is to apply herbicide to remove grass competition, and then, after the herbicide has degraded, to oversow the field with seeds of indigenous shrub and grass species of early successional stages to increase overall species diversity.



Opsomming

Weskus Renosterveld is een van die mees bedreigde plantegroei soorte in Suid Afrika. Minder as 5% van die oorspronklike omvang van hierdie plantegroei tipe is oor, en dit hoofsaaklik (80%) op privaatlande. Saam met fragmentasie, is baie Renosterveld areas ook omgeploeg vir boerdery en dan net so gelos, met die gevolg dat uitheemse plante hierdie areas ingedring het. Restorasie of herstelling van sulke bewerkte lande kan dalk die bewaringsstatus van hierdie plantegroei tipe verbeter. Natuurlike vestiging van Renosterveld spesies op sulke ou bewerkte lande gebeur nie, selfs al is daar Renosterveld direk langs so 'n ou veld. Die hervestiging van inheemse spesies is dus tot saadverspreiding or saailingbevestiging beperk. Die doel van hierdie studie is om die stadige terugkoms van inheemse plantegroei na verlate bewerkte velde te verduidelik.

Renosterveld is 'n struikveld waarin die renosterbos (*Eytropappus rhinocerotis*) domineer, maar kan ook 'n grasveld of 'n grasveld-struikland mengsel wees. Groot herbivore was algemeen in die Wes Kaap toe die eerste settelaars gearriveer het, maar intussen het omtrent al die groot wild spesies verdwyn. Dit is dus ontmoontlik om die ekologiese prosesse en funksionering van Renosterveld presies so te herstel.

Die eerste deel van hierdie studie bestudeer die effek van graskompetisie, weiding deur inheemse groot herbivore, en die interaksie tussen hierdie twee faktore op die vestiging, groei en oorlewing van oorgeplante Renosterveld saailinge in 'n verlate ou veld. Die eksperimentele oorplanting van inheemse struik in 'n ou land het gewys dat die meeste van hierdie plante kompeteer vir hulpbronne met kweekgras wat op die ou veld groei. Kompetisie het die saailinge deur die hele eksperiment geaffekteer. 'n Hoër mortaliteit en verminderde groei in saailinge wat aan gras kompetisie blootgestel was, is waargeneem. Met die uitsondering van *Olea europaea spp. africana*, het herbivorie alleen geen betekenisvolle impak op plant spesies gehad nie. Weidingsdruk was laag (20 ha/groot vee eenheid); 'n groter weidingsdruk sou miskien 'n ander uitkoms gehad het. Geen interaksie tussen kompetisie en herbivorie is waargeneem in die bestudeerde plantspesies nie. Dit wil

dus voorkom of kompetisie en weiding die saailinge onafhanklik van mekaar beïnvloed.

Die tweede deel van hierdie studie was onderneem om die effek van verskillende behandelings (kontrole, sny, brand en herbisied toediening) op plantspesie vestiging en samestelling te bestudeer asook om bestuurmetodes te toets was deur boere op groot skaal gebruik kan word om Renosterveld te herstel. In 'n vergelyking van verskillende bestuur metodes (kontrole, besnoeiing, brand en herbisied) om eenjarige uitheemse gras te beheer, is gewys dat die behandelings nie betekenisvol van mekaar verskil in hulle effek op spesierykheid nie. Vuur het struikbedekking verminder en totale spesies rykheid en diversiteit verhoog. Die gebruik van 'n herbisied het die probleem van grasindringing opgelos en het ook struikspesiesrykheid verhoog. Die herbisied het nie lang termyn negatiewe effekte op grond kwaliteit gehad nie. Sny het nie gras biomassa verlaag op die ou land nie. Eksperimentele plant van inheemse grasse en struike in die behandelde areas, het lae vestiging tot gevolg gehad.

My algemene afleiding is dus dat gras die hervestiging en groei van baie inheemse struikspesies verminder. Ek stel voor dat herbisied gebruik moet word om gras kompetisie te verminder. Nadat herbisied residue in die grond afgebreek is, moet die ou land met inheemse struik en grasspesies, wat in vroeë suksessie stadiums is, beplant word om sodoende totale spesiediversiteit te verhoog en uiteindelik ou bewerkte lande in Weskus Renosterveld te herstel.

Acknowledgements

I extend my gratitude to the Gabonese Government, which provided the financial support of my studies in South Africa, as well as to the TMF / WWF SA for project funding. The same gratitude goes to Mike Gregor, Nicola Farley and Bernard Wooding for logistic support, Mrs Elizabeth Parker for allowing me to work on the farm, WCNCB for the permit, and Prof Nel for assistance with statistics. I am deeply indebted to my supervisors, professor Sue Milton and Dr Cornelia Krug for their support, directions and willingness to share their knowledge. I am grateful to Benjamin Walton for his help and effort with the plant species identifications. Thanks to all my colleagues in Conservation Ecology Department for their support and friendship, especially Rainer Krug for his assistance while I was carrying out this research.

Finally, I thank my parents and family for their financial support and faith in me.



Dedicated to the Renosterveld Restoration Project

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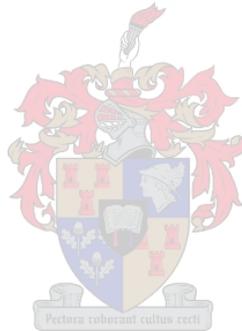
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Thesis structure

The thesis comprises an introduction (Ch 1) dealing with the history and ecology of the Renosterveld vegetation. This is followed by a literature review that explores the effects of competition and herbivory on vegetation development (Ch 2). The experimental component of this research is presented in two self-contained scientific articles that deal with the field experiments (Ch 3 and Ch 4). Chapter 3 deals with the effects of competition and herbivory on survival and growth of seedlings of five species of shrubs. Chapter 4 presents the results of larger scale experiments investigating the use of burning, brush-cutting and herbicide to re-establish indigenous plant communities on old fields. The outcomes of these two studies and my recommendations for land owners are presented in the conclusion (Ch 5). The thesis style is consistent with *African Journal of Ecology*.



Chapter 1: General Introduction

1.1 Introduction

Situated at the south-western tip of the African continent between latitudes 31° 30'S, the area referred to as the Cape Floristic Region has a very rich flora (Goldblatt and Manning 2000), and to a less extent fauna (Stuckenberg, 1962). The flora is sharply distinct from that of the lands surrounding it, and it has impressed naturalists from the time of its discovery by European explorers in the sixteenth century. Indeed, the floristic characteristics of the Cape Region are so unusual that it is regarded as one of the world's six-floral kingdoms (Goldblatt and Manning, 2000). Comprising a land area of about 90 000 km², less than 5% of the total area of the southern Africa subcontinent (Goldblatt, 1978, 1997), the Cape Floristic Region is one of the world's richest regions in terms of botanical diversity.

An estimated 9 030 species of vascular plants (ferns and fern allies, gymnosperms, and flowering plants) are native to this area, almost 70% of which are endemic (Goldblatt and Manning, 2000). The great majority of these species, some 8 888 in total, are flowering plants. Thus, the flora of the Cape Region comprises almost 44% of the approximately 20 500 species that occur in all of southern Africa (Arnold and De Wet, 1993). There are no accepted criteria for distinguishing floral kingdoms and recognition of the Cape Floral Kingdom is not universal (Goldblatt and Manning, 2000). The use of the neutral term Cape Floristic Region (CFR) is used here simply for convenience (Arnold and De Wet, 1993).

The climate of Cape Floristic Region is largely Mediterranean; strictly so in the West, with the eastern half of the Cape Floristic Region receiving substantially more summer precipitation. Rain falls mainly in the winter months and while summers are hot and dry, they are relatively less so in the east. Rainfall is highly variable locally, especially in mountainous areas. Mountain slopes facing prevailing winds receive considerably more precipitation than those facing away from these winds. Rainfall patterns in Cape Region show also dramatic variation in amount received at

localities, dropping from 2 000 mm per year on the high mountains ranges (Coetzee, 1993) to 250 mm in the coastal lowlands.

In addition, elevation and aspect affect precipitation depending on the direction of moisture-bearing winds. The eastern and western parts of the Cape Floristic Region are considered to be under fundamentally different climatic controls, probably a long enduring pattern that has affected the evolutionary histories of the areas and, hence, resulted in their distinctive floras and fauna (Cowling *et al.*, 1999).

The mosaic of soil types alone contributes to an increased diversity, but the peculiar nature of nutrient-poor soils may result in more pronounced effects on plant diversity, and hence plant gene flow (Goldblatt and Manning, 2002). The vegetation of the Cape Floristic region is thus far from being uniform. The Cape Region encompasses five biomes with several distinctive vegetation types (Cowling and Holmes, 1992; Rutherford and Westfall 1994), each with their own suites and physical characteristics.

The most common and distinctive is a heathland, locally called Fynbos. Shrubs with ericoid or short, arrow-like, or needle-like leaves predominate, but most species of *Proteaceae*, a family common to this vegetation, have broad sclerophyllous leaves. Fynbos typically occurs on soils derived from sandstone (Cowling and Holmes, 1992). The second distinctive vegetation type is Renosterveld, which is usually restricted to richer, fine-grained soils, which are derived from shales and granites. Although these two vegetation types often grow adjacently to one another, they share few species. Microphyllous *Asteraceae* are common in Renosterveld, which is a dense shrubland with a rich herbaceous understorey that becomes evident after clearing or fire, but is often suppressed under a mature shrub cover. On dry sites with rainfall of less than 200 mm per year, a vegetation of small succulent-leaved shrubs, including many *Aizoaceae* and *Asteraceae* species, establishes, forming the karoo steppe or succulent shrubland biome. The last biomes in the Cape Floristic region are the forest thicket (a dense, semi-succulent and spinescent evergreen shrubland to low forest) and the evergreen, afro-montane forests in the eastern parts of the region (Goldblatt and Manning, 2000).

Fire is integral part of the ecology of the Cape Region and accounts for several aspects of the vegetation (Cowling, 1987). Mature Fynbos and Renosterveld vegetation forms a relative uniform, closed, low canopy of twiggy and microphyllous to sclerophyllous shrubs. These vegetation types are highly prone to periodic fire (Cowling, 1987). Fire itself has a disruptive effect on the vegetation (Cowling, 1987). It has been a feature of the ecology for so long that there is a large flora of ephemerals, geophytes, other perennials, and short-lived shrubs that appear in the years following a fire, often flower profusely, and subsequently disappear, as they are succeeded by longer-lived shrubs (Goldblatt and Manning, 2000). The long-term ecological consequence of fire on the flora is the existence of a niche for species that grow rapidly after fire to persist and bloom in the immediate post-fire years. This fire-adapted suite of species contributes substantially to the overall diversity in the flora. Mature vegetation is affected by fire in more subtle ways, but fire may cause local perturbations in species composition and the elimination of some taxa (Cowling, 1987).

1.2. General Renosterveld history and ecology

1.2.1 What is Renosterveld?

The general public often confuses the definition of Renosterveld and Fynbos, as both are shrub dominated plant communities growing in winter rainfall areas of the Western Cape. Renosterveld is found in the southern part of the Western Cape and in the Eastern Cape; and is described as a shrubland dominated by asteraceous shrubs, particularly *Elytropappus rhinocerotis* (Renosterbos) with a grassy component and high species richness of geophytic plants (chiefly in the Iris family (*Iridaceae*) and Lily family (*Liliaceae*), but also belonging to the Orchid family (*Orchidaceae*)). Although Renosterveld and Fynbos vegetation share few species, there are not many species endemic to Renosterveld vegetation alone. However, species endemic to the Cape Floral Kingdom comprise about one-third of the plant species found in Renosterveld (Boucher, 1995). This vegetation type is typically confined to fine-grained soil (clays and silts) in areas receiving between 250 and 700

mm rainfall per year where at least 30% falls in winter (Boucher and Moll, 1981; Rebelo, 1998). Where the rainfall is higher, the soils become leached and Renosterveld is replaced by asteraceous Fynbos (McDowell and Moll, 1992). Because of its high soil fertility, it is probable that all the herds of large game in the Fynbos biome occurred in Renosterveld (Rebelo, 1998).

1.2.2 History and Ecology of Renosterveld

The name Renosterveld does not have a clearly defined origin. Levyns (1972) suggests that the colours and textures of the rhinoceros hide are reflected in the shrubby grey-green vegetation. Another explanation is that Renosterbos provided shelter for the rhinoceros, hence the name Renosterveld (literally rhinoceros field), which is characterized by Renosterbos. A number of terms for Renosterveld have been used, and Boucher (1980) suggests that the term Renosterveld should be used preferably over renosterbosveld, rhenosterveld or rhenosterbosveld. Renosterveld in its current state is a shrubland, but whether it was originally a shrubland or grassland is still under debate (Cowling *et al.*, 1986). Renosterveld has been used for centuries as natural grazing by Khoi-Khoi pastoralists for their livestock. With the arrival of the European settlers, but especially since the 1920s (Kemper, 1997), Renosterveld has been extensively transformed due to agriculture, and an estimated 160 000 ha of natural vegetation have been transformed to cereals and artificial pastures between 1918 and 1990 (Cowling *et al.*, 1986; Hoffman, 1997). Today, < 10% of the original area of Lowland Renosterveld habitat still exists, and < 1% is formally conserved (Von Hase *et al.*, 2003). Most of this vegetation type remains as a series of small fragments within cereal and pasturelands that are subjected to grazing, trampling, crop spraying and frequent burning (Kemper, 1997). Remnant patches of Renosterveld have high conservation or priority value (Pressey *et al.*, 1994, 1996), since almost all remaining habitat is required to meet a conservation goal of 10% of the pre-colonial extent of this vegetation type. Furthermore, owing to the relatively high agricultural value of Renosterveld soils, the remaining fragments are vulnerable to clearance (McDowell and Moll, 1992). For these reasons, Renosterveld is a major conservation priority in South Africa. There are four major blocks of Renosterveld in

South Africa, each with own characteristic features: South West Coast Renosterveld, South Coast Renosterveld, Mountain Renosterveld and West Coast Renosterveld.

South West Coast Renosterveld has a higher grass cover than the West Coast form, and co-dominants are species in the genera *Relhania* and *Helichrysum*, both Asteraceae, and *Hermannia*, (Sterculiaceae) (Rebelo *et al.*, 1991). South Coast Renosterveld contains a much higher proportion of perennial grasses, while central Mountain Renosterveld has a greater proportion of succulents and is dominated by *Relhania spp* and *Pteronia incana*, (Low and Rebelo, 1996). Most of the vegetation types of Mountain Renosterveld (North-Western mountain, Escarpment mountain and central mountain), are not well known, and are locally restricted. Northwestern Mountain Renosterveld is largely confined to the Kamiesberg highlands around Leliefontein where the higher elevation ensures sufficient rainfall to support this vegetation type (Low and Rebelo, 1996). This vegetation type grades with Succulent Karoo at lower and Fynbos at higher elevations. The Escarpment Mountain Renosterveld is located on the slopes and foothills of the great Escarpment, ranging from Calvinia to Sutherland and towards Beaufort West, on the Roggeveld, Koms and Nuweveld mountains (Adamson, 1938). Central Mountain Renosterveld is found on the fringes of the basins of little and great Karoo, and westward towards the Worcester valley. This vegetation type borders Fynbos and Succulent Karoo vegetation (Moll *et al.*, 1984). Most of the Mountain Renosterveld types are dominated by Renosterbos (*Elytropapus rhinocerotis*) and Gumbush (Gombos), *Relhania genisfolia* (Boucher, 1995).

Of the Renosterveld vegetation types, West Coast Renosterveld (comprising Boland and Swartland Coast Renosterveld types *sensu* von Hase *et al.*, 2003) is the focus of this study, and of particular interest are the conservation of remnant patches, and restoration of this vegetation type on abandoned fields in agricultural areas.

Little is known about the role of large herbivorous mammals and fires in the ecology of Renosterveld vegetation. Large game no longer occurs naturally in the area, although some of the species have been reintroduced to a number of private and

state owned nature reserves. Adamson (1938) states that grazing eliminates some plant species, while fire has an unspecified influence on the vegetation.

The ecology of Renosterveld was generally integrated with the Fynbos vegetation types, which are fire-prone, with plant recruitment occurring predominantly after fires (Boucher 1995). The plant species in Renosterveld vegetation were often managed under a fire regime appropriate for Fynbos. The fire return interval in Renosterveld is probably shorter than Fynbos (less than 10 years), owing to the more fertile soils that promote a high coverage of grasses, which in turn produce flammable biomass relatively quickly. In addition, post-fire recruitment of plants is by germination from seeds stored in the soil or by basal resprouting from buds protected from fire (Boucher, 1995).

1.2.3 West coast Renosterveld history and ecology

West Coast Renosterveld (Boland and Swartland Coast Renosterveld), once prevalent in the south-western lowlands of the floristically rich Cape Floral Kingdom, is now South Africa's scarcest vegetation type (Boucher, 1995). Only 5% of the original extent of the vegetation type remains, and remnants of natural vegetation are scattered amongst agricultural lands (von Hase *et al.*, 2003). Originally, the West Coast Renosterveld forelands, with their true Mediterranean type climate, used to cover an area of 512 266 hectares (Boucher, 1981), mostly on the rich shale soils of the Swartland, now famous for its wheat. It is ironic that the word Swartland is derived from Renosterveld, which has a characteristic dark green, grey, or sometimes almost black (swart), appearance from a distance. West Coast Renosterveld has a sparser grass cover than South Coast Renosterveld, a higher diversity of geophytes and annuals, and has *Eriocephalus africanus* and *Leysera graphalodes*, both Asteraceae, together with Renosterbos, as major elements. Especially on granitic soils there may also be a strong Fynbos element (Cowling and Richardson, 1995).

The area is typically Mediterranean with most of the rain falling in winter and rainfall varying from 300 mm to 600 mm per year. The summers are hot and dry and conductive fires are observed (Boucher and Moll, 1981). The geology of the soil is

confined to Cape granite suite and Klipheuwel formation shales, which weather to form heavy clays and loamy soils. In areas of higher rainfall, Fynbos elements become prominent and the boundary between Renosterveld and Fynbos vegetation types becomes diffuse (Boucher, 1981).

The overstorey is dominated by Renosterbos *Elytropappus rhinocerotis*, with subdominants *Eriocephalus africanus*, *Leysera gnaphalodes*, Jakkalsstert *Anthospermum aethiopicum*, *Athanasia trifurcata*, *Felicia filifolia*, *Metalasia muricata* and *Stoebe spiralis*. The understorey is mainly annual and herbaceous with perennial grasses. *Themeda triandra* and *Cymbopogon marginatus* are locally abundant (Rebelo, 1995). Geophytes, mainly Irises (Iridaceae), Lilies (Liliaceae) and Sorrels (Oxalidaceae) are characteristic and may be abundant.

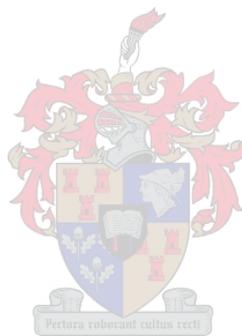
Another important feature in the Renosterveld landscape are clumps of taller, woody re-sprouting shrubs, mainly occurring on “heuweltjies”, underground termitaria, or among rocks and along river. These areas are more nutrient rich and moister than the surrounding areas. These bush clumps are dominated by typical Thicket Biome species, such as Wild Olive *Olea europaea* subsp. *africana*, Dune Taaibos *Rhus laevigata* and Bush Guarri *Euclea racemosa* (Rebelo, 1992).

Little is known about the early dynamics of West Coast Renosterveld. Records of large herds of big game suggest that grazing by large herbivores was an important ecological factor. Grazing strongly affects vegetation structure, and is also believed to be one of the factors contributing to the evolution and maintenance of species diversity in any region (Cowling, 1983). This is based on the intermediate disturbance hypothesis, which states that: “In the absence of disturbance, a competitive equilibrium results with one or few species dominating and the diversity is low ” (Connell, 1978). At high frequencies of population reduction, only the species capable reproducing under the heavy disturbance regime will persist and diversity will be low. The highest species diversity will therefore occur at an intermediate disturbance level, at which most species can co-exist (Connell, 1978).

In response to burning, *E. rhinocerotis* could regenerate far above its usual rate and also at higher densities than other species (Levyns, 1956). This is because *E.*

rhinocerotis seeds show an increased germination success when they are subjected to wide temperature fluctuations (Levyns, 1956). One of the main reasons for burning is to stimulate grass growth to provide grazing where herbivores have depleted the supply. The previous grazing will have removed all the palatable species and probably most of their seed bank. Renosterbos is not a palatable grazing species; therefore dominates the seed rain in heavily-grazed areas (Levyns, 1935). Grazing alone can substantially advantage Renosterveld seedlings as denudation of the soil increases the surface temperature fluctuations and thereby increasing the germination rate of Renosterveld seedlings.

Today few large tracts of Renosterveld remain. Among these, the Tygerberg Nature Reserve, and Elandsberg Private Nature Reserve between Wellington and Voëlvlei, are the best conserved (Figure1.1).



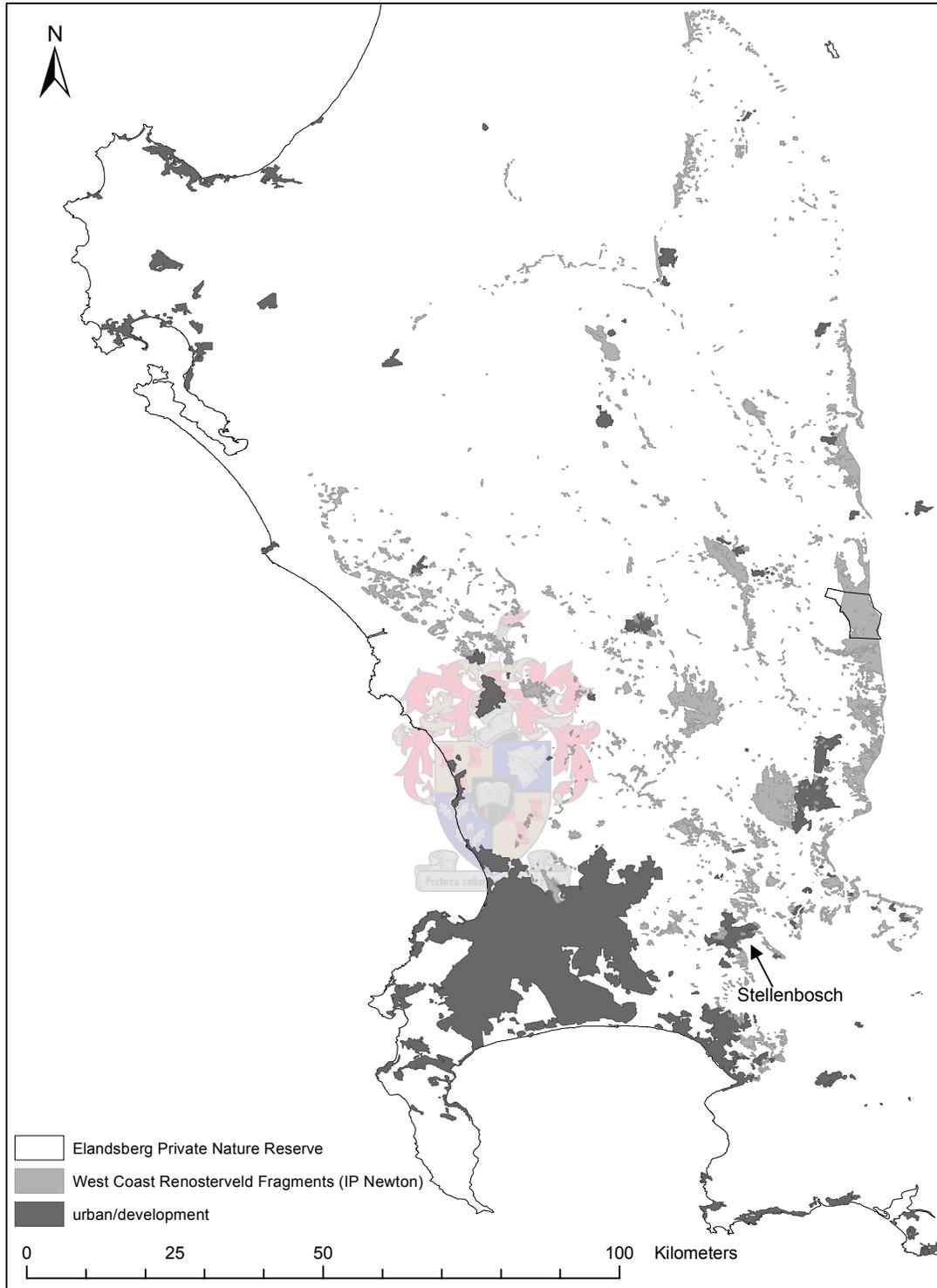


Figure 1.1: West Coast Renosterveld Fragments. Data from Ian Newton (Renosterveld Fragments) and Western Cape Nature Conservation Board (Conservancy, Private Nature Reserve and CFR boundary). Map created by CB Krug in ESRI®ArcMap™ 8.3 (ESRI 2002)

1.2.4 Current conservation problems of Renosterveld

The conservation of lowland in general is dismal, certainly when compared to the mountains where large areas of Fynbos vegetation are conserved. There is a lot of biodiversity that is threatened in the lowlands of South Africa (Heydenreych and Littlewort, 1995). From a conservation point of view, Renosterveld has shown the greatest decline of the major vegetation types in the Western Cape (McDowell and Moll, 1992). According to the Western Cape Lowlands Conservation working group, there are about 2 135 ha coastal Renosterveld under protection in private, provincial and national reserves. This includes the private nature reserve at Elandsberg which encompasses a total of 3800 ha of natural veld, of which about 1 000 ha is Renosterveld.

To be able to conserve 10% of Renosterveld as recommended by the International Union for Conservation of Nature and Natural Resources (IUCN), it is necessary to reclaim abandoned fields, and restore Renosterveld on the old fields and in degraded areas. Renosterveld vegetation apparently re-establishes easily after fire, because most Renosterveld species resprout or have wind dispersed seeds (Shiponeni 2003; Cowling *et al.*, 1994). Sprouters are able to persist for long periods (Midgley, 1996). Unlike fire, ploughing removes resprouters and most geophytes, revegetation of old fields is therefore slow and mainly results in monospecific stands of Renosterbos, *Elytropappus rhinocerotis*. Many other plants occurring in natural Renosterveld, especially geophytes do not return even after decades of abandonment. Observations in Elandsberg Nature Reserve support this: the natural vegetation does not return into old fields (fields abandoned when they are no longer suitable for crop production or due to the changes of land use) even after years, and even if they are adjacent to natural vegetation (Shiponeni, 2003). This can be for two reasons: the return of indigenous species is either seed and seed dispersal limited or the seedlings of indigenous plants can not establish on the old fields due to the competition from lawn grasses and annuals that dominate old fields. Furthermore, the large herds of game once found in the Western Cape have diminished drastically, and it is therefore nearly impossible to determine which role these herbivores have played in the ecology of Renosterveld. Game species have been

reintroduced to Elandsberg Private Nature Reserve, and grazing by these herbivores might also have an influence on the establishment of indigenous shrub species and the maintenance of plant communities.

To date no research has been conducted on restoring indigenous vegetation on degraded or cultivated areas that previously supported Renosterveld. As this vegetation type is highly threatened, it is important to investigate techniques to best restore degraded areas, as these potentially may contribute to the conservation network by providing new habitats for endangered species. The only way to ever attain 10% of Renosterveld as conserved is to reclaim it, not only from alien plant infestation and degradation, but also from vineyards and wheatfields. The old land site at Elandsberg Nature Reserve is suitable to investigate effect of competition between grasses and Renosterveld seedlings, to examine factors that effect herbivore feeding behavior, to investigate how these factors ultimately influence the plant communities of lowland Renosterveld, and to assess whether herbivore species maintain grazing lawns.

In order to facilitate re-establishment of Renosterveld we need to understand competitive and facilitative interactions among species, and need to identify “nurse species” that facilitate establishment of other species, especially geophytes and grasses. We need data on seed ecology, from dispersal and predation to germination and establishment. We need to know the regeneration niches of climax species, from both the shrubby and the grassy component (Levyns, 1935). Some restoration techniques need to be investigated to test management methods that can be used for re-establishment of Renosterveld.

The primary aim of this study is thus to explain the apparent slow return of indigenous vegetation to abandoned fields.

Three possible reasons for the slow return of Renosterveld species to ploughed lands are:

1. Seeds of indigenous shrub species are absent in the old-field. This may be the case for some species, however Shiponeni (2003) showed that seed of many wind-or dung-dispersed species are continually deposited onto the old field, or are present in the seed bank.
2. Competition from grass that presently dominates the fields prevents the establishment of indigenous shrubs.
3. Herbivory that appears to be concentrated on grassy patches prevents the establishment of indigenous shrub species.

1.3. Objectives, aims and predictions of the research

Many of the studies on large-scale disturbances have concentrated on fire (Bhandari *et al.*, 1998; Bond and van Wilgen, 1996; Hudak, 1999) and grazing (Cowling *et al.*, 1998; Hudak, 1999; Stohlgren *et al.*, 1999; Tracy and McNaughton, 1997). Grazing and fire are not excluded at Elandsberg Private Nature Reserve. For the future of this vegetation, it is therefore vital to understand any changes in species abundance due to the current disturbance regimes in the area. This project seeks to develop an understanding of the influence of grazing, competition and their interactions on the establishment of indigenous Renosterveld shrubs and perennial tussock grasses in the grazing lawns that establish on old fields. A second aim is to determine whether herbivores are implicated in the persistence of shrub-free grazing-lawns in Renosterveld, and whether herbivore exclusion would be a pre-requisite for Renosterveld restoration on old fields.

This research will investigate the hypotheses that Renosterveld shrub survival is influenced by both herbivory of large mammals and by competition from grasses, and that there is an interaction between these factors. This project will also test the management methods that can be used by farmers for large-scale restoration of Renosterveld using different disturbance regimes (burning, brush cutting, application of herbicide and untreated control).

The following specific questions were addressed:

1. Does grass removal, exclusion of large herbivores and a combination of these treatments improve shrub survival in old fields?
2. Under which disturbance regimes (burning, cutting or herbicide application) do shrubs and tussock grasses re-establish on abandoned fields?
3. Which of the applied methods (burning, cutting or herbicide application) is most suitable and cost-effective for farmers?

We predict that indigenous Renosterveld seedlings cannot establish on old abandoned fields due to the competition by grasses or by grazing from large herbivores, or a combination of both factors.

1.5. References

Adamson, R.S. 1938. Bush (Schlerophyll) vegetation. In: *Vegetation of South Africa*. London.

Arnold, T.H., and de Wet, B.C (eds) 1993. Plants of Southern Africa. Names and Distribution. *Memoir of Botanical Survey of southern Africa* **62** National Botanical Institute, Pretoria.

Bhandari, B.S., Mehta, J.P., and Tiwari, S.C. 1998. Animal behaviour and carrying capacity of burnt and unburnt submontane grazing lands. *Tropical Ecology* **38**: 149-152.

Bond, W., and van Wilgen, B.W. 1996. *Fire and plants*. Chapman & Hall. London. pp: 179-182.

Boucher, C. 1980. Note on the use of the term Renosterveld. *Bothalia* **13**: (1& 2): 237.

Boucher, C. 1981. Western Cape Provincial lowland alien vegetation. Page 67 in Moll, E.J., editor. Proceeding of a symposium on Coastal Lowlands of the Western Cape, 19-20 March 1981, Bellville, South Africa. University of Western Cape, Bellville, South Africa.

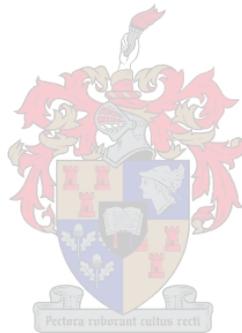
- Boucher, C. 1995. Overview of management of Renosterveld. In: Low, A.B., and Jones, F.E. (editors) The sustainable use and management of Renosterveld remnants in the Cape Floristic Region, pp: 47-50, FCC report 95/4 Botanical society of South Africa.
- Boucher, C., and Moll, E.J. 1981. South African Mediterranean Shrublands. In: di Castri. Goodall, D.W. & Specht, R.L. (editors) *Mediterranean-Type Shrublands*, Pp: 233-248, Elsevier, Amsterdam.
- Coetzee, J.A. 1993. Africa floran since the terminal Jurassic' pp: 37-61 in Goldblatt, P. (editors), Biological Relationships between Africa and South America. Yale Univ. Press, New Haven.
- Connell, J.H. 1978. Diversity in tropical rainforest and coral reefs. *Science* **199**: 1302-1310.
- Cowling, R.M. 1983. Diversity relations in Cape shrublands and other vegetation in the southeastern cape, South Africa. *Vegetatio* **54**: 103-127.
- Cowling, J.H. 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. *South Africa Journal of Science* **83**: 106-112.
- Cowling, R.M., Pierce, S.M., and Moll, E.J. 1986. Conservation and utilization of south coast renosterveld, an endangered South African vegetation type. *Biological Conservation* **37**: 363-377.
- Cowling, R.M., and Holmes, P.M. 1992. Flora and vegetation. In: Cowling, R.M. (Ed.). The ecology of Fynbos, nutrients fire and diversity. Oxford University Press. Cape Town, pp: 62-112.
- Cowling, R.M., Mustart, P.J., Laurie, H., and Richards, M.B. 1994. Species diversity, functional diversity, and functional redundancy in fynbos communities. *South Africa Journal of Science* **90**: 333-337.
- Cowling, R.M., and Richardson, D.M. 1995. Fynbos: South Africa's unique floral kingdom. Fernwood Press, Cape Town.

- Cowling, R.M., Rundell, P.W., Desmet, P.G., and Esler, K.J. 1998. Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons. *Diversity and distributions* **4**: 27-36.
- Cowling, R.M., Cartwright, C.R., Parkington, J.E., and Allsopp, J.C. 1999. Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: Implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. *Journal of Biogeography* **26**: 367-378.
- ESRI 2002. ESRI@ArcMap™ 8.3. www.esri.com.
- Goldblatt, P.1978. An analysis of flora of southern Africa: Its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden* **65**: 369-436.
- Goldblatt, P. 1997. Floristic diversity in the Cape Flora of South Africa. *Biodiversity and Conservation* **6**: 359-377.
- Goldblatt, P., and Manning, J.C. 2000. Cape Plants. National Botanical Institute, Cape Town.
- Goldblatt, P., and Manning, J.C. 2002. Plant diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden* **89**: 281-302.
- Heydenrych, B., and Littlewort, P. 1995. Flora survey of Darling. A preliminary investigation into the conservation of the renosterveld remnants in the Darling area. Flora Conservation Committee Report no. 95/3. Botanical Society of South Africa, Cape Town.
- Hoffman, M.T. 1997. Human impacts on vegetation. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (eds), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Hudak, A.T. 1999. Rangeland mismanagement in South Africa: failure to apply ecological knowledge. *Human Ecology* **27**: 55-78.

- Kemper, J. 1997. The effects of fragmentation of South Coast Renosterveld on vegetation patterns and processes. M.Sc. University of Cape Town, South Africa.
- Levyns, M.R. 1935. Germination in some South Africa seeds. *South Africa Journal of Botany* **1**: 161-170.
- Levyns, M.R. 1956. Notes on biology and distribution of the rhenoster bush. *South Africa Journal of Science* **52**: 141-143.
- Levyns, M.R. 1972. The rhenosterbush. *Veld and Flora* **2**: 7-9.
- Low, A.B., and Rebelo, A.G. (eds) 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.
- McDowell, C., and Moll, E.J. 1992. The influence of agriculture on the decline West Coast Renosterveld, South-Western Cape. *South Africa Journal of Environment management* **35**: 173-192.
- Midgley, J.J. 1996. Why the world's vegetation is not totally dominated by resprouting plants: because resprouters are shorter than reseeders. *Ecography* **19**: 92-95.
- Moll, E.J., Campbell, B.M., Cowling, R.M., Bossi, L., Jarman, M.L., and Boucher, C. 1984. A description of major vegetation categories in and adjacent to the Fynbos Biomes. **83**: 11-14. Pretoria, Council for scientific and Industrial Research. South African National Scientific Programmes Report.
- Pressey, R.L., Johnson, I.L., and Wilson, P.D. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. *Biodiversity and Conservation* **3**: 342-262.
- Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tulley, S.T., and Weinmann, K.M. 1996. How well protected are the forests of north-eastern New South Wales? Analysis of forest environments in relation to formal protection measures, land tenure and vulnerability to clearing. *Forest Ecology and Management* **85**: 311-333.

- Rebello, A.G. 1992. Reservation of biotic diversity. In: The ecology of fynbos- Nutrients, fire and diversity (Ed. Cowling, R.M.). Oxford University Press. Cape Town.
- Rebello, A.G. 1995. Renosterveld: Conservation and research. In: the Sustainable Use and Management of Renosterveld Remnants in the Cape Floristic Region. Proceedings of a Symposium (eds Low, A.B., Jones, F. E.), PP: 32-42. Flora Conservation Committee, Report 1995/4. Botanical Society of South Africa, Cape Town.
- Rebello, A.G.1998. Renosterveld. In: Low, A.B., and Rebello, A.G. (editors) Vegetation of South Africa, Lesotho and Swaziland, pp: 63-67, Department of Environmental Affairs and Tourism, Pretoria.
- Rebello, A.G., Cowling, R.M., Campbell, B.M., and Meadows, M. 1991. Plant communities of the Riversdale plain. *South African Journal of Botany* **57**: 10-28.
- Rutherford, M.C., and Westfall, R.H. 1994. Biomes of southern Africa: An objective categorization. *Memoir of Botanical Survey of South Africa* **63**.
- Shiponeni, N.N. 2003. Dispersal of seeds as a constraint in revegetation of old field in Renosterveld vegetation in the Western Cape, South Africa. M.Sc. University of Stellenbosch, South Africa.
- Stohlgren, T.J., Schell, L.D., and Heuvel, B.V. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* **9**: 45-64.
- Stuckenberg, B.R. 1962. The distribution of the montane palaeogenic element in the South Africa invertebrate fauna. *Annals of the Cape provincial Museums* **2**: 190-205.
- Tracy, B.F. and McNaughton, S.J.1997. Elk grazing and vegetation responses following a late season fire in Yellowstone National Park. *Plant Ecology* **130**: 111-119.

Von Hase, A., Rouget, M., Maze. and Helme, N. 2003. A Fine-Scale Conservation Plan for Cape Lowlands Renosterveld: Technical Report. Cape Conservation Unit, Botanical Society of South Africa.



Chapter 2: Literature review

2.1 Introduction

This review focuses on the influence of competition among shrub seedlings and established grass, as well as on the effects of grazing by large herbivores. The aim of the review is to gain a predictive understanding of the effects of these processes on vegetation, and in particular on the recovery of natural vegetation on abandoned agricultural fields. This understanding will be used as a basis for interpreting the experimental component of this thesis conducted in a West Coast Renosterveld plant community situated at Elandberg Private Nature Reserve (EPNR) in the Western Cape, South Africa.

More specifically this a review of how grass competition and grazing by large mammals limit the recruitment of indigenous shrub species and how this influences survivorship of these seedlings. This review will also look at different types of competition and competition interactions between individual plants, and discuss how large herbivores influence competition between plants, thereby driving or changing succession of vegetation and thus influencing the structure and function of ecosystems. Theories and predictions about competition and grazing at different stages will be developed to see whether competition between grasses and indigenous seedlings occurs on old agricultural lands.

2.2 Disturbance ecology

Disturbance is considered to play a primary role in determining both the composition and diversity of the vegetation community (Chaneton and Facelli, 1991; Collins, 1992). Both the system affected, and the disturbance itself can influence the nature of the induced changes via selective damage or mortality (Hulme, 1994), altered competitive interactions (Belsky, 1992; Clarke *et al.*, 1996), effects on abiotic conditions (Bazely and Jefferies, 1986; Ford and Grace, 1998), and effects mediated through altered trophic interactions (Coffin *et al.*, 1998). The definition of disturbance, and what actually constitutes a disturbance in any given community, has been much

debated. Useful definitions include those of White and Pickett (1985), who defined a disturbance as any relatively discrete event in time that disrupts an ecosystem, community, or population structure and changes resources, substrate availability, or physical environment. Disturbance can be regarded as an important source of uncertainty for plant species in mostly herbaceous vegetation.

Grime (1979) considered disturbance as one of the two most important factors that drive the evolution of plant life histories, morphology and defences, and shape the composition of plant communities. Although disturbances have specific and complex effects, the response of plant communities to an abrupt reduction in the intensity of competition, is assumed to be general. Disturbance that is too frequent or severe to enable re-colonization will preclude many species and reduce diversity. The tension between removal and competitive exclusion is thought to explain co-existence of competing species and is the basis of the intermediate disturbance hypothesis (Connell, 1978; Grime, 1973), as well as other models of community dynamics such as the dynamic equilibrium model (Huston, 1979).

The disturbance created by agriculture on the old field investigated, might pose a problem for the establishment, survival and growth of indigenous shrub seedlings. However, investigating the disturbance on this old abandoned field using plant removal treatments to study competition and exclosure cages to study grazing, might improve our understanding of the problem of indigenous seedling establishment on old fields.

Established vegetation has been shown to inhibit germination for many but not all plant species (Thompson *et al.*, 1977) and the suppression of germination by established vegetation has been described as a cryptic form of competition (Grace, 1999). This is thus an important interaction when considering the effects of disturbance. Some disturbance at the field boundaries can be caused by regular farming operations or by spot application of broad-spectrum herbicides, as is the case for the study site. Disturbance induces plant mortality that might decrease species diversity, but opens up space for colonisers from elsewhere, which might increase species diversity (Begon *et al.*, 1996). Disturbance can also reduce density

of perennial plants to the advantage of weaker competitors. Milton (1995) found, in the Succulent Karoo, that density of annuals increased in plots cleared of shrubs, compared to surrounding undisturbed vegetation. This prediction will be tested on the old abandoned field by removal of grasses in some of the plots to examine the response of indigenous shrubs growth and survival.

Fire, grazing, trampling, burrowing and digging, as well as human activities such as mowing, haying or tilling, are all common agents of disturbance in grasslands (Hulbert, 1988; Maret and Wilson, 2000). Moisture stress affects the competitive interactions between seedlings of certain species, and hence determines their recruitment success during dry years, which may lead, in turn, to changes in community composition (Milton *et al.*, 1994). For the purposes of biodiversity conservation, it is important to know the degree to which plant species in a system depend on specific forms of disturbance or whether various types of disturbance have equivalent effects.

2.3 Competition between plants

In order to understand the reactions of plant communities on the study site, and their reactions to the treatments, it is necessary to understand some of the basic principles governing their development. Competition between plants and grazing by large mammals can be also included among the most important concepts in ecology shaping plant communities and are the subject of large literature and numerous reviews (McNaughton, 1976, 1979; White, 1984; Goldberg and Barton, 1992; Goldberg *et al.*, 1999; Jolliffe, 2000). But these two concepts still continue to cause confusion. Competition may be intraspecific, between individuals of the same species, or interspecific, between individuals of different species (Stiling, 1999). The definitions of plant competition are based largely on observation and experience or measurements of effects on plants, rather than on understanding of mechanisms (Tilman, 1988). Plant competition is an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned (Begon *et al.*, 1996).

However, plants living in close proximity are likely to interact in some manner; these interactions may be small or large, direct, or indirect. These interactions may be beneficial to one or all of the species or they may be deleterious to one or all species (Tilman, 1988). Plants are often thought to suffer more from competition than animal populations because plants are rooted in the ground and cannot move to escape competitive effects.

There are two different types of competition, above and below ground. Plants have a physiological need for light, carbon dioxide, water, nutrients, and space. However, the relative importance of above and below ground competition is uncertain. Wilson (1988) analysed 23 competition studies and concluded that root competition is usually more important than shoot competition in determining competitive balance between species. For our study, it is expected that removal of above- and below-ground grass biomass will benefit the establishment, growth and survival of indigenous seedlings.

Competitive interaction between grass and other species involves two separate processes, the effect of grass on other species in the community and the response of grasses to non-grasses. Some authors have preferred to consider the term “interference” for plants growing in such proximity that they modify each other’s growth (Wardle *et al.*, 1998). Clearly, interference includes both beneficial and damaging influences, and competition is only one aspect of it.

One of best examples of plant competition is illustrated by Schulte *et al.*, (2003), who explored intrinsic ecosystem properties and processes and illustrated these using a simple dynamic simulation model of grass and clover interactions. Competition by grasses results in clover being shaded during its early growth, unless grazing is sufficiently intensive to remove grass as it grows. This situation fits the general use of the term competition, since it involves a common need for a limiting resource. In this example the limiting resource is light and the grass absorbs nearly all the light that falls on the pasture, thus preventing the clover plant from receiving sufficient radiation / energy. The ability of grasses to produce early growth that shades clovers

depends also on other requirements being met, including adequate soil nitrogen (Schulte *et al.*, 2003).

2.3.1 Effects of grass competition in particular

Grasses are monocotyledonous plants belonging to the family *Poaceae*, a well-defined natural group of plants. They are found all over the world, and altogether comprise more than 10 000 species (Bews, 1918). Their reproductive mechanism, plant anatomy and genetic variability result in high level of adaptability, thus enabling grass species to grow in most terrestrial habitats. Grasslands are one of the most widespread vegetation types in the low rainfall areas of the world and in temperate regions, where man has cleared the vegetation to create additional pastures (Donald, 1990).

Grasses, particularly alien grasses, are commonly regarded as a problem for regeneration of other types of plants because they interfere with growth and survival of seedlings of forbs and woody plant species in most of the grassland areas (Davies, 1985). For this reason it is possible that alien annual pasture grasses and indigenous lawn grasses (*Cynodon dactylon*) that invade abandoned agriculture fields in the Renosterveld might retard succession by precluding the establishment of indigenous shrubs. Several factors are involved in the interaction between grasses and the establishment of indigenous seedlings. The most important factor of alien grass dominance is its ability to aggressively compete for nitrogen and other nutrients (Orlander *et al.*, 1996). No information is available on how to facilitate the establishment of indigenous shrub species by clearing or reseeding abandoned agricultural fields within Renosterveld, and whether indigenous shrub seedling establishment, survival and growth may be enhanced by controlling alien grass competition and indigenous grasses.

There are a number of factors that influence invasion dynamics of species, including life history traits of native and exotic species, and physical characteristics of the site, such as soil texture and climate. Most researches have a limited understanding of the relative importance of these different processes and environmental conditions on invasion dynamics. Most studies of invasive perennial grasses have focused

exclusively on management methods and have been met with limited success (Donald, 1990; Benz *et al.*, 1999). A broader understanding of the ecological processes underlying the invasion and spread of exotic perennial weeds can contribute to our understanding of plant ecology as well as improve our ability to control and eliminate weed infestations (Cousens and Mortimer, 1995).

The aggressive vegetative spread and potential for dominance of grasses have been attributed to a number of mechanisms. Grass absorbs nearly all the light that falls on the pasture, thus preventing other plant species from receiving sufficient radiation (Stevens, 1986). Some exotic perennial species are known to release allelochemicals into the soil (Goslee *et al.*, 2001), which has negative impacts on the growth and recruitment of surrounding species and leads to loss of biomass and reduction in abundance of these species through time (Fletcher and Renney, 1963). Shrub seedlings establishing on old fields at EPNR could be exposed to a similar negative impact from grass biomass, thus leading to poor recruitment of shrub species on old fields

2.4 Herbivory

Large herbivores have well documented effects on plant establishment (Watt, 1919; Shaw, 1968; Gashwiler, 1970), growth (McNaughton, 1976, 1979, 1983a; Morrow and LaMarche, 1978); and also reproductive success (Janzen, 1969; Chew and Chew, 1970). They also have substantial effects on plant form (McNaughton, 1976, 1979). Herbivores, such as browsing mammals (Vessey-Fitzgerald, 1973a) or insects (Hartnett and Abrahamson, 1979) feeding on trees and herbs, alter plant form dramatically by activating lateral buds that produce a dense, bushy geometry. Among the most conspicuous effects of large mammalian grazers upon grasslands are a drastic reduction of canopy height and the activation of tillers that lead to a prostrate, dense canopy (McNaughton, 1976, 1979), hereafter referred to as grazing lawn.

Maintenance of grazing lawns increases the quality of food available to herbivores, particularly through enhanced nitrogen content in terrestrial habitats (McNaughton,

1979). Grazing also increases the digestibility of forage so that both nutrient content and relative yield to herbivores are greater in grazing lawns (Olubajo *et al.* 1974). Quantitative characterization of effects of herbivory upon the structural characteristics of vegetation indicates that grazing lawns have a high plant biomass concentration (forage mass per unit volume). This is because of the plant growth response that packs productive, nutritious, and palatable tissues into a small volume near the soil surface (McNaughton, 1976, 1979; Stobbs, 1973a, 1973b).

Similarly, grazing commonly produces a dense, highly branched canopy surface analogous to a grazing lawn that has a high foliage density but which protects the interior foliage from grazing by making it physically less accessible (Vesey-Fitzgerald, 1973a). The higher biomass concentration represents a potentially higher food yield to herbivores per mouthful eaten, but it also creates a spatial refuge that renders a portion of the foliage unavailable (McNaughton, 1979, 1983a).

The effects of large herbivores on plant survival and fitness are largely mediated by changes in interactions between plants, including competition, facilitation and mutualism. These effects can be positive or negative. For example, natural populations of large grazing mammals are reported to increase plant diversity (McNaughton, 1985). The same is found when domesticated large grazers are managed at low stocking rates on productive grasslands (Hobbs and Huenneke, 1992). Intermediate-sized, digging herbivores, such as prairie dogs (*Cynomys* sp.), rabbits (*Oryctolagus cuniculus*) and pocket gophers (*Geomys* sp.), create extensive, intense but aggregated soil disturbances that increase plant diversity in prairie habitats (Huntly and Reichman, 1994). This can be related to the optimal grazing hypothesis, which states that “herbivores can enhance plant primary production” (McNaughton, 1979; Hilbert *et al.*, 1981). Primary production can increase with low grazing intensity and reach an optimum at intermediate grazing, before production decreases again when grazing becomes too high.

Several authors have gone further and have suggested that grazing optimization can lead to mutualistic interactions between plants and their herbivores (Owen and Weigert, 1981; Petelle, 1982; Vail, 1992), based on a few studies that show a

positive effect of herbivory on plant fitness (Paige and Whitham, 1987; Bergelson and Crawley, 1992; Lennartsson *et al.*, 1998). Such a claim has attracted a lot of criticism (Silvertown, 1982; Belsky *et al.*, 1993; Mathews, 1994). According to Belsky *et al.*, (1993), no plausible explanation of a real benefit for the individual plant from herbivory has ever been proposed, and plants nearly always develop a defence strategy. One possible mechanism that could explain a positive effect of herbivory on primary production under certain conditions is the positive indirect effects of herbivores through nutrient cycling. Such mechanism could be at work in systems where grazing by large herbivores have been shown to increase primary production, e.g. the Serengeti in Tanzania (McNaughton, 1985).

In the low veld savanna of South Africa, palatable deciduous woody plant species lose less than 10% of their foliage to browsing ruminants during the growing season (Owen-Smith and Cooper, 1987). Leaf losses were more severe for the more palatable species among evergreens, and some of these had virtually all of their foliage below 2 m height consumed by kudus and impalas by the late dry season. Certain unpalatable tree and shrub species were browsed for a brief period, when they grow a flush of new leaves before the onset of the rain.

Milton and Dean (1990); Milton (1994) found, in the succulent karoo, that severe browsing by sheep greatly reduced the canopy size of the dwarf shrub *Osteospermum sinuatum*, with a consequent reduction in flower and hence seed production. This favoured the competitive replacement of this palatable shrublet with unpalatable or spinescent dwarf shrubs and ephemeral herbs. This can also be explained by greater seedling recruitment of the latter species under conditions of heavy stocking coupled with droughts. Grazing at EPNR might also change species composition of shrubs and enhance grass competition on Renosterveld shrub species.

2.5 Combined effect of competition and herbivory

Ecologists have long debated the relative importance of competition and herbivory in determining the distribution and abundance of plants in natural communities (Hairston *et al.*, 1960). Both herbivory and competition are thought to influence plant population dynamics, as demonstrated above and their relative importance is relevant to the general issue of top-down and bottom-up control of plant populations. Many field experiments (Rausher and Feeny, 1980; Parker and Salzman, 1985; Bonser and Reader, 1995; Edwards *et al.*, 2000; Parmesan, 2000; Van der Wal *et al.*, 2000) and models (Maron and Gardner, 2000) have investigated herbivory and competition together. Some experimental studies have suggested that competition between plants may increase the negative effect of herbivory and that herbivory may alter the outcome of competition (Bonser and Reader, 1995; Edwards *et al.*, 2000).

The effects of natural variation in levels of competition and herbivory have rarely been studied together. Recently, theoretical models have been developed that include both plant competition and herbivory (Huisman and Weissing, 1995; Leibold, 1996). Those that consider interactions between the effects of both herbivory and competition for nutrients and plant growth, predict that grazing pressure increases with increasing productivity (Grover, 1995; Leibold, 1996). This is accompanied by a shift in community composition from plant species that are good competitors for nutrients to those that can tolerate or avoid grazing.

Huisman *et al.* (1999), on the other hand, consider interactions between herbivory and competition for light and predict that, at high productivity, the small plant species with higher forage quality that are preferred by herbivores, will be outshaded by taller unpalatable plants. Competition for light should then be most evident where high productivity and a reduction in grazing pressure both contribute to increased biomass. Maintaining plant diversity is a central goal in the management of biodiversity throughout the world (Olf and Ritchie, 1998). Herbivores are generally thought to enhance plant diversity by their direct consumption of competitively dominant plant species (McNaughton, 1985). Consequently, management of

herbivores and competition have become a crucial component in efforts to restore or maintain biodiversity.

2.6 Conclusion

If nutrient enrichment causes increased competitive exclusion, how do herbivores affect this process? Herbivores can regulate diversity in various ways. Whether or not herbivores function as disturbance agents and maintain higher diversity than would occur without them is debatable (Milchunas *et al.*, 1988; Pacala and Crawley, 1992). Does herbivory increase or decrease cover of Renosterveld shrubs on the old field? The few studies examining the interaction between herbivory and competition have produced conflicting results (Swank and Oechel, 1991; Goldberg and Barton, 1992; Belsky, 1992; Burger and Louda, 1995). Because there is still debate about the effects of herbivores on plant primary productivity (Milchunas and Lauenroth, 1993), perhaps it is not surprising that no one can draw solid conclusions as to the effect of herbivory on competitive interactions (Taylor *et al.*, 1997). Large herbivores generally do not kill the plants that they feed upon, but they do affect their competitive ability (Taylor *et al.*, 1997). This may eventually lead to competition exclusion of some species and to herbivory-induced succession, leading to changes in vegetation composition.

Based on my understanding of the literature reviewed above, I predict that shrub seedlings will perform worse in the presence than in the absence of grass biomass, but that if grazing is sufficiently intense to remove grass as it grows, and does not damage shrub seedlings, then, this will facilitate the establishment of indigenous Renosterveld seedlings.

2.7 References

- Bazely, D.R., and Jefferies, R.L. 1986. Changes in the composition and standing crop of saltmarsh communities in response to removal of a grazer. *Journal of Ecology* **74**: 693-706.
- Begon, M., Harper, J.L., and Townsend, C.R. 1996. Ecology: Individuals, populations and communities, 3rd ed. Blackwell Science, Boston, USA.
- Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* **3**: 187-200.
- Belsky, A.J., Carson, W.P., Jense, C.L., and Fox, G.A. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* **7**: 107-121.
- Benz, L.J., Beck, K.G., Whitson, T.D., and Koch, D.W., 1999. Reclaiming Russian knapweed infested rangeland. *Journal of Range Management*. **5**:351-356.
- Bergelson, J., and Crawley. 1992. Herbivory and *Ipomopsis aggregata*: the disadvantages of being eaten. *American Naturalist* **139**: 870-882.
- Bews, J.W. 1918. The grasses and grasslands of South Africa. P. Davis & Sons, LTS. Printers, Longmarket Street.
- Bonser, S.P., and Reader, R.J. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* **76**: 2176-2183.
- Burger, J.C., and Louda, S.M. 1995. Interaction of diffuse competition and insect herbivory in limiting brittle prickly pear cactus, *Opuntia fragilis* (Cactaceae). *American Journal of Botany* **82**: 1558-1566.
- Chaneton, E.J., and Facelli, J.M. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* **93**: 143-156.
- Chew, R.M., and Chew, A.E. 1970. Energy relationships of the mammals of a desert shrub. *Ecological Monographs*. **40**: 1-21.

- Clarke, P.J., Myerscough, P.J., and Skelton, N.J. 1996. Plant coexistence in coastal heaths: between- and within-habitat effects of competition, disturbance and predation in the post-fire environment. *Australian Journal of Ecology* **21**: 55-63.
- Coffin, D.P., Laycock, W.A., and Lauenroth, W.K. 1998. Disturbance intensity and above-and below-ground herbivory effect on long-term (14y) recovery of a semiarid grassland. *Plant Ecology* **139**: 221-233.
- Collins, S.L. 1992. Fire frequency and community heterogeneity in tall grass prairie vegetation. *Ecology* **73**: 2001-2006.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1310.
- Cousens, R., and Mortimer, M., 1995. In: *Dynamics of Weed Populations*, Cambridge University Press, Cambridge, p. 332.
- Davies, R.J. 1985. The importance of weed control and the use of tree shelters for establishing broadleaved trees on grass-dominated sites in England. *Forestry* **58**: 167-180.
- Donald, W.W. 1990. Management and control of Canada thistle (*Cirsium arvense*). *Reviews of Weed Science* **5**: 193-250.
- Edwards, G.R., Bourdot, G.W., and Crawley, M.J. 2000. Influence of herbivory, competition and soil fertility on the abundance of *Cirsium arvense* in acid grassland. *Journal of Applied Ecology* **37**: 321-324.
- Fletcher, R.A., and Renney, A.J., 1963. A growth inhibitor found in *Centaurea* spp. *Canadian Journal of Plant Science* **43**: 475-481.
- Ford, M.A., and Grace, J.B. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *Journal of Ecology* **86**: 974-982.
- Gashwiler, J.S. 1970. Further study of conifer seed survival in a western Oregon clearcut. *Ecology* **51**: 849-854.

- Goldberg, D.E., Rajaniemi, T., Gurevich., and Stewart-Oaten, A. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* **80**:1118-1131.
- Goldberg, D.E., and Barton, A.M.1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**: 771-801.
- Goslee, S.C., Peters, D.P.C., and Beck, K.G. 2001. Modeling invasive weeds in grasslands: the role of allelograthy in *Acroptilon repens* invasion. *Ecological Modelling*.**139**: 31-45.
- Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in plant Ecology, Evolution and Systematics* **2**:1-28.
- Grime, J.P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* **1**: 151-167.
- Grime, J.P.1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester. In: Jutila, H.M., and Grace, J.B. 2002. Effects of disturbance on germination and seedling establishment in coastal prairie grassland: a test of the competition release hypothesis. *Journal of Ecology* **90**: 291-302.
- Grover, J.P. 1995. Competition, herbivory, and enrichment: nutrient based models for edible and inedible plants. *American Naturalist* **145**: 746-774.
- Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* **94**: 421-425.
- Hartnett, D.C., and Abrahamson, W.G. 1979. The effects of stem gall insects on life history patterns in *Solidago canadensis*. *Ecology* **60**: 910-917.
- Hilbert, D.W., Swift, D.M., Detling, J.K., and Dyer, M.I. 1981. Relative growth rates and the grazing optimisation hypothesis. *Oecologia* **51**: 14-18.
- Hobbs, R.J., and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**: 324-337.

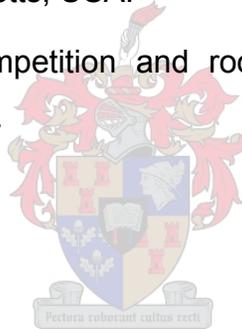
- Huisman, J., and Weissing, F. 1995. Competition for nutrients and light in mixed water column: a theoretical analysis. *American Naturalist* **146**: 536-564.
- Huisman, J., Grover, J.P., Van der Wal, R., and Van Andel, J. 1999. Competition for light, plant species replacement, and herbivores abundance along productivity gradients In: *Herbivores: between plants and predators* (eds Olff, H., Brown, V.K., Drent, R.H.), Pp: 239-269. Blackwell Science, Oxford.
- Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* **69**: 46-58.
- Hulme, P.E. 1994. Seedling herbivory in grasslands: relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* **82**: 873-880.
- Huntly, N., and Reichman, O.J. 1994. Effects of subterranean mammalian herbivores on vegetation. *Journal of Mammalogy* **75**: 852-859.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**: 81-101.
- Janzen, D.H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* **23**: 1-27.
- Jolliffe, P.A. 2000. The replacement series. *Journal of Ecology* **88**(3): 371-385.
- Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**: 784-812.
- Lennartsson, T., Nilsson, P., and Tuomi, J. 1998. Induction of overcompensation in field gentian, *Gentianella campestris*. *Ecology* **79**: 1061-1072.
- Maret, M.P., and Wilson, M.V. 2000. Fire and seedling population dynamics in western Oregon prairies. *Journal of Vegetation Science* **11**: 307-314.
- Maron, J.L., and Gardner, S.N. 2000. Consumer pressure, seed versus safe-site limitation and plant population dynamics. *Oecologia* **124**: 260-269.
- Mathews, J.N.A. 1994. The benefits of overcompensation and herbivory: the difference between coping with herbivores and linking them. *American Naturalist* **144**: 528-533.

- McNaughton, S.J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* **191**: 92-94.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* **113**: 691-703.
- McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* **40**: 329-336.
- McNaughton, S.J. 1985. Ecology of grazing ecosystem: the Serengeti. *Ecological Monographs* **53**: 291-320.
- Milchunas, D.G., Sala, O.E., and Lauenroth, W. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**: 87-106.
- Milchunas, D.G., and Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **6**: 327-366.
- Milton, S.J. 1994. Growth, flowering and recruitment of shrubs in grazer and in protected rangeland in the arid Karoo, South Africa. *Vegetatio* **111**: 17-28.
- Milton, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid karoo shrubland. *Journal of applied Ecology* **32**: 145-156.
- Milton, S.J., and Dean, W.R.J. 1990. Seed production in rangelands of the southern Karoo. *South African Journal of Science* **86**: 231-233.
- Milton, S.J., Dean, R.J., du Plessis, N.A., and Siegfried, W.R. 1994. A conceptual model of arid rangeland degradation. *BioScience* **44** (2): 70-76.
- Morrow, P.A., and LaMarche. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine Eucalyptus. *Science* **201**: 1244-1246.
- Olf, H., and Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**: 261-265.
- Olubajo, F.O., Vansoest, P.J., and Oyenuga, V.A. 1974. Comparison of four tropical grasses grown in Nigeria. *Journal of Animal Science* **38**: 149-153.

- Orlander, G., Nilsson, U., Hällgren, J.E., and J.A. Griffith, J.A. 1996. Competition for water and nutrients between ground vegetation and planted *Picea abies*. *Newzealand Journal of Forest Science* **26**: 99-117.
- Owen, D.F., and Weigert, R.G. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. *Oikos* **36**: 376-378.
- Owen-Smith, N., and Cooper, S.M. 1987. Palatability of woody plants to browsing ruminants in a South Africa savanna. *Ecology* **68**: 319-331.
- Pacala, S.W., and Crawley, M.J. 1992. Herbivores and plant diversity. *American Naturalist* **140**: 243-260.
- Paige, K.N., and Whitham, T.G. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* **129**: 407-416.
- Parker, M.A., and Salzman, A.G. 1985. Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. *Journal of Ecology* **73**: 903-913.
- Parnesan, C. 2000. Unexpected density-dependent effects of herbivory in a wild population of the annual *Collinsia torreyi*. *Journal of Ecology* **88**: 392-400.
- Petelle, M. 1982. More mutualisms between consumers and plants. *Oikos* **38**: 125-127.
- Rausher, M.D., and Feeny, P. 1980. Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* **61**: 905-917.
- Schulte, R.P., Lantinga, E.A., and Struik, P.C. 2003. Analysis of the production stability of mixed grasslands: I: A conceptual framework for the qualification of production stability in grassland ecosystems. *Ecological Modelling* **159** (1): 43-69
- Shaw, M.W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. Acorn losses and germination under field conditions. *Journal of Ecology* **56**: 661-666.

- Silvertown, J.W. 1982. No evolved mutualism between grasses and grazers. *Oikos* **38**:253-259.
- Stevens, K.L. 1986. Allelopathic polyacetylenes from *Centaurea repens* (Russian knapweed). *Journal of Chemical Ecology* **12**: 205–1211.
- Stiling, P.1999. Ecology, theories and application. Prentice Hall, Upper Saddle River, New Jersey.
- Stobbs, T.H. 1973a. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Australian Journal of Agricultural Research* **24**: 809-819.
- Stobbs, T.H. 1973b. The effect of plant structure on the intake of tropical pastures. II. Differences in sward structure, nutritive value, and bite size of animal grazing *Setaria anceps* and *Chloris gavana* at various stages of growth. *Australian Journal of Agricultural Research* **24**: 821-829.
- Swank, S.E., and Oechel, W.C. 1991. Interaction among the effects of herbivory, competition, and resource limitation on chaparral herbs. *Ecology* **72**: 104-115.
- Taylor, K.L., Grace, J.B., and Marx, B.D. 1997. The effects of herbivory on neighbor interactions along a coastal marsh gradient. *American Journal of Botany* **84**: 709-715.
- Tilman, D.1988. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* **1**: 304-315.
- Thompson, K., Grime, J.P., and Mason, G. 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* **267**: 147-149.
- Vail, S.G. 1992. Selection for over compensatory plant responses to herbivory: a mechanism for the evolution of plant-herbivore mutualisms. *American Naturalist* **139**: 1-8.
- Van der Wal, R., Egas, M., Van der Veen, A., and Bakker, J. 2000. Effects of competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* **88**: 317-330.

- Vesey-Fitzgerald, D.F. 1973. Animal impact on vegetation and plant succession in Lake Manyara National Park, Tanzania. *Oikos* **24**: 314-325.
- Wardle, D.A., Nilsson, M.C., Gallet, C., and Zackrisson, O. 1998. An ecosystem-level perspective of allelopathy. *The Botanical review* **73**: 305-319.
- Watt, A.S. 1919. On the causes of failure of natural regeneration in British oakwoods. *Journal of Ecology* **7**: 173-203.
- White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* **63**: 90-105.
- White, P.S., and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. In: Meffe, G.K., Carroll, C.R. and contributors. 1997. *Principles of conservation Biology*, second edition, pp: 308-309. Sinauer Associates, INC. Sunderland, Massachusetts, USA.
- Wilson, J.B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* **25**, pp: 279-296.



Chapter 3: Effects of competition and herbivores on survival and growth of seedlings of five species of shrubs

3.1 Introduction

For many years ecologists have debated the relative importance of competition and herbivory in influencing the distribution and abundance of plants in natural communities (Hairston *et al.*, 1960; Parker and Salzman, 1985). However, competition from neighbouring plants and herbivory could be important factors that determine the growth, survival and reproduction of individual plants, and consequently the sizes of plant populations (Gurevitch *et al.*, 2000). Most authors who worked on competitor removal experiments (Fowler, 1981; Robberecht *et al.*, 1983) and herbivory exclosure experiments (Rausher and Feeny, 1980; Parker and Root, 1981; Louda, 1983) clearly demonstrate that plant success can be affected by either process acting alone. Field observations further suggest that manipulation of plant neighbours and herbivore densities frequently have synergetic or substitutive effects on plant performance, e.g. the removal of plant neighbours may either relax or intensify herbivory. The interactive effect of herbivory and plant competition may arise through two major routes. First, rates of herbivory may increase or decrease when the abundance of plant neighbours, or some factor correlated with plant abundance, is altered (Lubchenco, 1978; Holt and Lawton, 1994). Secondly, herbivory might increase or decrease the competitive effect of one plant on another by impacting on plant regrowth ability (Willis *et al.*, 1998; WallisDeVries *et al.*, 1999; White *et al.*, 2000). In greenhouse experiments, various interactions between the effects of competition and herbivore damage on plant performance have been observed (Bentley and Whittaker, 1979; Windle and Franz, 1979; Lee and Bazzaz, 1980). Yet for natural plant populations, little is known about the relative impact of these forces, or about the nature of interactions between them.

The aim of this study is thus to explain the apparent slow return of indigenous Renosterveld vegetation to abandoned fields. Three hypotheses explaining the slow return of the natural vegetation were tested, namely that:

1. Seeds of indigenous shrub species are absent in old-field soil, this possibly due to their rapid predation, short dispersal distances in wind and ant dispersed forms and in bird dispersed forms an absence of suitable perching sites. This may be the case of some species, however Shiponeni (2003) showed that seed of many wind-or dung-dispersed species are continually deposited onto the old field, or are present in the seed bank.
2. Competition from grasses that presently dominate the fields prevents the establishment of indigenous shrubs.
3. Herbivory that appears to be concentrated on grassy patches prevents the establishment of indigenous shrub species.

We report here on an experimental field study on how plant competition and herbivory damage simultaneously affect Renosterveld shrub seedlings in the winter rainfall region of the Western Cape, South Africa. In this study, we examine the importance of competition and herbivory on establishment, growth and survival of transplanted seedlings, addressing the following questions:

1. How do competition and herbivory separately affect survival and growth of Renosterveld seedlings?
2. How important are interactions between competition and herbivory, or, in other words, how do the effects of herbivore damage depend on whether competitors are present or absent, and vice versa?

3.2 Study site and methods

3.2.1 Study area

Landuse

The study was carried out on Elandsberg Private Nature Reserve (EPNR), situated on the Farm Bartholomew's Klip, near Hermon, approximately 25 km north of Wellington in the Tulbach district in the Western Cape Province of South Africa. It lies between 33°24'17" S and 33°29'8" S, and 18°58'30" E and 19°05'10" E (Bard, 1990).

The reserve was proclaimed in 1973 (Parker 1982), initially to protect the endangered geometric tortoise (*Psammobates geometricus*) and in 1988; the reserve was declared a Natural Heritage Site (Farley, *pers. comm.*). This is the highest status of protection a privately owned property can be awarded. This means that the land is safe from agricultural intensification and development. This status assists the private or public landowners in protecting their natural areas, no matter how small, because of their scientific, aesthetic and/or cultural value (WCNCB, 2000). Elandsberg is registered as a Private Nature Reserve with Western Cape Nature Conservation.

The reserve is fenced in on three sides, preventing large game movement to the surrounding fields, and is open to the Elandskloof Mountains on the eastern side of the reserve (Farley, *pers. comm.*). These mountains reach altitudes of 1378 m. Most of the reserve has a gentle slope, which increases to a steep slope in the eastern part. The area receives runoff water from the mountains predominantly in winter, and during this time of the year large floodplains form.

The reserve currently covers 3900 ha of natural veld, including Mountain Fynbos and Renosterveld, which at approx. 1000ha, is the largest remaining patch of West Coast Renosterveld. Apart from the reserve, there are 2600 ha of farmland, which maintains merino sheep, cattle, wheat, oats, barley, canola, lupines, clover and other feeding crops (Mike Gregor, *pers.com.*).

Most of the low-lying areas were subjected to grazing by sheep and cattle between 1958 and 1983. From 1972 to 1982 large indigenous game species (Table 1) were added to the small antelopes already present in the reserve. An extensive fire in March 1982 burnt 2880 ha of the farm, including the low-lying areas. Two successive fires, in February and March 1988, burnt most of the Mountain Fynbos (Jarman, 1986).

Previously ploughed abandoned agricultural fields are being incorporated into the reserve and are referred to as old fields (Fig. 3.1 and 3.2). The particular field, where this study was conducted, was used for cultivation of oats (*Avena sativa*) from 1960 until 1985, then oversown with European pasture grasses, and used for livestock grazing until 1987 when all agricultural activity was abandoned, and the field was incorporated into the reserve (Mike Gregor, *pers. comm.*). The plant community on this abandoned agricultural field is dominated by alien herbaceous plants, and differs from the natural vegetation not only in the degree of woody cover but also in the relative abundances of the herbaceous species. The open grassy area of the old field is dominated by the perennial African lawn grass, *Cynodon dactylon* (L.) Pers, in summer, and alien pasture grasses such as *Briza maxima* (L.), *B. minor* (L.), *Bromus diandrus* Roth, *B. pectinatus* Thunb., *Lolium perenne* L., *Poa annua* L., *Vulpia myuro* (L.) C.C. Gmel., after winter rainfall (Shiponeni, 2003).

The old field part of the reserve, which is bordered by agricultural cultivation to the west, acts as a buffer zone between the farming area and the natural vegetation to the north and east of the reserve. In this transition zone, the natural Renosterveld vegetation returns slowly, and *Elytropappus rhinocerotis* is the dominant shrub. Other Renosterveld species that have colonised the field include the shrubs *Helichrysum* sp., *Hermannia* sp. and *Thesium* sp., and an indigenous perennial forb, *Leysera gnaphalodes*. The authorities for plant names are given in appendix A.

Geology

The underlying geological formation of the reserve is the Malmesbury group, consisting of sedimentary rocks, which were deposited in a geosyncline (Visser, 1984). The Malmesbury group has one of the oldest sediments that developed

during the final stages of the welding together of the Namaqualand section of the earth's crust almost 1 000 million years ago. The Malmesbury rocks are exposed over an extended area in the southwestern Cape and are important, together with the granites, as they form base-rich substrates (Cowling, 1992). Excluding the eastern (mountain) part of the reserve, which has mainly rocky and stony sand stone derived soils, the rest of the reserve has sandy clay soils that are more fertile.

On weathering these predominantly clayey substrates release exchangeable cations such as calcium, potassium, magnesium and sodium, which are important in soil formation and plant nutrient cycling (Cowling, 1992; Deacon *et al.*, 1992; Cowling and Richardson, 1995). It is this richer substrate on which Renosterveld occurs and thus makes it more prone to clearance of agriculture than Fynbos (Baard, 1990).

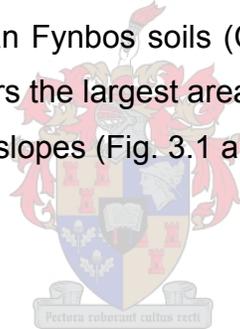
Climate

The reserve falls within the Mediterranean climate zone of the southwestern part of the sub-continent (Baard, 1990). The weather is influenced by the South Atlantic anticyclonic system with dry and hot summers from December to February, and cold and wet winters, which occur from June to August (Engelbrecht, 1995). The southwestern Cape region receives most of its rain in autumn, winter and early spring, which is from May to September (500mm per year annum). The mean annual temperature is 17.4°C, with a winter mean of 12.2°C and summer mean of 23.8°C (Baard, 1990).

The prevailing wind during summer and spring is usually southwesterly, with occasional gale force southeasterly winds. During winter, northwesterly winds usually bring cooler, rainy conditions (Baard, 1990). Due to the Elandsbloof Mountains in the east, Föhn-like winds are formed which cause an increase in fog when winds and clouds are blown against the mountain and condensation increases (Baard, 1990).

Vegetation

According to Acocks (1988) the vegetation at the Elandsberg Nature Reserve can be divided in two main types: Coastal Renosterveld (Veld Type 46) and Mountain Fynbos (Veld Type 69), both belonging to the Fynbos biome. Low and Rebelo (1998) included West Coast Renosterveld in vegetation type 62 with a total area of 6141 km², part of the Fynbos biome. The vegetation of the reserve in the low-lying areas has been classified as West Coast Renosterveld, and the vegetation in the mountain slopes is classified as Mountain Fynbos veld type 64 (Low and Rebelo, 1998). Renosterveld comprises those communities where renosterbos, *Elytropappus rhinocerotus*, generally is a co-dominant component with other asteraceous species such as *Eriocephalus africanus* and *Leyserra gnaphalodes* (Baard, 1990). Renosterveld can be distinguished from Fynbos in that restioids and proteoids contribute little to the vegetation cover, and it grows on clay-rich soils that are always less sandy and more fertile than Fynbos soils (Cowling and Richardson, 1995). On the reserve, Renosterveld covers the largest area of the reserve whereas the Fynbos mainly occurs on the mountain slopes (Fig. 3.1 and 3.2).



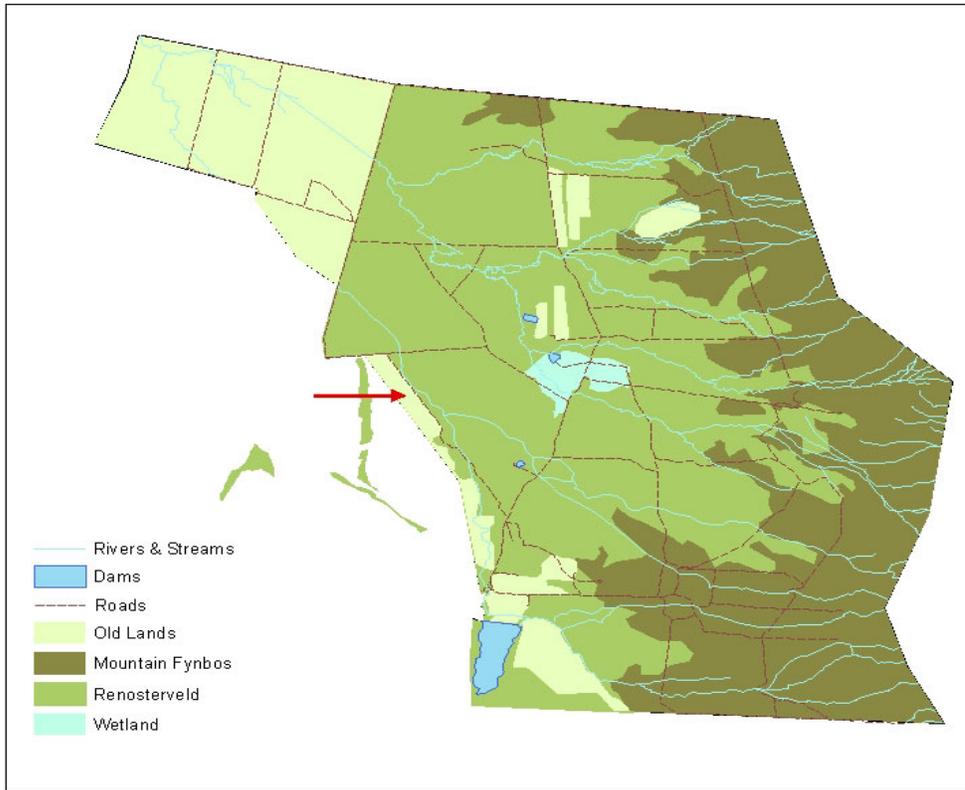


Figure 3.1: Map of Elandsberg Private Nature Reserve, with vegetation types and landmarks. The red arrow indicates location of the study site. GIS data supplied by Sean Ranger, Western Cape Nature Conservation Board. Map created by CB Krug in ESRI®ArcMap™ 8.3 (ESRI 2002).

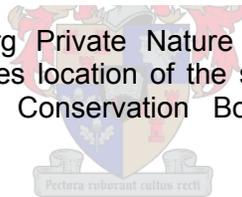




Figure 3.2: Overview picture of the previously ploughed field at Elandsberg Private Nature Reserve (EPNR), with an old field in the foreground

Indigenous herbivorous large mammals are thought to play important role in controlling the structure and composition of the Renosterveld vegetation. The large animal unit (LAU) approach converts all animals to standard units based on the metabolic equivalent of a 453 kg head of cattle. This only gives a broad indication of the grazing capacity of a given area (Bothma, 1996). Elandsberg Private Nature reserve makes available a total area of about 3900 ha to large herbivores, including the old field investigated (about 18ha in size) (*Mike Gregor, pers.comm.*). Table 3.1 gives an overview of the large mammals present in the reserve and indicates whether they graze or browse. The stocking density of the reserve is approximately 20 ha/ LAU throughout the reserve (3900 total ha/192.32 total LAU) (Grossman, 1991) (Table 3.1).

Table 3.1: Estimated number of stock present at Elandsberg Private Nature reserve for the period of 2002 (Farley, 2002) and their feeding category. The feeding categories were obtained from Skinner and Smithers (1990). The large animal units equivalents (LAU) were obtained from Bothma (1996). One LAU is the metabolic equivalent of a medium-sized head of cattle

Species	Number	Major feeding category	LAU equivalent	LAU's
Springbok (<i>Antidorcas marsupialis</i>)	120	Mixed feeder	0.15	18.0
Bontebok (<i>Damaliscus dorcas dorcas</i>)	100	Short grass grazer	0.22	22.0
Eland (<i>Taurotragus oryx</i>)	90	Mixed feeder	1.08	97.2
Black wildebeest (<i>Connochaetes gnou</i>)	40	Short grass grazer	0.46	18.4
Burchell's zebra (<i>Equus burchelli</i>)	30	Mixed feeder	0.66	19.8
Red hartebeest (<i>Alcelaphus buselaphus</i>)	12	Short grass grazer	0.37	4.44
Gemsbok (<i>Oryx gazella</i>)	11	Long grass grazer	0.56	6.16
Cape mountain zebra (<i>Equus zebra</i>)	4	Long-medium grass grazer	0.63	2.52
Grey rhebok (<i>Pelea capreolus</i>)	10	Mixed feeder	0.10	1
Grysbok (<i>Raphicerus melanotis</i>)	20	Unknown	0.07	1.4
Steenbok (<i>Raphicerus campestris</i>)	20	Unknown	0.07	1.4
TOTAL			----	192.32

3.2.2 Methods and materials

A field experiment was conducted to understand the role of herbivory and competition on establishment of shrub seedlings translocated into old lands.

Plant materials used in transplanting experiment

Six indigenous plant species belonging to five families commonly found in West Coast Renosterveld at Elandsberg were selected for use in the experiment. These were *Athanasia trifurcata* (L.) L., Asteraceae, *Leucadendron corymbosum* P.J. Bergius, Proteaceae, *Relhania fruticosa* (L.), K. Bremer, Asteraceae, and *Salvia chamelaeagnea* P.J. Bergius, Lamiaceae, all low microphyllous shrubs typical of open Renosterveld shrubland (Acocks, 1998; Low and Rebelo, 1998), and *Olea europaea subsp. africana* L., Oleaceae, an evergreen tree of fire refuge habitats such as drainage lines, screes and termitaria, and *Crassula glomerata* P.J. Bergius, Crassulaceae, an annual succulent understory forb. Nomenclature follows Germishuizen and Meyer (2003). These species differed in dispersal mechanism

and palatability to large herbivores, as well as in life form (Table 3.3). Since only one species of each genus was included in the experiment, the species will be referred to by species name only: *A. trifurcata*, *C. glomerata*, *L. corymbosum*, *O. europaea ssp. africana*, *R. fruticosa* and *S. chamelaeagnea*. This convention will be followed throughout the thesis.

Table 3.2: Target species, their life cycle and number of seedlings per plot and treatment, life form was obtained from Goldblatt and Manning (2000). Seed dispersal attribute was obtained from S.J. Milton (*pers.comm*)

Species	Family	Life form	Seed dispersal attribute	seedlings per plot	Seedlings per treatment
<i>Athanasia trifurcata</i>	Asteraceae	perennial shrub	Pappus – wind dispersed	5	25
<i>Crassula glomerata</i>	Crassulaceae	annual forb	Dust – wind dispersed	5	25
<i>Leucadendron corymbosum</i>	Proteaceae	perennial tree	Wing – wind dispersed	5	25
<i>Olea europaea subsp. africana</i>	Oleaceae	perennial shrub	Fleshy fruit – bird dispersed	4	20
<i>Relhania fruticosa</i>	Asteraceae	perennial shrub	Anti-telechorous	5	25
<i>Salvia chamelaeagnea</i>	Lamiaceae	perennial shrub	Nutlet - Mammalian endozoochory	1	5

Seeds of *A. trifurcata*, *L. corymbosum*, *R. fruticosa* and *O. europaea ssp. africana*, were collected from natural vegetation of the study site in September/ October 2002. Seeds of *S. chamelaeagnea* were bought from the seedroom, National Botanical Institute, Kistenbosch. *C. glomerata* germinated from the soil collected from the study site, which was used for the experiment. Seedlings were grown in the glass-house at the University of Stellenbosch and transplanted to the study site in July 2003, where seedlings were 5-6 cm height.

Experimental design

The experimental design comprised 20 (1m x 1m) 1m² plots arranged in two parallel rows positioned on a uniform substrate and slope adjacent to an area of natural vegetation. The four treatment combinations were arranged in alternate caged

(herbivore exclusion) and non-caged paired plots with the weeding treatments randomised among these paired plots (Fig. 3.3). Seedlings of each species were allocated randomly to one of the twenty treatment plots. Unfortunately, no rain fell for two weeks after seedlings were transplanted, so that some seedlings died after the first data collection.

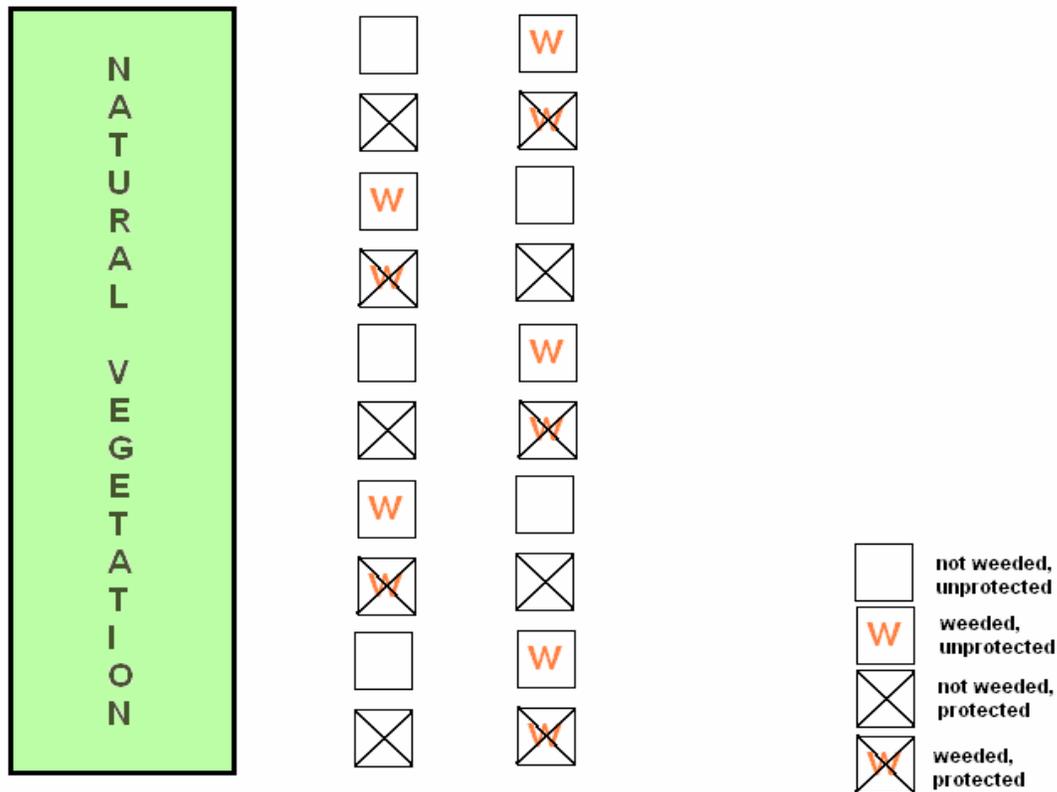


Figure 3.3: Layout of the experimental design in the study site (not to scale).

Treatments were:

- PW: Protected from large herbivores and weeded to remove grass (assumes no herbivory by large mammals and no grass competition),
- PNW: protected from large herbivores and not weeded (assumes no herbivory by large mammals but active grass competition),

- NPW: Not protected and weeded (assumes exposure to herbivory by large mammals but no grass competition),
- NPNW: Not protected and not weeded (assumes exposure to herbivory by large mammals and grass competition).

Each treatment was replicated five times. Throughout the results section of this chapter the various treatments will be referred to by acronyms given (Table 3.2).

Table 3.3: Factors influencing shrub growth and establishment in each of the four treatments. PW: protected from herbivory and weeded to remove competition, PNW: protected and not weeded, NPW: not protected and weeded, NPNW: not protected and not weeded

Treatment	Competition	Herbivory
PW		
PNW	X	
NPW		X
NPNW	X	X

The above and below grass biomass was removed in the weeded plots at ground level using a short-handled spade. Seedlings in these plots were thought not to receive any competition. Seedlings in plots not cleared of grass were considered to experience competition from the grass (10-30 cm in height) that covered 60-100% of the plot surface area (Shiponeni, 2003). In other words, the competition effect was estimated by comparing survivorship, growth, number of leaves and canopy area of the target plants in weeded plots and not weeded plots under herbivore exclusion. Large herbivores were excluded by positioning wire cages (Fig. 3.4 and 3.5) over selected plots. Grazing intensity in the herbivory trial can be considered low (see table 3.1). However, smaller mammals (e.g. rodents) and insects were not prevented from entering the cages. It was assumed that the cages did not significantly reduce light availability inside the cages. The herbivory effect by large mammals was determined by comparing survivorship, growth, number of leaves and canopy area of target plants in protected plots and unprotected plots. A combined effects of competition and herbivory were determined by comparing survivorship, growth,

number leaves and canopy area of target plants in unprotected and unweeded plots vs. protected weeded plots.

3.2.3 Data collection and analysis

Seedlings were monitored monthly from July 2002 until October 2003 for growth and survival, starting the first month after transplantation in July 2002. The following parameters were monitored at monthly intervals: number of surviving plants per species, and height and canopy area of each seedling. Number of leaves and branches per seedling were counted. When the number of leaves were too numerous to be counted, the numbers of leaves per branch were counted. The total number of leaves was estimated by multiplying the number of leaves per branch by the total number of branches. The height and canopy diameter measurements were taken using a 50 cm ruler. The survivorship of transplanted seedlings was calculated as the mean number of surviving seedlings per species and per treatment.

All measurements were log transformed to reduce inequality of variance in the raw data. A 2-factor analysis of variance tested the main effects of herbivores and competition and their interaction on measured plant parameters, viz plant height, leaf number and canopy area, in each species. Significantly different treatment means were separated using a scheffé post-hoc test in STATISTICA (STATISTICA 6.1, StatSoft, Inc. 2003). Canopy area was calculated using the following formula (Bronstein and Semendjajew 1991): $Cover = \pi * \frac{canopy1}{2} * \frac{canopy2}{2}$ with canopy1 and canopy2 two perpendicular diameters of the plant as seen from above.

Seedling survival at each recording stage was examined in terms of the proportion of seedlings that survived relative to the total number of planted seedlings. A two-factor analysis of variance tested for differences in the proportions of seedlings that survived between the 4 different treatment combinations. The Bonferroni test was used as post-hoc test to determine significant differences between pairs of treatments. Repeated measures ANOVA was also used to assess survival of shrub seedlings over time of sampling (STATISTICA 6.1, StatSoft, Inc. 2003).



Figure 3.4: An example of a protected and weeded plot after planting (August 2002). Note the dense grass cover outside the plot and the sunlight reaching the soil surface inside the plot.

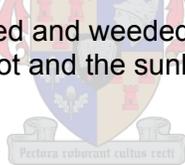




Figure 3.5: An example of a protected and weeded plot 13 months later in September 2003. Note well-established and flowering *Athanasia trifurcata*.



3.3 Results

3.3.1 Seedling growth

To examine seedling growth, the average height of seedlings under different treatment combinations was plotted separately for each of the six species in Fig. 3.6 and Fig. 3.7. Competition (NW) was the most important factor affecting the height of *A. trifurcata*, *L. corymbosum* and *R. fruticosa* (Table 3.4). Seedlings were significantly smaller in non-weeded (NW) plots than on plots where grass was removed (W), regardless of grazing treatment. Seedlings of *S. chamelaeagnea* growing on non-weeded plots were also smaller than seedlings growing on weeded plots, but this difference was not significant. Growth data indicated that *O. europaea ssp. africana* was mostly affected by grazing. Competition and grazing did not have any negative effect on *C. glomerata* (Fig. 3.6 and 3.7).

The growth of *O. europaea ssp. africana*, a tree usually growing on nutrient rich soil around termitaria, was not affected by grass competition (Fig. 3.6 and 3.7), but seedlings were smallest in unprotected, weeded plots. The growth of *C. glomerata*, an annual forb, was also not influenced either by grass removal or exposure to grazing. For most of the plant species in plots protected from grazing, growth was greater with grass removal than when grass biomass was left intact (Fig. 3.7).

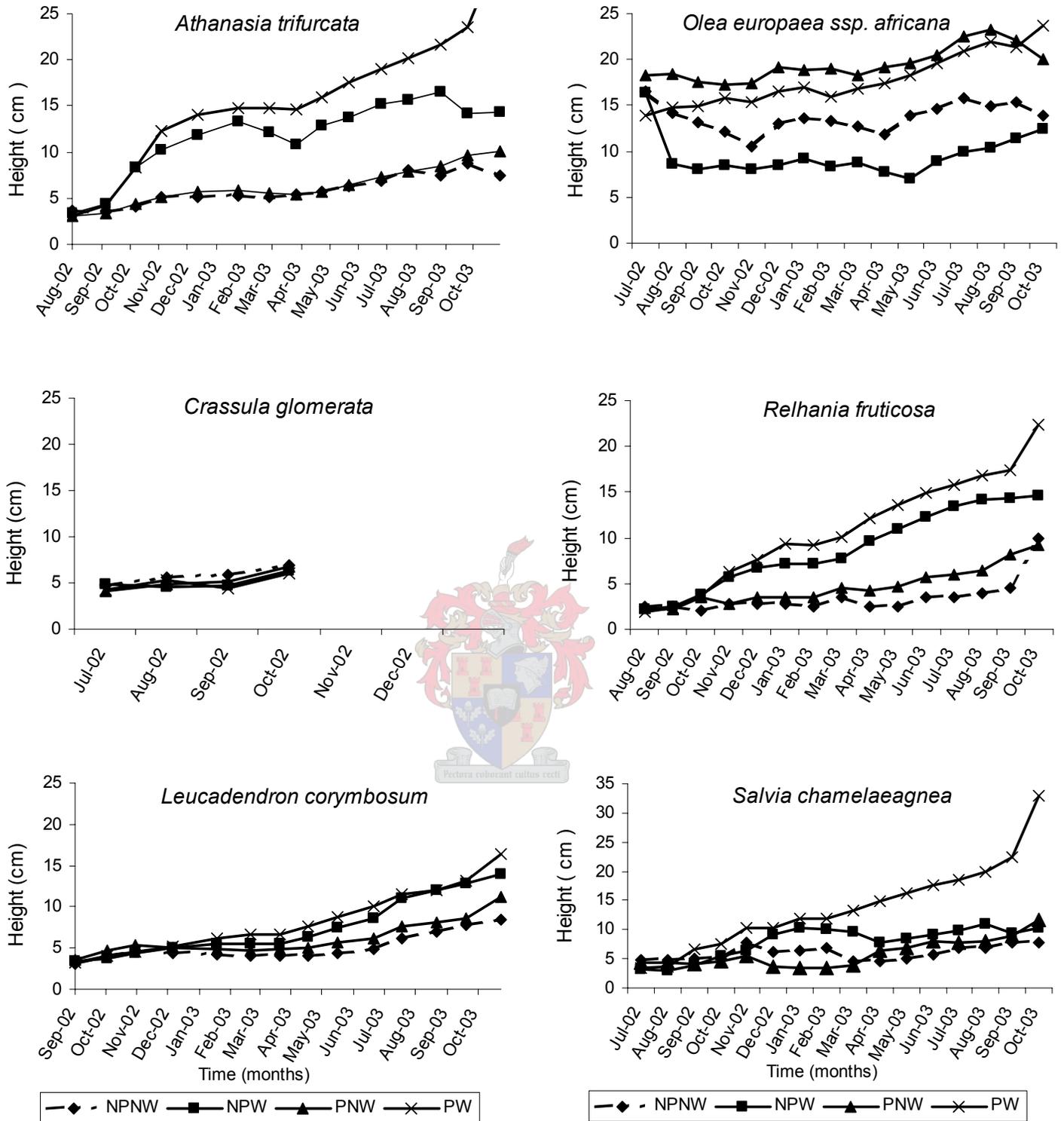


Figure 3.6: Effect of the four different treatments on the growth of the six target species: (Factors influencing shrub growth and establishment in each of the four treatments. PW: protected from herbivory and weeded to remove competition, PNW: protected and not weeded, NPW: not protected and weeded, NPNW: not protected and not weeded).

3.3.1.1 Direct effect of competition

No significant ($p \geq 0.05$) effects of grass competition were found on the height of *O. europaea ssp. africana* (Table 3.4), however, at the end of the treatment a significant ($p \leq 0.05$) negative effect of grass competition on the height of *A. trifurcata*, *L. corymbosum*, *R. fruticosa* and *S. chamelaeagnea* was found (Table 3.4).

3.3.1.2 Direct effect of grazing

Effects of grazing on plant height are indicated in Fig. 3.7. Grazing reduced the final heights of *A. trifurcata*, *L. corymbosum* and *S. chamelaeagnea* in weeded plots. Reduction in height due to grazing was less than height reduction attributed to competition, so in unweeded plots grazing effects were generally insignificant. Grazed seedlings of *O. europaea ssp africana*, *L. corymbosum*, *S. chamelaeagnea* and *A. trifurcata* (Table 3.4) were significantly smaller than ungrazed seedlings at end of treatment. No significant effect of grazing was found on the height of *C. glomerata* and *R. fruticosa*, (Table 3.4) and it appeared that herbivores avoided these species.

3.3.1.3 Interaction of grazing and competition

In general, grazing and competition had statistically independent effects, as shown for most species. The combined effect of grazing and competition, showed that the height of all the target plants was greater with grass biomass removal and protected plots than with grass biomass left intact and plants not protected (Fig. 3.7). Only in *A. trifurcata* was there a significant interaction, between grazing and grass competition (Table 3.4).

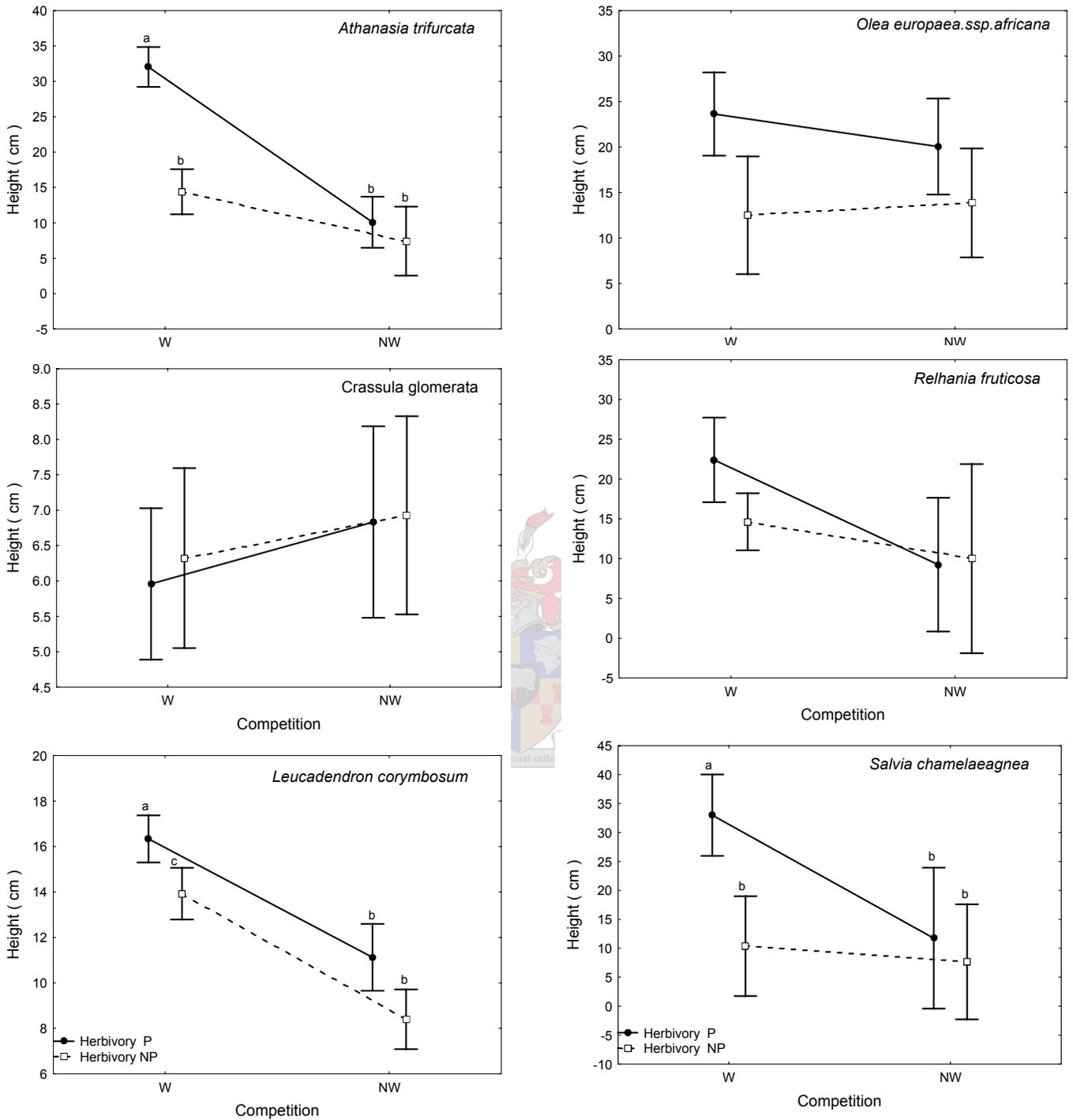


Figure 3.7: Interaction effect of grazing and competition on the average height at end of treatment of the six target Renosterveld species. Corresponding significance values given in Table 3.4. Different letters indicate significant differences between treatments. Vertical bars indicate SD.

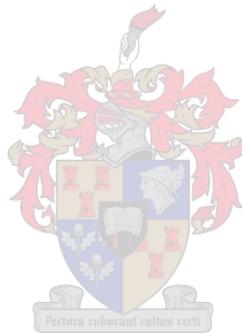
Table 3.4: Interaction effect of grazing and competition (factorial ANOVA) on the average height at the end of treatment of all target Renosterveld species. Corresponding graphs plotted in Fig. 3.7 df equals 1 for all species, significant p values indicated in bold

Species	Source of variation	SS	F	p	Significance level
<i>Athanasia trifurcata</i>	Competition	2173.82	61.9149	0.000	***
	Grazing	1072.56	30.5486	0.000	***
	Competition*Grazing	582.02	16.5771	0.000	***
<i>Crassula glomerata</i>	Competition	9.181	1.3327	0.252	NS
	Grazing	0.889	0.1290	0.721	NS
	Competition*Grazing	0.305	0.0443	0.834	NS
<i>Leucadendron corymbosum</i>	Competition	476.71	73.486	0.000	***
	Grazing	109.04	16.809	0.000	***
	Competition*Grazing	0.41	0.064	0.801	NS
<i>Olea europaea ssp. africana</i>	Competition	9.711	0.1613	0.691	NS
	Grazing	595.475	9.8881	0.004	**
	Competition*Grazing	48.160	0.7997	0.378	NS
<i>Relhania fruticosa</i>	Competition	176.645	5.68757	0.031	*
	Grazing	27.467	0.88438	0.362	NS
	Competition*Grazing	40.472	1.30311	0.272	NS
<i>Salvia chamelaeagnea</i>	Competition	459.201	7.50575	0.019	*
	Grazing	570.668	9.32770	0.011	*
	Competition*Grazing	275.035	4.49551	0.058	NS

3.3.2 Seedling survival

Numbers of surviving seedlings decreased gradually during the first months after transplanting. Thereafter, seedling numbers remained low and fairly stable (Fig. 3.8). Species in the control treatment (protected and weeded) however showed high survival except for *R. fruticosa* (0.20 ± 0.15), and *O. europaea ssp. africana* (0.60 ± 0.15) (Table 3.5), (Fig. 3.8). Both grazing and competition negatively affected survival of seedlings in the old field, but competition was again the more important factor affecting survival of indigenous species in the old field (Table 3.5). The survival was higher in the weeded treatment with or without herbivory exclusion for all species, except for *O. europaea ssp. africana* (Fig. 3.8).

Seedlings of *O. europaea ssp. africana* were not affected by grass competition and survival rates were better under grass competition, regardless of exclusion of grazing (Fig. 3.8). There were, however, only significant differences in the effect of grazing and competition on the survival of *C. glomerata* ($p < 0.05$; $F_{3,16} = 4.471$) and *L. corymbosum* ($p < 0.05$; $F_{3,16} = 6.966$) seedlings (Table 3.5). Repeated measures ANOVA, showed no significant difference between mean survival for each treatment in different months, for most of the target species, *A. trifurcata* ($F_{45,240} = 1.122$; $p = 0.287$), *C. glomerata* ($F_{6,32} = 1.338$; $p = 0.269$), *O. europaea ssp. africana* ($F_{42,224} = 0.961$; $p = 0.543$), *R. fruticosa* ($F_{42,224} = 0.307$; $p = 0.999$), *S. chamelaeagnea* ($F_{42,224} = 1.205$; $p = 0.195$) except for *L. corymbosum* ($F_{36,192} = 5.455$; $p \leq 0.001$) (Fig. 3.8).



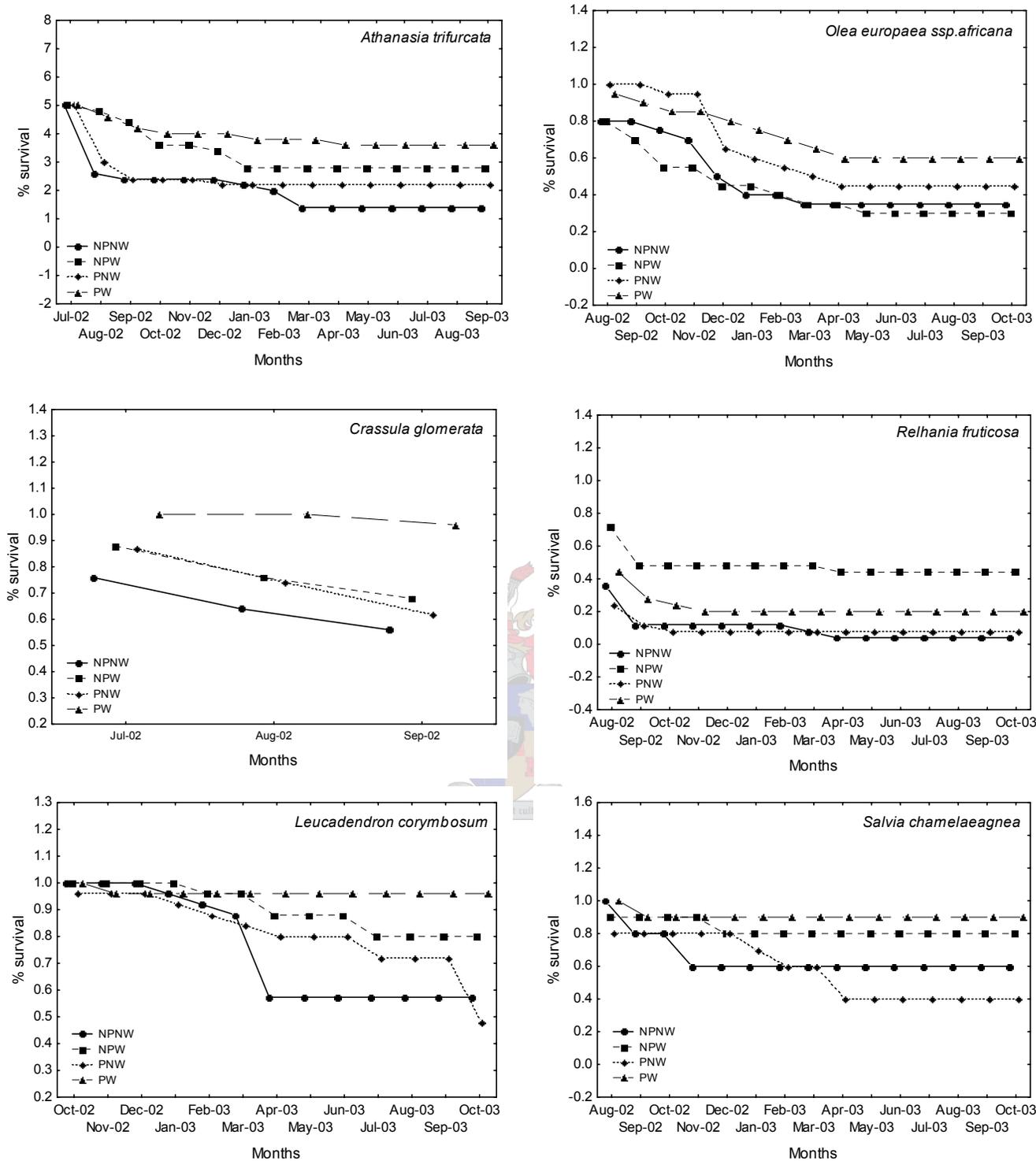


Figure 3.8: Repeated measures ANOVA of survival rate of target species under different treatments: (Factors influencing shrub growth and establishment in each of the four treatments. PW: protected from herbivory and weeded to remove competition, PNW: protected and not weeded, NPW: not protected and weeded, NPNW: not protected and not weeded).

Table 3.5: Mean % survival at end of treatment for each of the target species planted on experimental plots. Mean \pm Std.Err, df = 3 (4 treatments) and n = 20 (plots) for all species. (Factors influencing shrub growth and establishment in each of the four treatments. PW: protected from herbivory and weeded to remove competition, PNW: protected and not weeded, NPW: not protected and weeded, NPNW: not protected and not weeded). Letters indicated significant differences between columns and significant p values indicated in bold, (F (3,16) for each species and F(3,96) for all species).

Species	Treatment				F-value	P-value
	PW	NPW	PNW	NPNW		
<i>Athanasia trifurcata</i>	0.96 \pm 0.40	0.60 \pm 0.20	0.47 \pm 0.22	0.34 \pm 0.18	2.163	0.132
<i>Crassula glomerata</i>	0.96 \pm 0.04 ^a	0.68 \pm 0.08 ^{ab}	0.62 \pm 0.08 ^{ab}	0.56 \pm 0.11 ^b	4.471	0.018*
<i>Leucadendron corymbosum</i>	0.96 \pm 0.04 ^a	0.80 \pm 0.08 ^{ab}	0.51 \pm 0.09 ^b	0.57 \pm 0.07 ^b	6.966	0.003*
<i>Olea europaea ssp. africana</i>	0.60 \pm 0.15	0.30 \pm 0.05	0.45 \pm 0.09	0.35 \pm 0.10	1.600	0.228
<i>Relhania fruticosa</i>	0.20 \pm 0.15	0.44 \pm 0.23	0.08 \pm 0.04	0.04 \pm 0.04	1.588	0.231
<i>Salvia chamelaeagnea</i>	0.90 \pm 0.10	0.80 \pm 0.20	0.40 \pm 0.24	0.60 \pm 0.24	1.156	0.356
All species combined	0.76 \pm 0.06 ^a	0.60 \pm 0.06 ^{ab}	0.42 \pm 0.06 ^{bc}	0.41 \pm 0.06 ^c	6.527	0.004*

3.3.3 Number of leaves per plant

3.3.3.1 Effect of competition

To facilitate the comparison between all six target species on the different treatment plots, all results were summarized together in Table 3.6 and in Figure 3.9, showing the mean number of total leaves per species at end of the experiment. Although all plants started at approximately the same size, similar patterns were observed for grazing and competition on the total number of leaves for all target species as for plant height. Total leaf number was higher in weeded plots than in unweeded plots (competition treatment) for all species regardless of grazing. Nevertheless, where herbivores were excluded, the total number of leaves of all the target plant species was higher with grass biomass removal than with grass biomass left intact (Fig. 3.9).

Competition had a strong effect ($p \leq 0.05$) on the total number leaves per plant in all the species: *A. trifurcata*, *R. fruticosa*, *S. chamelaeagnea*, *O. europaea ssp. Africana* and *L. corymbosum* (Table 3.6).

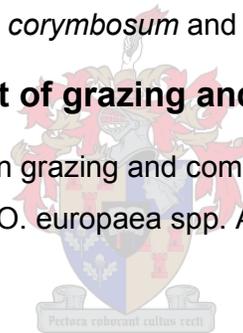
3.3.3.2 Effect of grazing

Grazing by large mammals appeared to reduce the total number of leaves for all target species. The total number of leaves was higher in the ungrazed treatment than in grazed treatment in both weeded and unweeded plots. However, the total number of leaves was higher in the grazed treatment without competition and lower in grazed treatment with competition (Fig. 3.9). Once again, the results show that, where grass biomass is removed, the total number of leaves per plant was greater for protected plot plants than for plants exposed to grazing (Fig. 3.9). Similarly, where grass biomass remained in the plots, the total number of leaves was higher for protected than un-protected plants (Fig. 3.9).

For grazing, a significant ($p \leq 0.05$) negative effect on leaf number was only found on *O. europaea ssp. africana* and *S. chamelaeagnea* (Table 3.6). There were no significant ($p \geq 0.05$) differences in leaf number between ungrazed and grazed treatments for *A. trifurcata*, *L. corymbosum* and *R. fruticosa* (Table 3.6).

3.3.3.3 Interaction effect of grazing and competition

The interaction effect between grazing and competition on leaf number was significant ($p \leq 0.05$) only for *O. europaea ssp. africana* (Table 3.6)



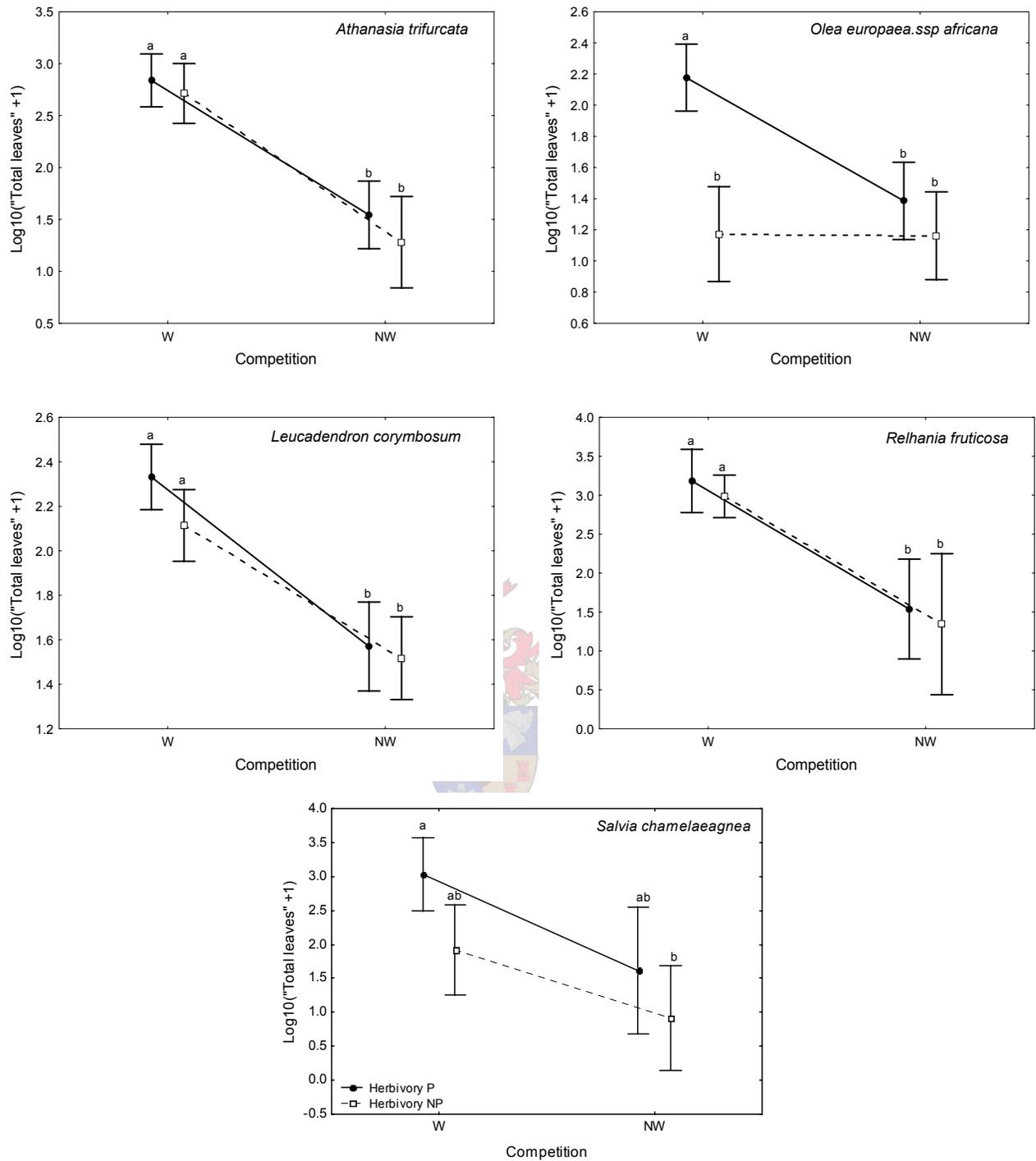


Figure 3.9: Effect of grazing and competition on the average number of leaves of the target Renosterveld species. Corresponding significance values given in Table 3.6 *C. glomerata* was not regarded. Different letters indicate significant differences between treatments. Vertical bars indicate indicate SD.

Table 3.6: Results of factorial ANOVA comparing the effect of grazing and competition of the total number of leaves of the target Renosterveld species. Corresponding graphs plotted in Fig. 3.9 df equals 1 for all species, significant p values indicated in bold

Species	Source of variation	SS	F	p	Significance level
<i>Athanasia trifurcata</i>	Competition	19.3395	67.2973	0.000	***
	Grazing	0.3942	1.3716	0.248	NS
	Competition*Grazing	0.0492	0.1712	0.681	NS
<i>Leucadendron corymbosum</i>	Competition	7.8584	60.176	0.000	***
	Grazing	0.3118	2.388	0.127	NS
	Competition*Grazing	0.1156	0.886	0.350	NS
<i>Olea europaea ssp. africana</i>	Competition	1.27790	9.5937	0.004	**
	Grazing	2.99601	22.4921	0.000	***
	Competition*Grazing	1.20771	9.0667	0.005	**
<i>Relhania fruticosa</i>	Competition	6.03575	33.3509	0.000	***
	Grazing	0.08659	0.4784	0.500	NS
	Competition*Grazing	0.00001	0.0000	0.996	NS
<i>Salvia chamelaeagnea</i>	Competition	4.65537	12.7429	0.004	**
	Grazing	2.62742	7.1919	0.021	*
	Competition*Grazing	0.14531	0.3978	0.541	NS

3.3.4 Canopy area

3.3.4.1 Effect of competition

The analyses of the effects of grass removal (competition) on canopy area of all the target species show a similar response for most of the plant species. The effects of treatment on canopy area are similar to those for height and total leaf number. The results show the direct effects of the removal of grass biomass on canopy area on all the target plant species (Fig. 3.10), indicating that grass competed with transplanted seedlings. Where herbivores were excluded, the canopy area of all the target plant species was higher in weeded plots than where grass biomass was left intact (Fig. 3.10). A significant difference ($p \leq 0.05$) was found between weeded and unweeded plots for canopy area of all the target plant species (Table 3.7).

3.3.4.2 Effect of grazing

For most of target plant species, the results of grazing on canopy area show that the canopy area of transplanted seedlings in protected plots was greater than in plots exposed to herbivory (Fig. 3.10). For *A. trifurcata*, *O. europaea ssp. africana*, *L. corymbosum* and *S. chamelaeagnea*, this effect was increased where grass biomass was removed (Fig. 3.10). Interestingly, competition by grasses reduced growth more than did large mammal herbivory for *A. trifurcata*, *R. fruticosa* and *L. corymbosum*. However, for the palatable plants like *O. europaea ssp. africana* and *S. chamelaeagnea*, the effect of grazing overrode that of competition and the plants grew larger in ungrazed plots, both in the presence and absence of grasses. For *C. glomerata*, competition reduced canopy growth but exposure to grazing had no significant ($p \geq 0.05$) effect (Fig. 3.10). Exposure to grazing had no significant ($p \geq 0.05$) effect on the canopy area of *A. trifurcata*, *C. glomerata*, *R. fruticosa* and *S. chamelaeagnea*. The canopy area of seedlings of *O. europaea ssp. africana* was significantly ($p \leq 0.05$) affected by grazing and also the canopy area of *L. corymbosum* seedlings (Table 3.7).

3.3.4.3 Direct interaction effect of grazing and competition

The combined effect of grazing and competition showed that the canopy area of all the species was larger with grass biomass removed in the plots and protected than with grass biomass left intact in the plot and not protected. There were no significant interaction effects of grazing and competition on the canopy area for any of the targets species (Table 3.7).

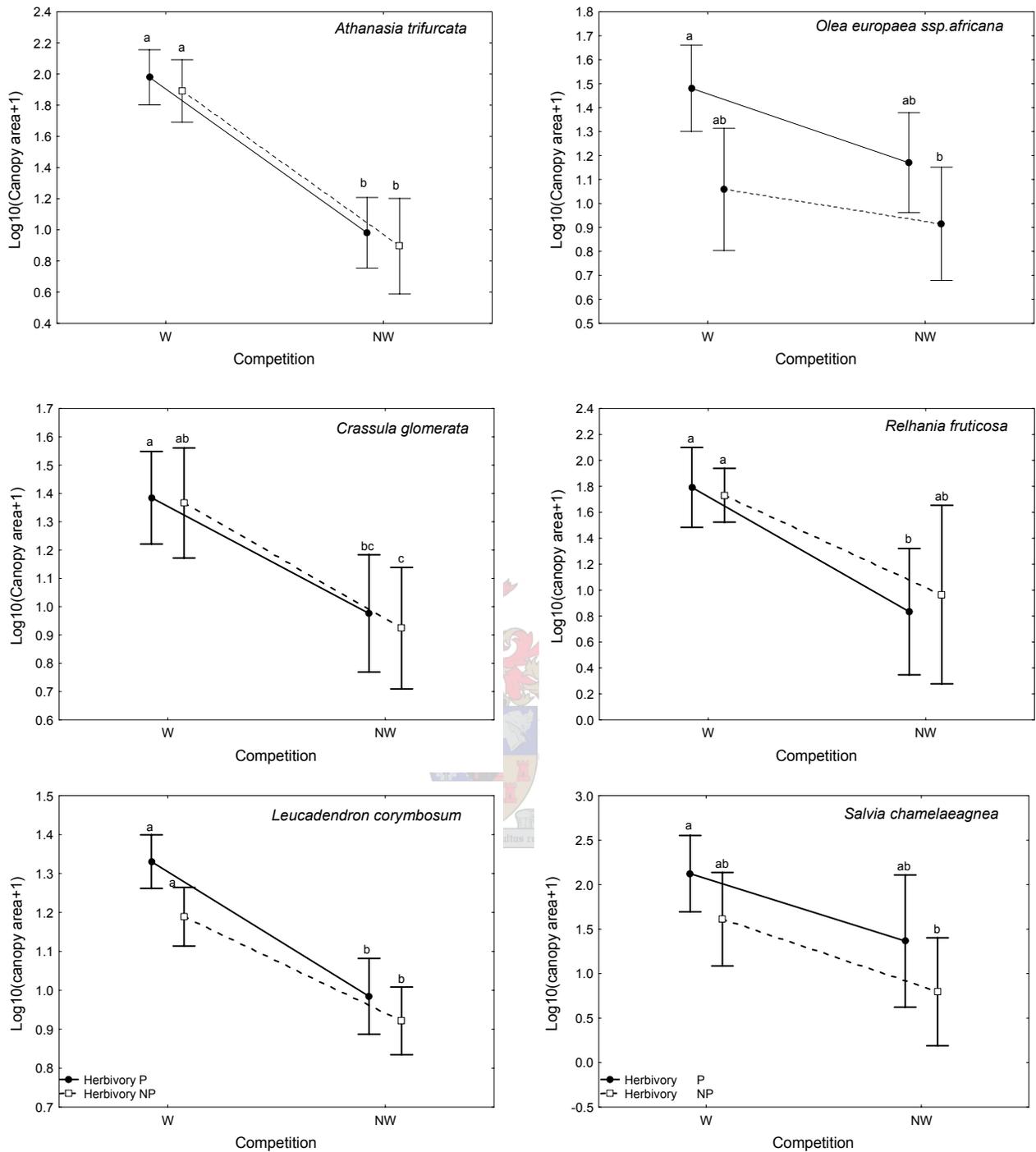


Figure 3.10: Interaction effects of grazing and grass competition on the canopy area of the target Renosterveld species. Corresponding significance values given in Table 3.7. Different letters indicated significant differences between treatments. Vertical bars indicate SD.

Table 3.7: Results of factorial ANOVA comparing the effect of grazing and competition of the canopy area of the target Renosterveld species. Corresponding graphs plotted in Fig. 3.10. df equals 1 for all species, significant p values indicated in bold

Species	Source of variation	SS	F	p	Significance level
<i>Athanasia trifurcata</i>	Competition	10.34670	74.6056	0.000	***
	Grazing	0.07832	0.5647	0.456	NS
	Competition*Grazing	0.00001	0.0001	0.993	NS
<i>Crassula glomerata</i>	Competition	10.34670	74.6056	0.000	***
	Grazing	0.07832	0.5647	0.456	NS
	Competition*Grazing	0.00001	0.0001	0.993	NS
<i>Leucadendron corymbosum</i>	Competition	1.55849	54.660	0.000	***
	Grazing	0.17289	6.064	0.016	*
	Competition*Grazing	0.02546	0.893	0.348	NS
<i>Olea europaea ssp. africana</i>	Competition	0.40931	4.3724	0.045	*
	Grazing	0.91096	9.7314	0.004	**
	Competition*Grazing	0.05548	0.5926	0.447	NS
<i>Relhania fruticosa</i>	Competition	1.65940	15.9154	0.001	**
	Grazing	0.00287	0.0275	0.870	NS
	Competition*Grazing	0.02073	0.1988	0.662	NS
<i>Salvia chamelaeagnea</i>	Competition	1.97797	8.6787	0.013	*
	Grazing	0.93733	4.1127	0.067	NS
	Competition*Grazing	0.00252	0.0111	0.918	NS

3.4. Discussion

3.4.1 General trends

This study was designed to examine the effects of grass competition, grazing by indigenous large herbivores, and interaction of these two factors on the establishment, growth and survival of Renosterveld target species seedlings on an abandoned field. To compare the effects of competition and herbivory on the six target species (*A. trifurcata*, *C. glomerata*, *L. corymbosum*, *O. europaea ssp. africana*, *R. fruticosa* and *S. chamelaeagnea*), the following three measures of plant performance were recorded for each species: height, total number of leaves and canopy area. The results clearly indicate the importance of grass competition and the effect of herbivory on Renosterveld species establishing on the old field. Herbivory and competition by grasses had an effect on the survival and growth of the transplanted Renosterveld species. In most cases, survival and growth of plants were reduced more in the competition treatment than the herbivory treatment, although the different Renosterveld species varied considerably in their response. These results support the suggestion of Goldberg (1987), and Miller and Werner (1987) that the response to competition may be highly species specific. The results indicate that most of the target plants competed for resources where the grass biomass was left intact in the treatment i.e., on the non-weeded plots. For example, overall survival of seedlings in the weeded plots was generally much higher than for those in the non weeded plots.

Large herbivores have profound effects on plant community structure, especially composition and dynamics (Augustine and McNaughton, 1998). These effects may be an indirect result of trampling (Salihi and Norton, 1987; Pitt *et al.*, 1998) and removal of plants by herbivores, subsequent reduction of nutrients and by change of the chemical composition of the nutrients (Olf and Ritchie, 1998). Herbivory is often seen as a confounding factor when measuring competition among plants (Reader, 1992). Experimental removal of neighbouring plants to exclude competition may simultaneously reduce food and shelter available to herbivores. Therefore, reduced competition rather than herbivory may be responsible for the improved performance of some target plants with this study.

The patterns observed in regard to the effects of herbivory are remarkably similar to those reported by Bonser and Reader (1995) who demonstrated that competition and herbivory each had a greater effect on plant growth at sites with higher biomass, and that herbivory had a lesser effect than competition on plant growth at sites with relatively low biomass. In this study the unweeded treatment can be considered as a high biomass treatment, which caused reduction of plant performance due to the competition among plants.

The combined effects of competition and herbivory are poorly studied (e.g. van der Wal *et al.*, 2000). In our results, the interaction of competition and herbivory on target species was not significant. Gurevitch *et al.* (2000), performed a meta-analysis of the relative effects of competition and herbivory on survival and growth of five plant species. They found that plant growth was affected equally by competition and herbivory, and that there was no significant interaction. In our results, competition has more impact on the plants than herbivory, and there is no significant interaction effect. Thus, these results disagree with Gurevitch *et al.* (2000) in regard equal effects of herbivory and competition, but agree with the insignificant interaction effects.

3.4.2 Effect of grass competition on growth and survival of transplanted seedlings

We found that competition had a greater effect on all variables measured in the field, than did herbivory. This was inconsistent with the expected result that herbivory would have a greater effect on target plant performance (Augustine and McNaughton, 1998). The results show that all plants increased in height in all the treatments. However, the height at the end of treatment of four of the target species was greatly affected by competition, since the removal of the grass biomass resulted in a height increase at the end of the treatment compared to when they were planted. While a decrease is observed in the non-weeded treatments (*A. trifurcata*, *L. corymbosum*, *R. fruticosa*, *S. chamalaeagnea*). Plants that are not surrounded by grass biomass experience less competition for resources such as light, nutrients and water, than plants where grass biomass is left intact (Reader *et al.*, 1994). This notion is supported by other old-field

experiments by (Goldberg, 1987) and by those of Bonser and Reader (1995) who report that competition will increase with increasing productivity.

In contrast, the height of *O. europaea ssp. africana*, usually growing on nutrient rich soil around termitaria, was not affected by grass competition. Presumably, tall growing seedlings of *O. europaea ssp. africana* are probably better competitors for light than short growing grasses like *Cynodon dactylon*. The root system of *O. europaea ssp. africana* might be developed and well established in an earlier stage than those other transplanted species, thus, this species is better equipped to compete with grass. Seedlings of the annual succulent plant *C. glomerata* were not affected by grass competition.

While neighbour removal is used commonly to measure competition (Aarssen and Epp, 1990), Campbell *et al.*, (1991) have questioned the use of removal experiments to study competition because nutrient supply in removal plots may increase from the decomposition of dead roots of neighbours, which are usually not removed completely. Consequently, the increase in canopy area and total number of leaves due to grass removal may be greater in weeded plots than in non weeded plots due to the nutrient release from the decomposition of roots.

The survival of transplanted seedlings was higher in weeded plots than in non-weeded plots for most of the target species. Primarily, this might be due to a reduction of grass biomass in weeded treatments, thus confirming the prediction made by Tilman (1988) and others (Slobodkin *et al.*, 1967; Newman, 1973), who state that, although competition intensity may be constant, a qualitative shift is expected from competition for soil resources at low productivity to competition for light at high productivity. The competition balance between all the target species may be a shift between microenvironments within plots. This might be due to specific differences of plot sites, such as soil composition, i.e. water availability, water holding capacity and infiltration in the weeded treatments.

Our results are consistent with previous research that shows that small plants are more likely to be impacted by competition than large plants (Thomas and Weiner, 1989; Pacala and Weiner, 1991). Those species that decreased in cover may have been suppressed by one of the species that subsequently increased in size (grass biomass), or they may have been dependent on the removed species for

shade, increased humidity, or soil stability (Hunter and Aarssen, 1988). Those species that increased in cover were most likely released from competition for limiting resources by the species removals (Aarssen and Epp, 1990).

3.4.3 Effect of herbivory on establishment, growth and survival of seedlings

Cages were used to exclude the effect of large herbivores on all target species. Where cages were used there was a significant increase in height at the end of the treatment, especially for *A. trifurcata*, *L. corymbosum*, *O. europaea ssp. africana* and *S. chamelaeagnea*. The reason for this could be that the protected plants lost less tissue to herbivores, but also due to the trampling effect, which can inflict mortality on plant seedlings (Salihi and Norton, 1987; Pitt *et al.*, 1998). Results of monthly monitoring indicated that unprotected plants showed obvious signs of herbivory, such as cropped stems and damaged leaves. Plants were also trampled.

The experiment was conducted for large herbivores, but we did not attempt to determine what type of herbivores actually removed tissue. So we can only speculate whether small mammals (rodents), insects (grasshoppers), and molluscs (snails, slugs) had an impact on the results, as the cages only excluded animals of rabbit size or bigger. Most of these animals were seen at least near one of the experimental plots during data collection (pers. obs.). However, these species would not have much impact on the results, as they all had the same probability to influence all the treatment plots in the field.

A significant negative effect of exposure to large herbivores on plant height was found for all species except *C. glomerata* and *R. fruticosa*. Since the target species differ in terms of palatability to large herbivores and in competitive ability, some plants will survive with grasses around them and some will not. Many authors have suggested that invertebrate herbivory effects are likely to be most conspicuous when grazed plants are competing with other plants for resources, since differential herbivory can provide a competitive advantage to the least damaged plants (Bentley and Whittaker, 1979). Selective grazing by large herbivores and target species palatability were not considered but this certainly could have had an effect on the results. However, a positive correlation has been

found between competitive ability and palatability for species in the grassland area (Crawley, 1990). This finding is consistent with the prediction of competitor release of unpalatable species when exposed to grazing (Pacala and Crawley, 1992).

In the field species like *A. trifurcata*, *O. europaea ssp. africana* and *S. chamelaeagnea* were strongly grazed and browsed and species like *L. corymbosum* and *C. glomerata* did not show any signs of herbivory (pers. obs.). Total leaf number of *O. europaea ssp. africana* and *S. chamelaeagnea* was considerably higher when protected from herbivory, but not for *A. trifurcata*, *L. corymbosum* and *R. fruticosa*. These last three species might be unpalatable or this can be due to species preference by large herbivores. It can also depend on which large herbivore species are habitually present in the old field.

A significant difference for canopy area between protected and non-protected plants was also found for *L. corymbosum* and *O. europaea ssp. africana* but not for *A. trifurcata*, *C. glomerata*, *R. fruticosa* and *S. chamelaeagnea*. These results are not surprising for *O. europaea ssp. africana* and *S. chamelaeagnea*, since they were highly grazed in the field and are likely palatable species (Goldblatt and Manning, 2000). It has often been predicted that herbivory would have the biggest effects on seedlings (Crawley, 1989). Some authors have challenged the idea that the magnitude of damage should be associated with the effects on plant performance (Crawley, 1989; Marquis, 1984). The surprising lack of effect that herbivory had on seedlings of some species might be due to their small size. It has been recognised that less apparent species will be more difficult for large herbivores to find than taller plant species (O'Connor, 1991; O'Connor, 1992). In the case of selective herbivory, however neighbouring species might reduce the grazing pressure on palatable plants by making them less obvious, which might ameliorate the direct grazing effects, as was shown in the study by Mulder and Ruess (1998) on *Triglochin palustris*. Although some seedlings may escape from herbivory because of their small size, we found that survival was lower in non-protected plots than in protected plots for all the target species.

3.4.4 Interaction between grazing and competition on seedling establishment, growth and survival.

Our results showed no interaction effect between herbivory and competition on the average height at the end of treatment for all but one of the target species (*A. trifurcata*). The height of plants at the end of treatment was higher in weeded and protected treatments than in the weeded and non-protected treatments. One could argue that grass removal might enhance the rate of herbivory, as the target plants were easily found by herbivores in the non-protected environment. Similarly, the heights of the target plants were slightly greater in the non-weeded and protected plots than in the non-weeded and non-protected plots, although the difference was not significant for all species. Herbivory pressure presumably increased, following experimental grass biomass removal, because plants in weeded plots were more apparent. It seems like herbivores fed more on plants translocated to plots without grass competition.

The same pattern was found for the total number of leaves and canopy area at the end of treatment for the target species. The total number of leaves per plant was higher in the weeded and protected treatment than in the weeded and non-protected ones. In most cases there was no significant difference, apart from *O. europaea ssp. africana*, where significant interaction was found on total leaves per plant. Observing the canopy area showed no significant difference for interaction for all the target species. The herbivory impact increased in non-weeded plots. Presumably, herbivory damage increased because plots with more biomass which were not protected attracted more herbivores, due to the great plant cover and food availability. Both Grover, (1995) and Leibold, (1996) predict that grazing pressure increases with increasing productivity.

Consequently, our results are consistent with the assumption that the individual effects of herbivory and competition from neighbouring plants are independent rather than interactive, with each factor reducing the performance of each plant. A possible reason for independent effects of herbivory and competition on the shoots of target species might be that herbivores have little effect on the competitive ability of some target plants if the plant is already at the bottom of competitive hierarchy. Generally, one species competes or disperses better than

another depending on their relative position in a hierarchy. The hierarchy has variously been based on an experimentally derived probability of one species invading a neighbouring site at the expense of another (Silvertown *et al.*, 1992) or on more general functional traits derived from experimentation (Colasanti and Grime, 1993). On sites where water is not a limiting factor, Richardson *et al.*, (1996) found that growth of juvenile plants was most restricted by tall, fast growing competitors. In contrast, in dryland areas, herbaceous broadleaved weed species were shown to have the most detrimental influence on juvenile plant growth (Richardson *et al.*, 1993).

Another possibility is that the competitive balance between Renosterveld species and the grass biomass may be unaffected by herbivory if herbivores feed on both the Renosterveld species and grass biomass. It might be also that the presence of the grass biomass may not affect the ability of target Renosterveld species to escape detection by herbivores if herbivore density is high in the old field or if herbivores use visual plus olfactory cues to locate the target plants. Further study is required however to determine the reasons for the independence of herbivory and competition effects in the old field at EPNR.

3.4.5 Conclusion

In most studies of the importance of competition or herbivory in plant communities, seedlings have been used rather than mature, established plants. It is argued that seedlings are more susceptible than established plants to effects of both herbivory (Reader, 1992) and competition (Goldberg and Barton, 1992). Hand weeding caused a threefold increase in plant size, which is clearly a result of the relaxation of competitive interactions with neighbouring plants (Rees and Brown, 1992). More experimental studies still need to be done before generalizations can be made about the role of herbivory and competition on seedling establishment, survival and growth on old-field in Renosterveld vegetation. However, this study shows that both grazing and competition play important roles in determining the performance and distribution of target plant species, and these two processes are not linked. It appears that herbivory and competition action observed where the grass was removed had an independent effect on plant performance, in which case their combined effect can be predicted

by simply multiplying the individual effect, quantified experimentally by using herbivore-exclusion and grass removal treatments.

The growth and survival of *A. trifurcata*; *L. corymbosum*; *R. fruticosa* and *S. chamalaeagnea*, all common shrubs of low open Renosterveld shrubland vegetation, are more likely to be impacted by competition. All regenerate by seed after fire. *O. europaea ssp. africana*, an evergreen tree associated protected habitats such as drainage lines, termitaria and boulder scree (Boucher and McDonald, 1982; Campbell, 1985), is more likely to be impacted by herbivory than competition, even at the low herbivore densities. Tolerance of competition may be expected of plants species in fire-free habitats. *C. glomerata*, an understory herb, showed a high tolerance of grass competition and was seldom browsed. We conclude that the performance of most of the Renosterveld species was more sensitive to competition effect than herbivory.

3.5 References

- Acocks, J.P.H. 1988. Veld Type of South Africa. Botanical Research Institute. South Africa.
- Aarssen, L.W., and Epp, G.A. 1990. Neighbor manipulations in natural vegetation: a review. *Journal of Vegetation Science* **1**: 13-30.
- Augustine, D.J., and McNaughton, S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* **62**: 1165-1183.
- Baard, E.H.W. 1990. Biological aspects and conservation status of the geometric tortoise *Psammobates geometricus*, PhD dissertation, University of Stellenbosch.
- Bentley, S., and Whittaker, J.B. 1979. Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. *Journal of Ecology* **67**: 79-90.
- Bonser, S.P., and Reader, R.J. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* **76**:2176-2183.
- Bothma, J. du P. 1996. Game Ranch Management. J.L. Van Schaik Publishers, Hatfield, Pretoria.

- Boucher C and McDonald AE 1982. An inventory of plant communities recorded in the western, southern and eastern Cape Province, South Africa up to the end of 1980. South African National Scientific Programmes Report 57, CSIR, Pretoria Pp: 62.
- Bronstein, I.N. and Semendjajew, K.A. 1991: Taschenbuch der Mathematik, 25 edn. B.G. Teubner Verlagsgesellschaft, Stuttgart.
- Campbell, B.M. 1985. A classification of the mountain vegetation of the Fynbos Biome. Memoirs of the Botanical Survey of South Africa 50. Botanical Research Institute, Pretoria.
- Campbell, B.D., Grime, J.P., Mackey, J.M.L., and Jalili, A. 1991. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology* **5**: 241-253.
- Colasanti, R.L., and Grime, J.P. 1993. Resource dynamics and vegetation processes: a deterministic model using two-dimensional cellular automata. *Functional Ecology* **7**: 169-176.
- Cowling, R.M. 1992. The ecology of fynbos-nutrients, fire and diversity. Oxford University Press: Cape Town.
- Cowling, R.M., and Richardson, D.M. 1995. Fynbos: South African's unique flora kingdom. University of Cape Town.
- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* **34**: 531-564.
- Crawley, M.J., 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* **27**: 803-820.
- Deacon, H.J., Jury, M.R., and Ellis, F. 1992. Selective regime and time. In: *The ecology of fynbos-nutrients, fire and diversity* (Ed. Cowling, R.). Oxford University Press. Cape Town.
- Engelbrecht, E. 1995. The diet, water and electrolyte balance, and thermoregulation of geometric tortoise, *Psammobates geometricus* (Linnaeus) (Cryptodira: Testudinidae). Faculty of Science, University of Stellenbosch.
- ESRI 2002. ESRI®ArcMap™ 8.3. www.esri.com.
- Farley, N. 2002 (*pers.comm.*) Elandsberg Farms, PO Box 38, Hermon. Unpublished material.

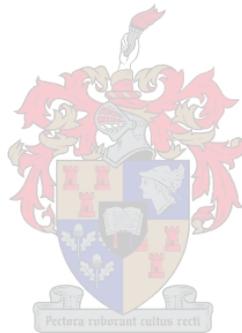
- Farley, N. 2001. Information booklet on Elandsberg Farms. Unpublished material.
- Fowler, N. 1981. Competition and coexistence in North Carolina grassland. *Journal of Ecology* **69**: 843-854.
- Germishuizen, G., and Meyer, N.L. 2003 (eds). Plants of southern Africa – an annotated checklist. Strelitzia 14. National Botanical Institute, Pretoria. pp:1231.
- Goldberg, D.E. 1987. Neighborhood competition in old-field plant community. *Ecology* **68**: 1211-1223.
- Goldberg, D.E., and Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **138**: 771-801.
- Goldblatt, P., and Manning, J.C. 2000. Cape Plants. National Botanical Institute, Cape Town.
- Grover, J.P. 1995. Competition, herbivory, and enrichment: nutrient based models for edible and inedible plants. *American Naturalist* **145**: 746-774.
- Grossman, D. 1991. Drakrag, wildgetalle en optimale benutting. Seminar: Game Ranch Management, PU for CHE, Potchefstroom. In Bothma, J. du P. 1996. Game Ranch Management. J.L. Van Schaik Publishers, Hatfield, Pretoria.
- Gurevitch, J., Morrison, J.A., and Hedges, L. V. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *American Naturalist* **155**: 435-453.
- Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* **94**: 421-425.
- Holt, R.D., and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* **25**: 495-520.
- Hunter, A.F., and Aarssen, L.W. 1988. Plants helping plants. *BioScience* **38**: 34-40.
- Jarman, M.L. 1986. Conservation Priorities in Lowland Regions of the Fynbos Biome, Pretoria: Foundation for Research Development CSIR.
- Lee, T.D., and Bazzaz, F.A. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *Journal of Ecology* **68**: 813-821.

- Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**: 784-812.
- Louda, S.M. 1983. Seed predation and seedling mortality in the recruitment of shrub, *Haplopappus venetus* (Asteraceae), along a climate gradient. *Ecology* **64**: 511-521.
- Low, A.B. and Rebelo, A.G. 1998. Vegetation of South Africa, Lesotho and Swaziland. Pretoria: Department of Environmental Affairs and Tourism, Pretoria.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* **1978**: 13-39.
- Marquis, R.J. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* **226**: 537-539.
- Mike, G. (*pers.comm.*) Elandsberg Farms, PO Box 38, Hermon.
- Miller, T.E., and Werner, P.A. 1987. competition effects and responses between plant species in a first-year old field community. *Ecology* **68**: 1201-1210.
- Mulder, C.P.H., and Ruess, R.W. 1999. Effect of herbivory on arrowgrass: interaction between geese, neighboring plants, and abiotic factors. *Ecological Monographs* **68**: 275-293.
- Newman, E.I. 1973. Competition and diversity in herbaceous vegetation. *Nature* **244**: 310-311.
- O'Connor TG (1992) Patterns in plant selection by grazing cattle in two savanna grasslands: A plant's eye view. *Journal of Grassland Society of Southern Africa* **9**:97-104.
- O'Connor, T.G. (1991) Local extinction in perennial grasslands: a life-history approach. *The American Naturalist* **137**: 753-773.
- Olf, H., and Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**: 261-265.
- Pacala, S.W., and Weiner, J. 1991. Effects of competitive asymmetry on a local density model of plant interference. *Journal of Theoretical Biology* **149**: 165-179.
- Pacala, S.W., and Crawley, M.J., 1992. Herbivores and plant diversity. *American Naturalist* **40**: 243-260.

- Parker, D. 1982. The Western Cape Lowland Fynbos: What is there left to conserve? *Veld & Flora* **68**: 98-101.
- Parker, M.A. and Root, R.B. 1981. Insect herbivores limit distribution of a native composite, *Machaeranthera canescens*. *Ecology* **62**: 1390-1392.
- Parker, M.A., and Salzman, A.G. 1985. Herbivory exclosure and competitor removal: effects on juvenile survivorship and growth in shrub *Gutierrezia microcephala*. *Journal of Ecology* **73**: 903-913.
- Pitt, M.D., Newman, R.F., Youwe, P.L., Wikeem, B.M., and Quinton, D.A. 1998. Using a grazing pressure index to predict cattle damage of regenerating tree saplings. *Journal of Range Management* **51**: 417-422.
- Rausher, M.D., and Feeny, P.P. 1980. Herbivory, plant density, and plant reproductive success: the effects of *Battus philenor* on *Aristolochia reticulata*. *Ecology* **61**: 905-917.
- Reader, R.J. 1992. Herbivory, competition, plant mortality and reproduction on a topographic gradient in an abandoned pasture. *Oikos* **65**: 414-418.
- Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilma, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olf, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., Grigulis, R., and Beisner, B.E. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* **75**: 1753-1760.
- Rees, M., and Brown, V.K. 1992. Interactions between invertebrate herbivores and plant competition. *Journal of Ecology* **80**: 358-360.
- Richardson, B., Vanner, A., Davenhill, N., Balneaves, J., Miller, K., and Ray, J. 1993. Interspecific competition between *Pinus radiata* and some common weed species-first year results. *Newzealand Journal of Forest Science* **23**: 179-193.
- Richardson, B., Vanner, A., Ray, J., Davenhill, N. and Coker, G., 1996. Mechanisms of *Pinus radiata* growth suppression by some common forest weed species. *Newzealand Journal of Forest Science* **26** (3): 421-437.
- Robberecht, R., Mahall, B.E., and Nobel, P.S. 1983. Experimental removal of intraspecific competitors-effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. *Oecologia*, Berlin, **60**: 21-24.

- Salihi, D.O., and Norton, B.E. 1987. Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. *Journal of Applied Ecology* **24**: 145-151.
- Shiponeni, N.N. 2003. Dispersal of seeds as a constraint in revegetation of old field in Renosterveld vegetation in Western Cape, South Africa. MSc University of Stellenbosch.
- Silvertown, J., Holtier, S., Johnson, J., and Dale, P., 1992. Cellular automaton models of interspecific competition for space—the effect of pattern on process. *Journal of Ecology* **80**: 527–534.
- Skinner, J.D., and Smithers, R.H.N. 1990. The mammals of the Southern African Subregion. University of Pretoria, Pretoria.
- Slobodkin, L.B., Smith, F.E., and Hairston, N.G. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *American Naturalist* **101**: 109-124.
- StatSoft, Inc. (2003). STATISTICA (data analysis software system), version 6. www.statsoft.com.
- Thomas, S.C., and Weiner, J. 1989. Including competition asymmetry in measures of local interference in plant populations. *Oecologia* **80**: 349-355.
- Tilman, D. 1988. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* **1**: 304-315.
- Van der Wal, R., Egas, M., Van der Veen, A., and Bakker, J. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* **88**: 317-330.
- Visser, D.J.L. 1984. Explanation of the 1:1 000 000 geological map, fourth edition. The geology of the Republics of South Africa, Transkei, Bophuthatswana, Venda and Ciskei and Kingdoms of Lesotho and Swaziland. Department of Mineral and Energy Affairs. South Africa.
- WallisDeVries, M.F., Laca, E.A., and Demment, M.W. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia* **121**: 355-363.

- WCNCB, 2000. State of Biodiversity: Western Cape Province, South Africa. Introduction. Scientific Services, Western Cape Nature Conservation Board, Private Bag 5014, Stellenbosch 7599.
- White, J.A., and Whitham, T.G. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* **81**: 1795-1803.
- Willis, A.J., Groves, R.H., and Ash, J.E. 1998. Interactions between plant competition and herbivory on the growth of *Hypericum* species: a comparison of glasshouse and field results. *Australian Journal of Botany* **46**: 707-721.
- Windle, P.N., and Franz, E.H. 1979. The effects of insect parasitism on plant competition: greenbugs and barley. *Ecology* **60**: 521-529.



Chapter 4: Effects of different management strategies on the re-establishment of shrubs and tussock grasses on old lands in Renosterveld

4.1 Introduction

Much of the biodiversity transformation of the natural vegetation has historically been created by farming practices (Bignal and McCracken, 1996; Clemente *et al.*, 2004). The intensification of agricultural practices during the last century has led to a rapid decline in species richness and diversity (Duelli, 1997). At both local and regional scales, land use changes are among the most immediate drivers of species diversity (Van der Putten *et al.* 2000; Clemente *et al.*, 2004).

However, much of the former biodiversity in the agricultural landscape is maintained in small-scale landscape elements such as field margins, hedgerows and road verges (Goedmakers, 1989). West Coast Renosterveld is one of the most threatened vegetation types in South Africa. Farming has been the most important activity since European settlement in the eighteenth century (i.e. 1700 to present), leaving less than 5% of the original extent of this vegetation type (Low and Rebelo, 1998). Most of the natural vegetation was transformed by ploughing mainly for wheat production and more recently vineyard expansion (Fairbanks *et al.*, 2004). The remaining natural vegetation is mostly found on private land and less than 2% is to date under formal protection (Low and Rebelo, 1998; von Hase *et al.*, 2003).

Conservation efforts in general over the past decade have been shifting from a focus on the preservation and protection of intact systems to the restoration of degraded systems (Hobbs and Norton, 1996; Dobson *et al.*, 1997). One of the major challenges is that degraded plant communities often do not respond predictably to management efforts, producing inconsistent and sometimes unexpected results (Hobbs and Harris, 2000; Klotzli and Grootjans, 2001; Zedler, 2000).

The aim of this part of the thesis is to determine whether removal of grass competition (by using fire, herbicide or brush cutting) in combination with reseeding, would hasten recovery of natural vegetation on old agricultural lands. The research was motivated by the need to find a cost-effective method for restoration of natural Renosterveld vegetation at a larger scale in Elandsberg Private Nature Reserve (EPNR). For this restoration experiment three different questions were asked:

1. Which treatment results in the quickest restoration?
2. Which treatment results in the highest species richness or diversity?
3. Which treatment is the cheapest or most feasible for the landowner or farmer?

4.2 Materials and methods

4.2.1 Study area

Experimental work was conducted at Elandsberg Private Nature Reserve (EPNR), on the farm Bartholomew's Klip (33°24'17" S and 33°29'8" S, and 18°58'30" E and 19°05'10" E), at the foot of the Elandskloof Mountains, Western Cape. The principal vegetation type on the farm is mountain fynbos, grading into West Coast Renosterveld at the foot of the mountain. For a more detailed description of the study site, see chapter 3.2.

4.2.2 Experimental design

In early April 2003 (autumn), a stratified repeated design was selected to avoid confounding experimental results with possible gradient effects and spatial heterogeneity of the area. The treatment area was established parallel to the edge old field / natural vegetation, with treatment strips running perpendicular to the edge. Twelve plots, four parallel strip treatments of 4 m x 20 m each were established in the study site. Strips were separated by 2 m wide walkways to avoid influence of each treatment on one another. Each treatment was replicated three times. The strip treatments were (1) burning, (2) mowing / brush cutting, (3) application of herbicide and (4) control (unmanipulated old-field vegetation) (Fig. 4.1). The burn treatments were established in April 2003, mowing / brush cutting and herbicide application were conducted in May 2003, with one week intervals between the application of each treatment. Seeds of two species (*Eriocephalus*

africanus, Asteraceae and *Ehrharta calycina*, Poaceae) were sown within all treatment plots after the first rain in May 2003.

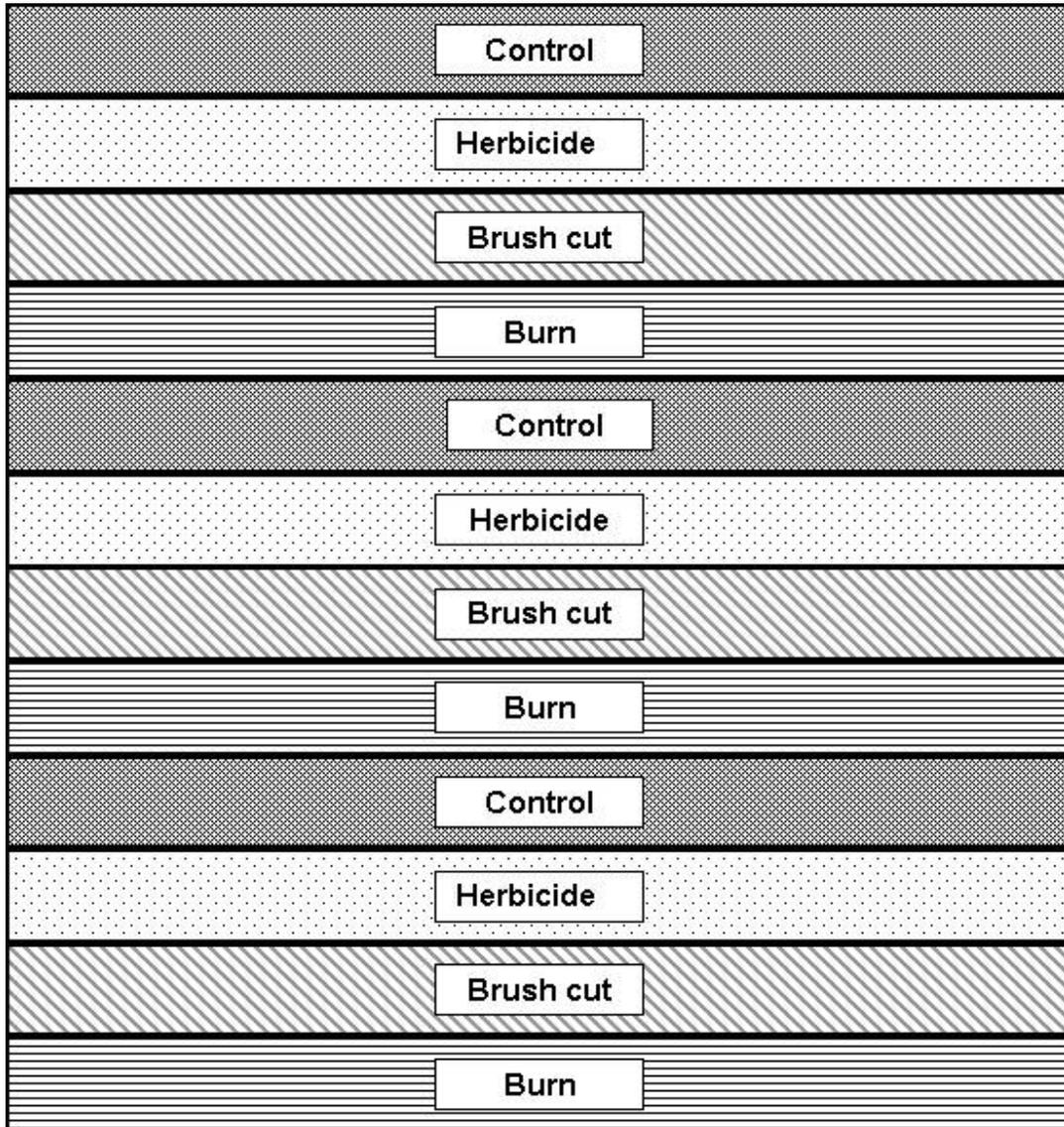


Figure 4.1: Experiment Layout (not to scale) 3 strips of 80 m² (4m * 20m) with 4 different treatments: Control, Herbicide: application of herbicides, Burn: controlled burn, Cut: vegetation mowed / brush cut

Treatment description

Burning was carried out within the firebreak established on the study site to prevent fire from spreading into surrounding treatment plots. The herbicide treatment involved application of “*Gallant Super*”[®], (2- (4-((3-Chloro-5-(trifluoro methyl)-2-pyridinyl)oxy)phenoxy) propanoic acid methyl)) which is a selective pre-emergence, systemic herbicide for the control of annual and perennial grasses. A spray tank of 10 litres was filled with clean water and mixed with approximately 4 ml of gallant super (application rate: 0.5 l/ha) and 10 ml of “*Curabuff*”[®] (application rate: 100 to 400ml per 100l water). This product, a buffer, lowers the pH of alkaline and increases the pH of acidic spray water of natural origin to an optimum range of pH= 4 to pH= 6.5. One spray tank was sprinkled over the soil surface for each of the three herbicide treatments. The soil surface was lightly raked to ensure penetration of the herbicide. The mowing / brush cutting treatment was done by using a cutter pulled by a small tractor. Following treatment application, each experimental treatment plot was marked with a 1.5 m iron stake, which was colour-coded to indicate the treatment applied. The trials were also delimited with rocks.

Sowing mix

Seeds of *E. calycina* were obtained from Agricol (Pty) Ltd, Brackenfell, and seeds of *E. africanus* were supplied by Worcester Veld Reserve, Western Cape Department of Agriculture. Seeds of each species were mixed with sawdust, 2 volumes of sawdust to 1 volume of seed. 500 ml sawdust were mixed with 250 ml of seeds. Of this sowing mix, 10 samples of 100 ml were taken and the number of seeds in each sample was counted. This gave the average number of seeds per 100 ml plastic bag of sowing mixed and average number of seeds sown in the plots. An average of 2000 to 2500 seeds per bag was found for *Ehrharta calycina* in 100 ml seed mix. For *Eriocephalus africanus* seeds, three handfulls of seeds were mixed with two handfulls of sawdust for each seeding bag. Number of seeds per seeding bag was not established, as the fluffy outer covering of the seeds made them difficult to count.

Preparing the sowing mix for field application:

The mixture of sawdust and seeds (2:1) were divided into 12 packets of equal volume / weight and one packet was used for each of the treatment plots (3 burns, 3 herbicides, 3 mowing / brush cutting, 3 controls). Each of the twelve packets was divided again into four small sowing bags of 500 ml for each treatment, giving a total of 48 sowing packets.

Sowing in the field:

To ensure that the seeds were equally distributed throughout the plots, each of the twelve (4 m x 20 m) treatment plots were divided in quarters (4 m x 5 m). Within each quarter plot, one of the 48 packets of sowing mix was sown.

Seed germination and viability

Seed germinability was tested in the nursery. For this purpose, 380 seeds of *Ehrharta calycina* and 120 seeds of *Eriosephalus africanus* were used. All the seeds were planted in soil from the study site in June 2003, watered 2 times a day and kept in the nursery under ambient temperature. Germinated seedlings were recorded in August 2003. The seed germinability was calculated by dividing the total number seeds germinated by the total number of seeds planted.

4.2.3 Soil bioassay

To determine whether the soil quality was affected by herbicide, Radish (*Raphanus sativus* L.) a dicotyledon, and wheat (*Triticum aestivum* L.), a monocotyledon, were selected as an indicator of soil toxicity in bioassays. Wheat grass was chosen as herbicide used in the treatment is grass specific. Both species germinate rapidly, are fast growing, and short lived. The effects of nutrient imbalances on their morphology are well documented. Three soil samples in each of the four different treatments were collected randomly to a depth of 15 cm using a hand trowel and soil augers. Soil samples from natural vegetation (untransformed area) were also collected and included in the experiment. These soils samples were collected one year (March 2004) after the experiment took place, to establish whether there was any persistent residual effect of the herbicide (Gallant Super®) on the soil. Soil samples were arranged in random order in the nursery with respect to treatments. Five radish and five grass wheat seeds were planted in the centre of each soil sample. After two weeks all

radish plants were removed, leaving the strongest radish plant in each pot. After six weeks the radish had developed a minimum of four leaves per seedlings and a swollen root.

The plants were removed from the soil by washing off the soil under running water. Photographs of each plant species and notes on the colour and shape of the leaves were taken for both species (leaf appearance). Leaves of each radish were placed in a separate, well labeled paper bag. The root of each radish was thinly sliced and placed in a clearly labeled paper packet. The root and leaf samples were dried for 48 hours at 60 degrees and weighed (leaf dry weight and root dry weight). The roots and leaves of the grass wheat were also dried and weighed. A single-factor analysis of variance tested the effects of different management strategies on measured plant parameters, viz above and below ground mass and their ratios. Significantly different treatment means were separated using a Scheffè post-hoc test in STATISTICA (STATISTICA 6.1, StatSoft, Inc. 2003).

4.2.5 Data collection and analysis

The plots in the field were sampled every month from April 2003 until March 2004. The sampling involved recording the number of species in the plot, and estimating species cover (sown, emerging from the seed bank and established) using visual estimation of percentage cover in 1m X 1m grid. A single-factor analysis of variance tested for differences in species richness and diversity between the different management strategies. Significantly different treatment means were separated using a Scheffè post-hoc test in STATISTICA (STATISTICA 6.1, StatSoft, Inc. 2003). To determine species diversity, the

Shannon-Wiener Index (H) was calculated using the formula: $H = -\sum_{i=1}^S p_i \ln p_i$ (S:

total number of species in the community and p_i : proportion of species i), in the programme “Species Diversity and Richness” (Henderson and Seaby, 2001). Diversity indices were performed using a Randomization Test (Solow, 1993), which uses a Shannon Wiener index with 10000 random partitions, also built into the programme to compare the diversity between treatments.

With the same statistical package, the upper and lower confidence intervals of the diversity indices were estimated using bootstrapping. All the cover data were transformed using arcsine transformation (Zar, 1999). The size distribution of seedlings establishing from sown seeds was also recorded to evaluate the recruitment of sown seeds in all the four different treatments. All species were classified into three main groups: grasses (indigenous and alien), shrubs and other species. By indigenous grasses, we mean native grass species and alien grasses are regarded as exotic non-natives grasses. By other species we mean non-grasses comprising geophytes, bulbs, sedges and forbs (Appendix A). A single-factor analysis of variance tested the effects of different management strategies on the average of total grass cover of alien grasses; indigenous grasses, shrubs and other species in different treatment plots at the end of the study separately. The ratio between alien grasses and indigenous grasses, the ratio between alien grasses and the total species cover as well as the ratio between indigenous grasses and the total species cover, and the ratio between other species and total species cover on different treatments were tested separately to determine the proportion of alien and indigenous grasses in relation to the total cover of all the species. Significantly different treatment means were separated using a Scheffé post-hoc test.

Multivariate technique of DCA (Detrended Correspondence Analysis) embedded in CANOCO (Canonical Community Ordination software package 4.5) was applied for separating the different disturbance treatments on the basis of their overall species composition and cover.

An analysis of the monetary costs of the different treatments will be given as a cost analysis table for this experiment to see which treatment is the most cost-effective for the landowner.

4.3 Results

4.3.1 Species richness and diversity

A comparison of the four treatments at the end of the experiment indicates that there were no significant differences in species richness ($p > 0.05$, $F_{3, 8} = 1.8370$) between treatments. However, at the end of sampling period, species richness was lowest on the plots treated with herbicide and highest in the control treatment (Fig. 4.2).

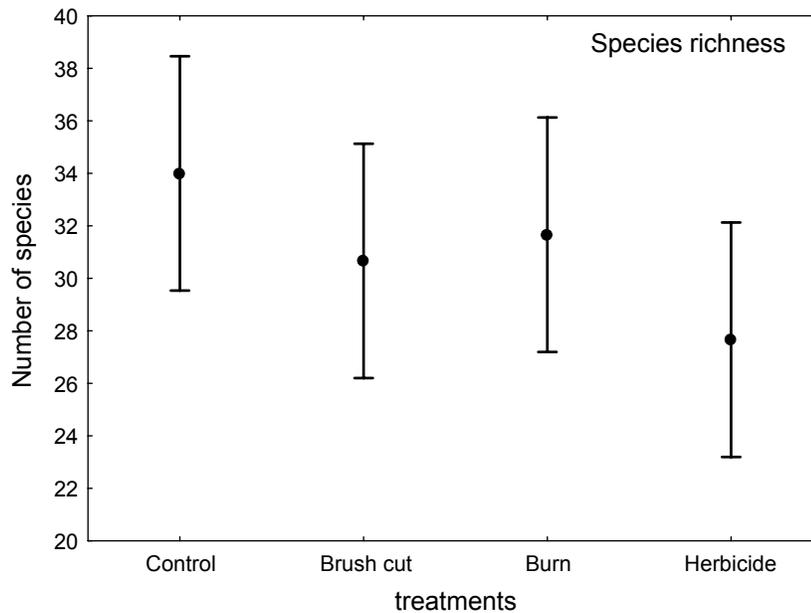


Figure 4.2: Effects of treatments on mean species richness at the end of the experiment. Vertical bars indicate SD.

Species diversity on the treatment plots did not follow the pattern of species richness (see table 4.1). Diversity, as calculated with the Shannon-Wiener diversity index (H), was highest in the burned plots, which was followed by the control plots. However, species diversity was found to be similar in the herbicide and brush cutting treatments.

Table 4.1: Shannon Diversity Index H, Variance of H and upper and lower 95% confidence intervals obtained by bootstrapping on the average of different treatments plots. Different letters indicate significant difference between treatments

Treatments	Shannon Diversity Index (H)	Variance H	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Control	2.6586 ^{ab}	0.0036	2.4960	2.7336
Burn	2.7912 ^a	0.0027	2.6411	2.8576
Brush cut	2.5804 ^b	0.0039	2.4106	2.6539
Herbicide	2.5046 ^b	0.0038	2.3416	2.5765

4.3.2 Cover by guild

4.3.2.1 Vegetation dynamics on different treatment plots

Changes in cover of the various components of the vegetation were plotted separately for the four different treatments throughout the sampling period (Fig. 4.3). Although some treatments reduced the cover of indigenous and alien grasses, these still dominated the vegetation after the trial. Vegetation cover followed a seasonal pattern.

In the control, cover of indigenous grasses decreased between May and July, and started increasing again in August. Cover increased rapidly between November and January, and stabilized thereafter (Fig. 4.3a). Alien grasses showed a decrease between May and August, however an increase was observed from August to October and stabilizing thereafter with a slight variation between January and March. The shrub species cover was almost stable throughout the sampling period, but a slight increase was observed between October and March. Other species showed a large increase from May to September. Rapid decrease was observed between September and October and cover then stabilized (Fig. 4.3a).

The pattern was different in the brush cutting treatment, where a large decrease in indigenous grass cover was observed from May to September. Cover increased again from September to March. Alien grass was only recorded from June and showed an increase in cover for this treatment. Shrub cover for this treatment showed a decrease from between May and October and a slight increase was observed between October 2003 and March 2004. Other species such as forbs, annuals, and bulbs showed the same pattern as in the control

treatment with an increase between May 2003 and September 2003, and decrease between September 2003 and October 2003 and stabilizes thereafter (Fig. 4.3b).

The scenario is similar in the burning treatment with small variation in indigenous grass cover between May 2003 and September 2003, and a cover increase from September 2003 to March 2004, which was followed by an increase of alien grasses (Fig. 4.3c). Shrub cover decreased between May 2003 and June 2003 and stabilized after that. Other species showed the same pattern as the previous treatment, with an increase in cover between May 2003 and September 2003, and a decrease between September 2003 and October 2003 and stabilization from then on (Fig. 4.3c).

In the herbicide treatment, great variation of indigenous grass cover was observed throughout the sampling period. A decrease of alien grass cover was recorded in this treatment between May 2003 and June 2003 and between September 2003 and March 2004. Shrub cover also decreased between May 2003 and July 2003, and stabilized afterwards. However, other species showed an increase in cover between May 2003 and September 2003 and a decrease was observed from September 2003 to October 2003. A slight increase of other species was observed again between October 2003 and February 2004 after dropping between February 2004 and March 2004 (Fig. 4.3d).

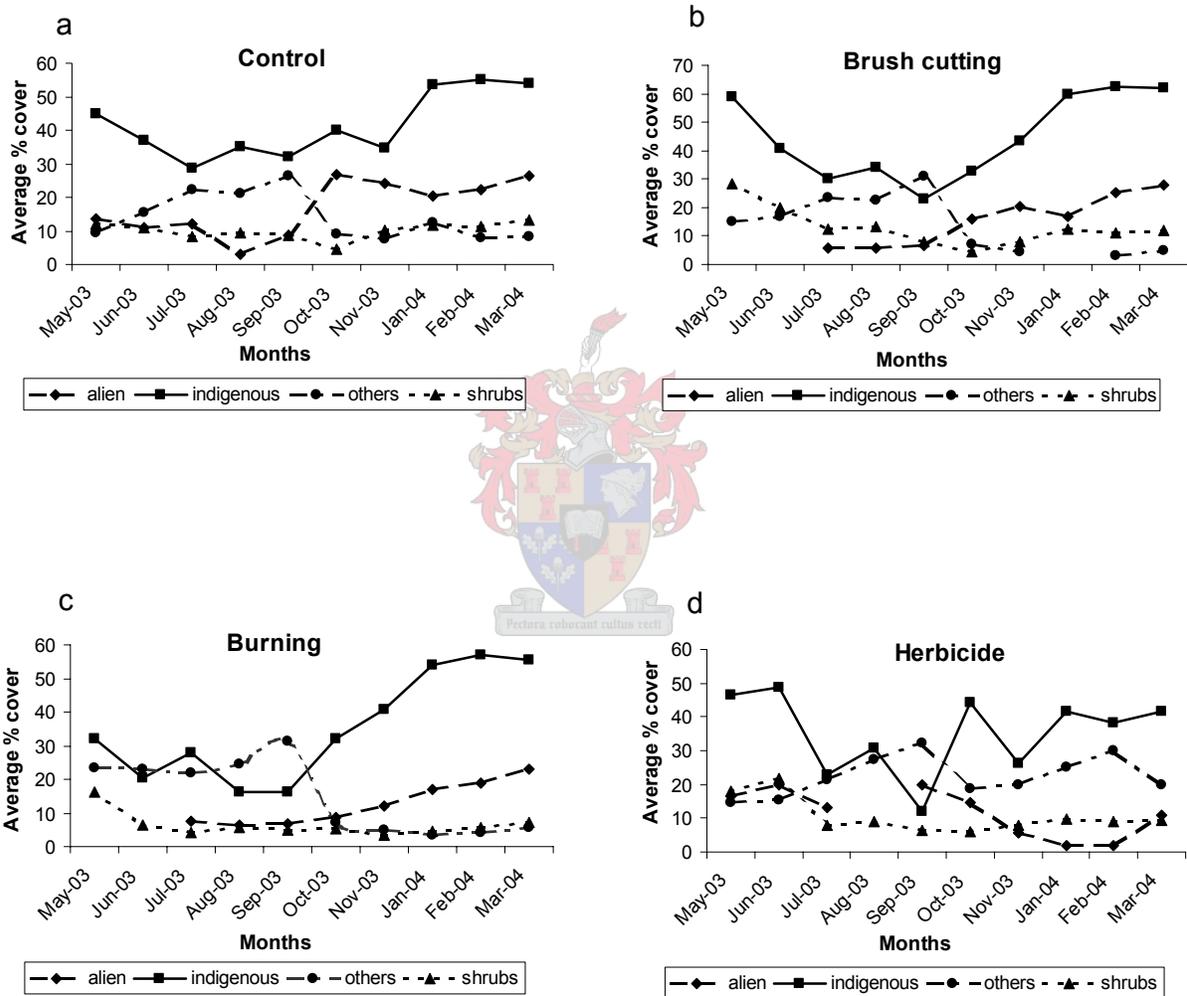
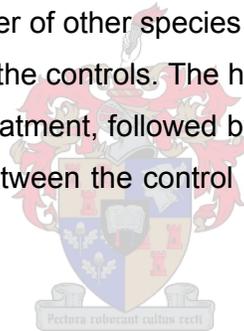


Figure 4.3: Changes in average percentage cover of, alien grasses, indigenous grasses, shrubs and other species in different treatment plots (Control, Brush cut, Burn and Herbicide) throughout the study period.

4.3.2.2 Response of cover to treatments

In March 2004 when the experiment was terminated; cover of indigenous grasses, was significantly greater in the brush cutting than the burn treatments ($p < 0.05$; $F_{3,8} = 4.8709$). Treatments had no significant effect on alien grass species cover (Fig. 4.4), but the highest alien species cover was recorded in the control treatment, followed by the brush cutting treatment. A lower alien grass cover was recorded in the herbicide and burn treatments but showed no significant difference ($p > 0.05$; $F_{3,8} = 2.4330$).

As the herbicide used targets grass species, cover of both alien and indigenous grass species were slightly lower in the herbicide treatment than for the other treatments. Shrub species cover was higher in the brush cutting, herbicide and control than in burning treatments. The lowest species cover for shrubs was recorded in the burn treatment. None of these differences were significant ($p > 0.05$; $F_{3,8} = 0.7772$). The cover of other species (forbs and geophytes) was higher in the disturbed plots than in the controls. The highest cover of these species was recorded for the herbicide treatment, followed by the burn treatment. A significant difference was only found between the control and the herbicide treatments ($p < 0.001$; $F_{3,8} = 8.6005$).



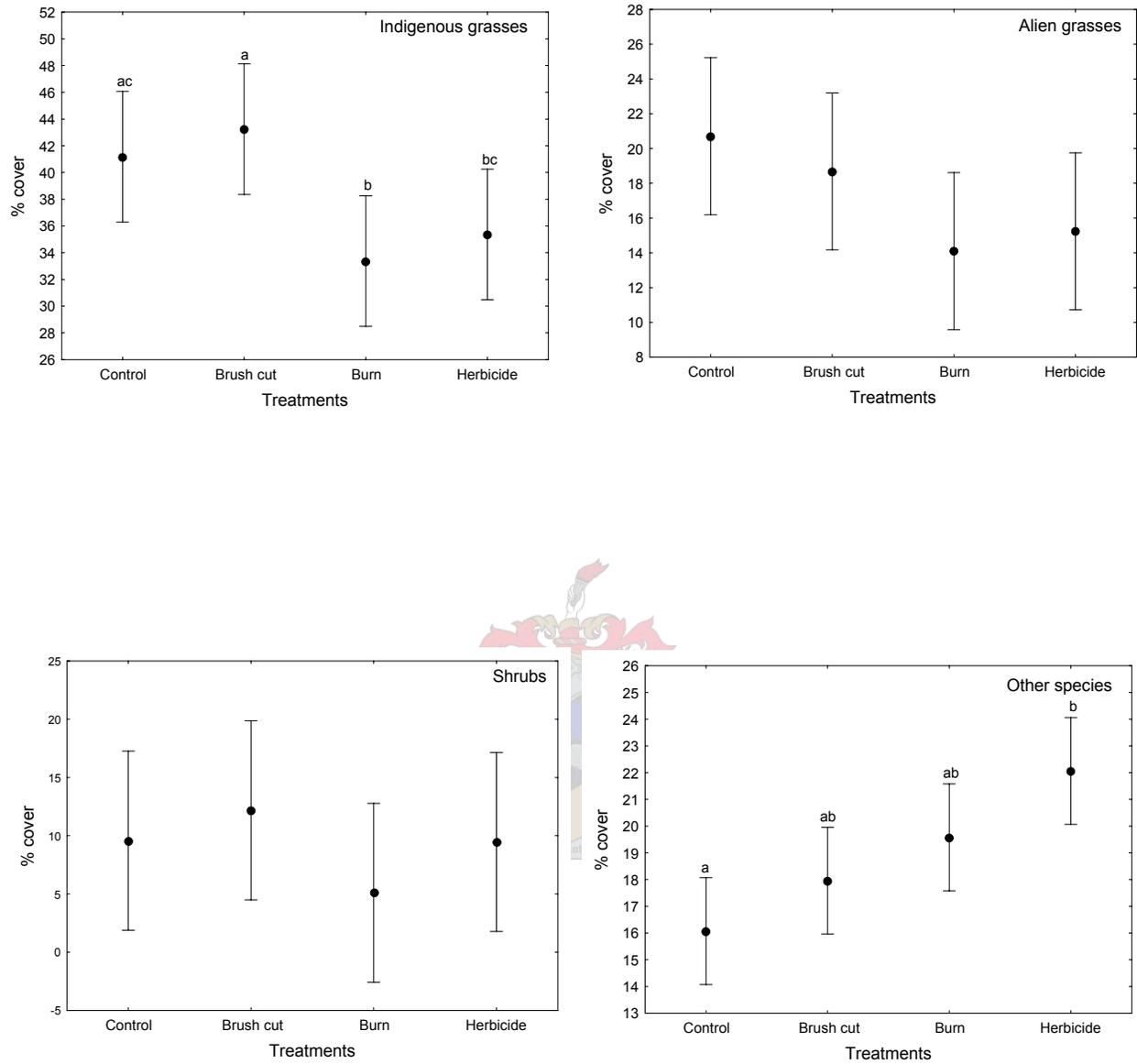
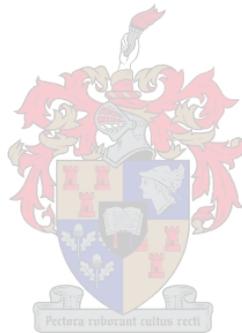


Figure 4.4 Effect of control, brush cutting, burn and herbicide treatments on the average percentage cover at the end of treatments for the four species groups. Different letters indicated significant differences between treatments.

4.3.2.3 Proportional cover by guild

The proportion of indigenous grass cover versus total cover did not differ significantly among treatments ($p > 0.05$; $F_{3,8} = 0.3899$). The proportion of cover of alien grass versus total cover appeared greatest in the control treatment, but the use of Scheffé post-hoc test revealed no significant difference between those two treatments (Fig. 4.5). Shrub cover appeared lower in the burn treatment, but the difference was not significant. The proportion of other species was high in the burn and herbicide treatments and lower in the control and brush cutting treatments. A significant difference was found between treatments ($p < 0.001$; $F_{3,8} = 42.749$). No significant difference in the ratio of alien to indigenous grass cover was found among treatments ($p > 0.05$; $F_{3,8} = 0.38560$).



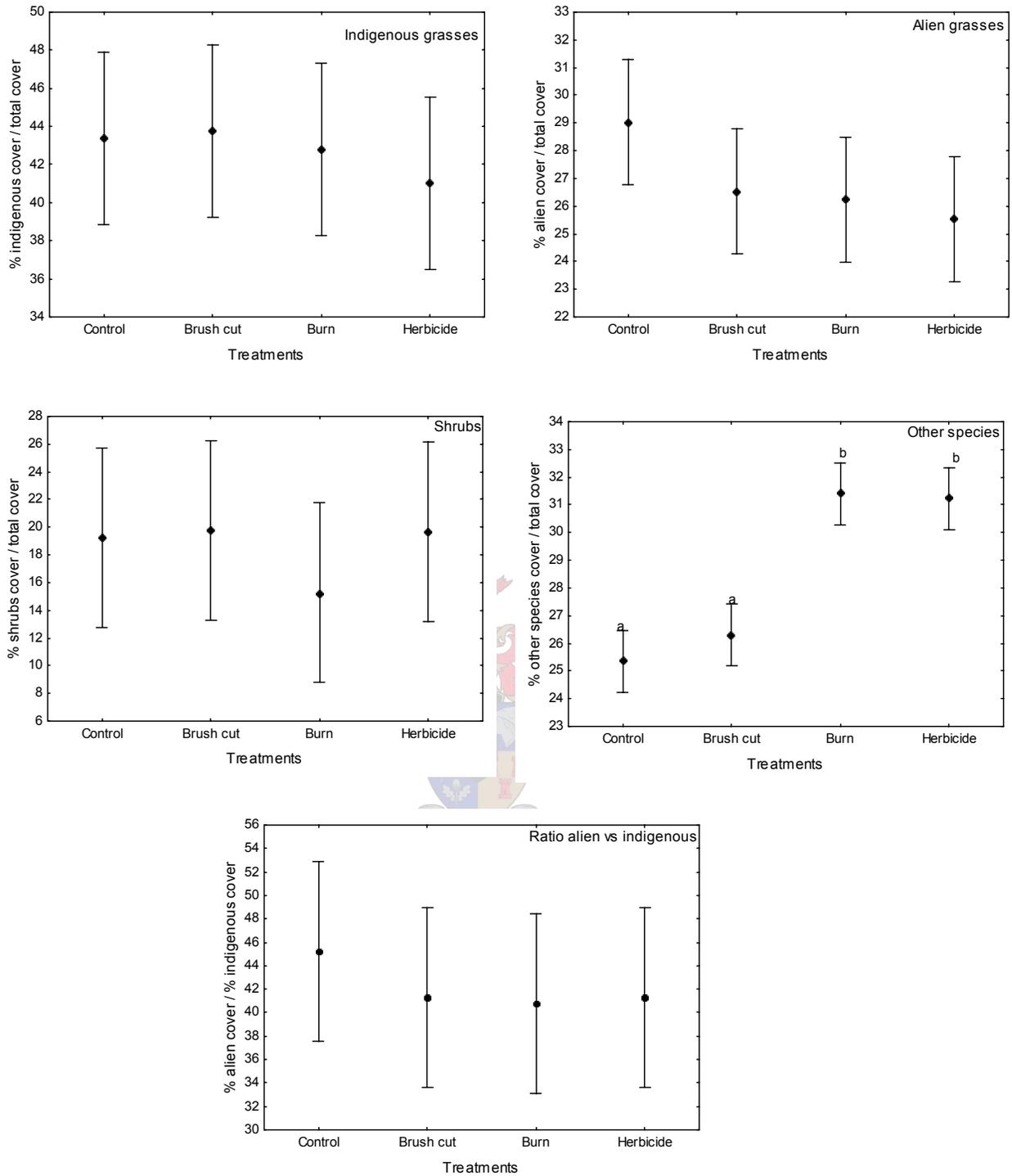


Figure 4.5: Effect of treatments on the proportion of the four different species groups. Different letters indicate significant differences between treatments revealed by Scheffe post-hoc tests.

4.3.3 Reseeding experiment

Seed viability

Seed viability was tested separately for the two species in the nursery. For *E. africanus*, of 120 seeds planted only 15 seedlings germinated. For *E. calycina*, 380 seeds were planted and 280 seedlings germinated. Therefore, 12.5% of the seeds germinated for *E. africana*, and for *E. calycina*, 73.68% of the seeds planted germinated.

Eriocephalus africanus

Recruitment of *E. africanus* was observed in all four treatments, but the emergence of seeds varied greatly among treatments. Seedling emergence was observed five months after sowing in all plots, seedlings were marked with tags to avoid double counting and to distinguish new recruitment (Fig. 4.6). No rain fall data were available in that period. In the control, the recruitment was observed from October 2003 throughout March 2004, but only two size classes were found. The brush cutting treatment showed the lowest recruitment and no recruitment was observed for this treatment after November 2004. The burning and herbicide treatments had more recruitment after sowing. The recruitment took place from October 2003 throughout the study period; all the size classes were represented in these two treatments. However, the herbicide treatment showed the best recruitment with more individuals from October 2003 until March 2004 when the sampling ended (Fig. 4.6).

Ehrharta calycina

No seedling emergence was recorded in the herbicide treatment. For the other treatments, the germination took place in June with the highest recruitment observed in the burn treatment. In this treatment, more individuals of small size classes were found than in the other treatments. The brush cutting treatment had the second highest recruitment after the burning treatment, but only with few individuals for most of the size classes. Almost all seedlings died after the October data collection (Fig. 4.7).

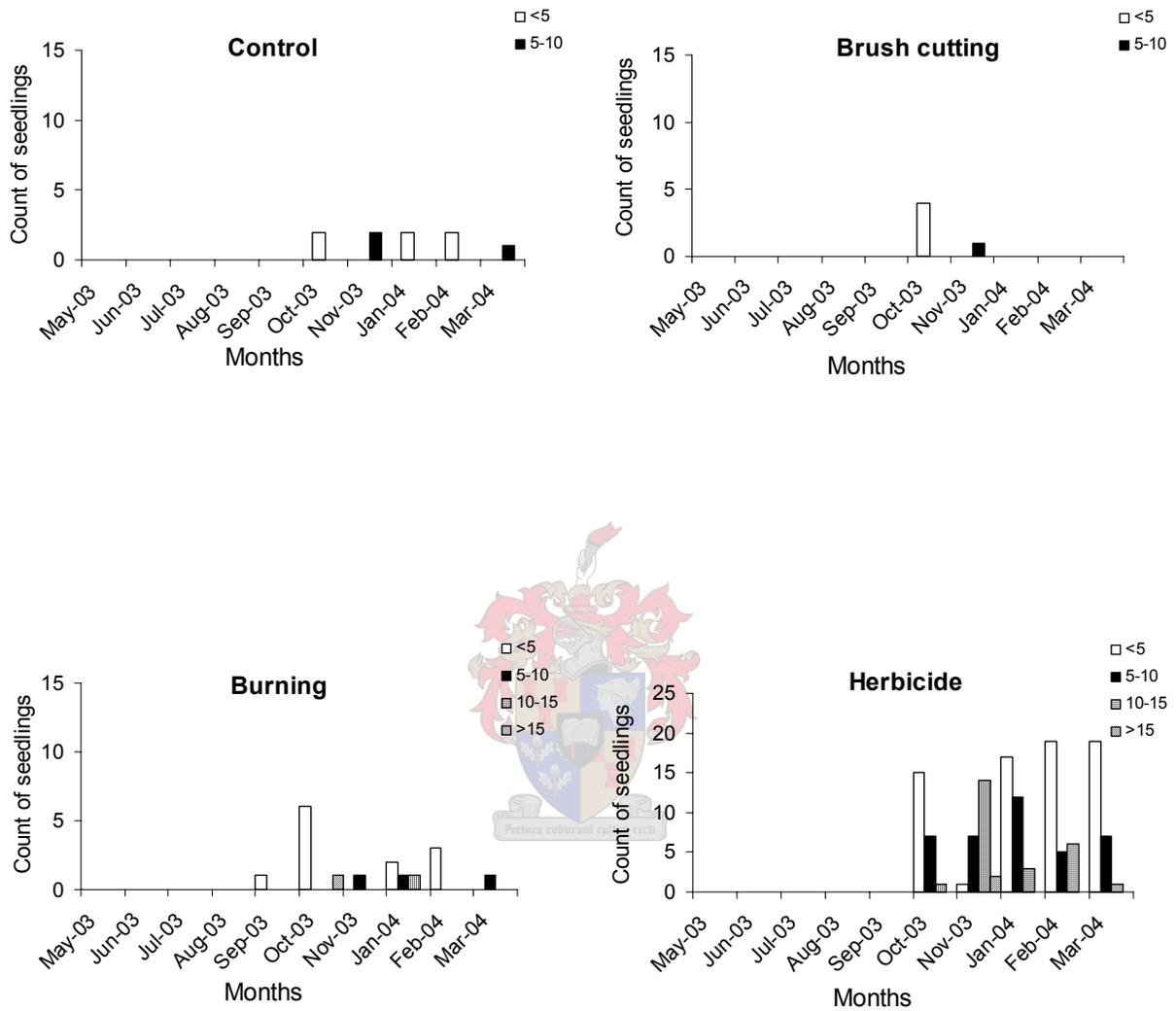


Figure 4.6: Monthly size class distribution of *E. africanus* in the Control, Brush Cutting, Burning and Herbicide treatments. Size classes (open, solid and shaded bars) are given in cm.

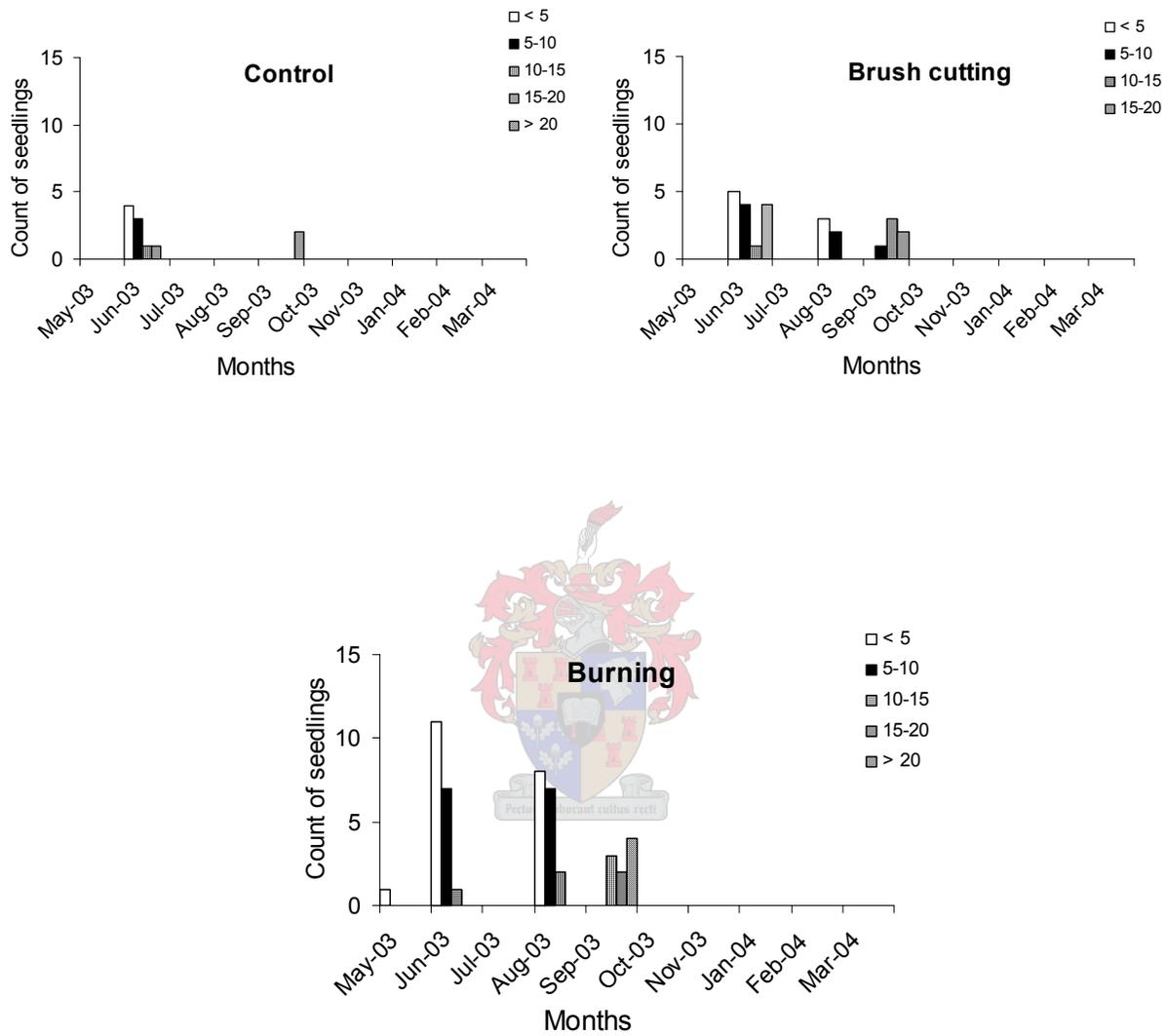


Figure 4.7: Monthly size class distribution of *E. calycina* in the Control, Brush cutting and Burning treatments. No seedlings germinated in the herbicide treatment. Size classes (open, solid and shaded bars) are given in cm.

4.3.3.1 Cover abundance of sown species (*Ehrharta calycina* and *Eriosephalus africanus*)

Eriosephalus africanus

After sowing the highest cover of *E.africanus* was recorded in herbicide treatment, followed by the burning and control treatments. The brush cutting treatment showed the lowest *E. africanus* cover. However, for *E. africanus* a high cover was recorded in January in all the treatments compared to other months.

Ehrharta calycina

Low cover of *E. calycina* was recorded after sowing throughout the sampling period in all the treatments. The highest cover of *E. calycina* was recorded in the burning and brush cutting treatments, with the control treatment showing the lowest *E. calycina* cover. June seemed to be the best months for *E. calycina* recruitment.

An interesting pattern was found in the burning treatment, which is not present in other treatments. In the burning treatment both species are well represented and, both *E. calycina* and *E. africanus* germinated one month earlier than in the other treatments. *E. calycina* seedlings were recorded from May and *E. africanus* from September (Fig. 4.8).



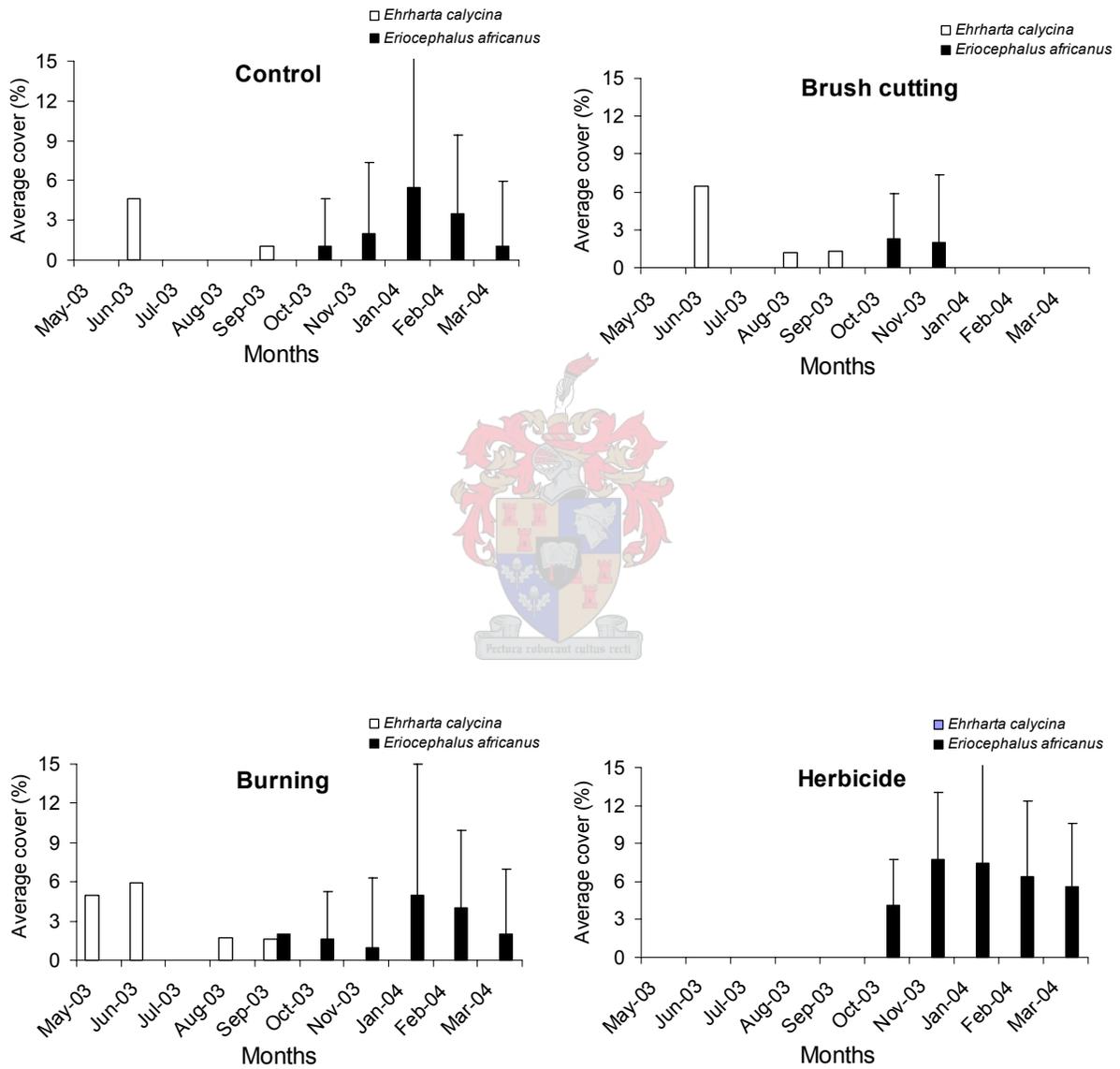


Figure 4.8: The effect of treatments on the projected canopy cover of *E. calycina* and *E. africanus*, throughout the sampling period

4.3.4 Plant community responses to disturbance treatments

DCA (Detrended Correspondence Analysis) results of the CANOCO (Canonical Community Ordination) separated plant species and their cover between the four different treatments that they naturally colonized (Fig. 4.9). Interesting is that herbicide plots were grouped more closely together than the plots of the other treatments. A clear separation could be seen between herbicide (H) treatments and the burning (B), brush cutting (Bc) and control (C) treatments. The burning and brush cutting treatments were much more similar. While the control plots also group, the similarities between them are not as big as between the herbicide plots. The DCA species data produced eigenvalues (measure the importance for each of the axes) of 0.146; 0.0038; 0.008; 0.003 for the first four axes. The sum of all the eigenvalues was 0.436.

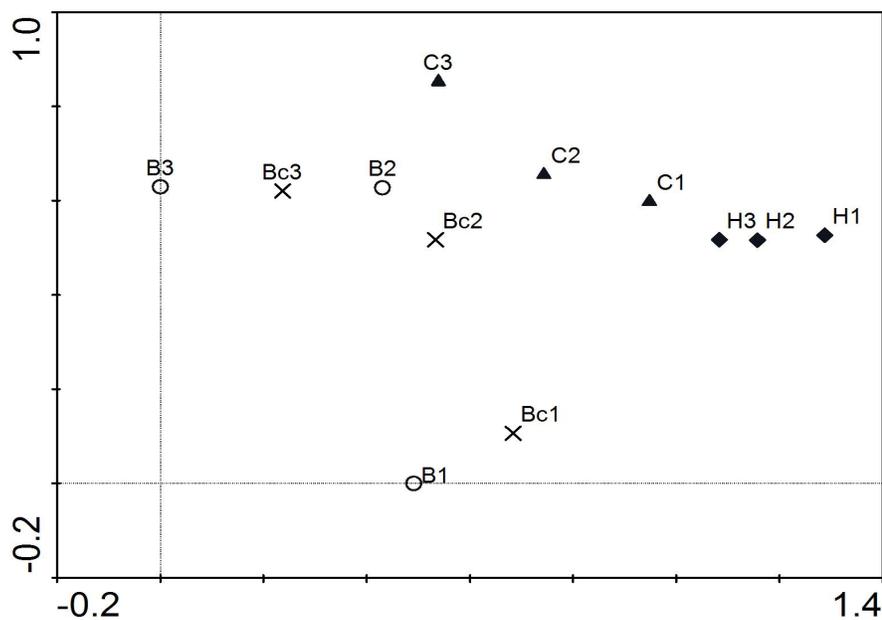
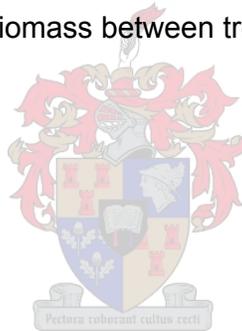


Figure 4.9: Detrended Correspondence Analysis (DCA) for the cover of the plant species in the four different treatment plots (CANOCO 4.5 (Software, 2004)) (C: Control; Bc: Brush cutting; B: Burning; H: Herbicide). Axes eigenvalues: 0.146; 0.0038; 0.008; 0.003.

4.3.5 Soil bioassay

To determine whether the soil quality was affected by herbicide, radish (*Raphanus sativus*) and wheat grass (*Triticum aestivum*) were selected as indicators of soil toxicity in bioassays. The highest radish leaf biomass was recorded in soil from unploughed natural vegetation followed by the burn and herbicide treatments (Fig. 4.10). The lowest leaf biomass was recorded in the soil from the control (unmanipulated old field) and brush cutting treatments. A significant difference between treatments on the leaf biomass was only recorded between natural vegetation and control ($p < 0.001$; $F_{4, 10} = 8.1129$) and between the natural vegetation and brush cutting treatments ($p < 0.05$; $F_{4, 10} = 8.1129$).

Root biomass and the ratio of above- to below-ground biomass did not differ significantly among treatments (Scheffè post-hoc test). Wheat leaf biomass showed the same pattern as the radish (Fig. 4.10), except that no significant difference was found in leaf biomass between treatments.



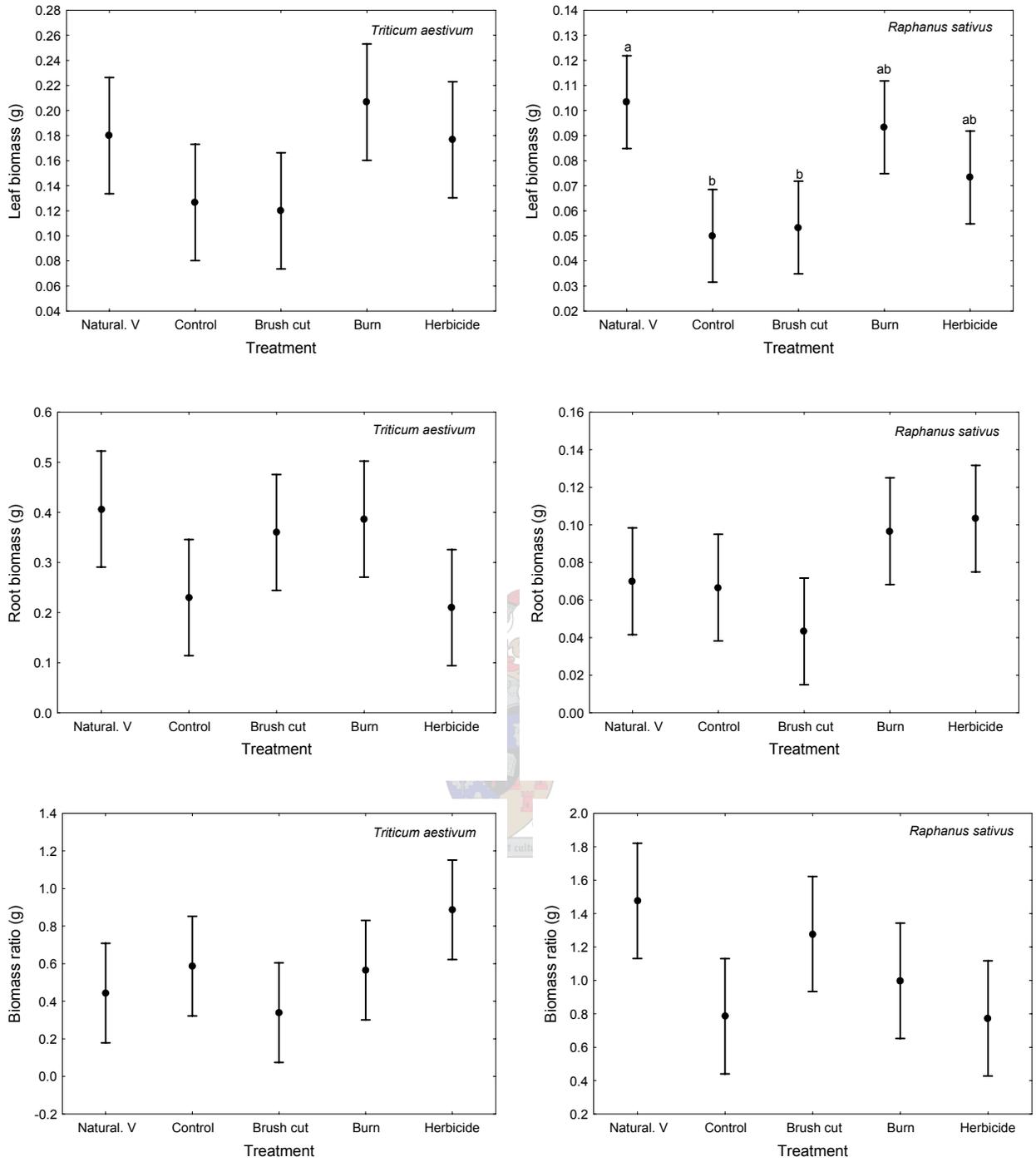


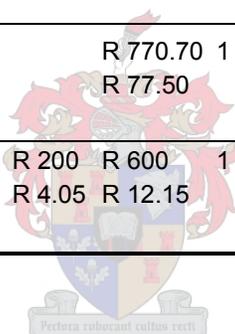
Figure 4.10: Mean leaf and root dry mass, and leaf:root biomass ratios obtained in a bioassay testing the effect of herbicide on biomass of *Triticum aestivum* (wheat grass) and *Raphanus sativus* (radish). Letters indicated significant differences between treatments. Vertical bars indicate SD.

4.3.6 Cost analysis of the four different treatments

A total area of 80 m² was used for each treatment plot, thus a total area of 240 m² (80m² x 3) for each treatment (0.0240 ha). The burning treatment was found to be the most expensive (R 1022.15), followed by the herbicide treatment (R 866.2). The cheapest was the brush cutting treatment (R630.15) see table below.

Table 4.2: Approximation of the budget spent for the experiment. The cost information of hire equipment per hour and labour per hour was obtained from the farm managers (Mike Gregor, *pers.comm* and Bernard Wooding, *pers.comm*).

Treatments		Equipments			Labour				
	Type	Hours	Hire/h	Cost	Persons	Hours	Hire/h	Cost	Total cost
Burning	Tractor for fire break	4	R 200	R 800	7	5	R 6	R 210	R 1010
	Petrol	3L	R 4.05	R 12.15					R 12.15
	Total cost / ha								R 42,589.58
Herbicide	Gallant super	25L		R 770.70	1	3	R 6	R 18	R 794.70
	Buffer	5L		R 77.50					R 77.50
Total cost / ha									R 36,091.66
Brush cut	Tractor	3	R 200	R 600	1	3	R 6	R 18	R 618
	Petrol	3L	R 4.05	R 12.15					R 12.15
Total cost / ha									R 26,256.25



4.4 Discussion

This study was conducted to assess the suitability of three treatments (brush cutting, burning, and herbicide application) to facilitate the restoration of Renosterveld on an abandoned agricultural field. This was done by examining plant species recruitment and community composition (diversity and richness) on a monthly basis after treatment. Diversity takes into account two factors: species richness i.e. number of species) and evenness (i.e. equal distribution of abundances) (Magurran, 1998). The higher the number of species and their evenness in an assemblage, the higher is the species diversity (Krebs, 1989; Margurran, 1998). No significant difference in species richness was found between treatments. Species diversity as calculated with the Shannon-Wiener Diversity Index is somewhat similar to the pattern of species richness, but diversity was highest in the burning treatment and lowest in the herbicide treatment.

Our results did not comply with the predictions of the intermediate disturbance hypothesis in that the least disturbed (control) and the most disturbed (herbicide) treatments did not have significantly lower diversity or species richness than the intermediate disturbance treatments (mow and burn). Possible reasons for this are that we had too few replicates, that the duration of the study was too short, or that the control (grazed old field) was continually subjected to an intermediate level of disturbance, and all additional disturbances simply reduced diversity.

A large number of studies have reported positive effects of burning on species richness of mature vegetation (Thanos and Rundel, 1995; Tyler, 1995; Bond and Wilgen, 1996; Benwell, 1998; Irene *et al.*, 2000). In our study, diversity, but not species richness was higher in the burn treatment than in the mowed and herbicide plots. This might be because the main difference between these treatments is that burning adds nutrients to the soil, mainly nitrogen (De Bano and Conrad, 1978; Kutiel and Kutiel, 1989), which is available to the species present. Therefore, the post-fire environment provides opportunities for successful recruitment (Holmes and Richardson, 1999).

In addition, burning might open up additional niches allowing colonisation of new species into the area (Scott, 1986). In this study, fire increased seedling emergence more than brush cutting and herbicide.

4.4.1 Response of species group cover to treatments

Species groups differed in their response to the different treatments while, the burning and herbicide treatments reduced both indigenous and alien grass cover, only the results for indigenous grasses were significant. In contrast, to the previous treatments, brush cutting increased grass cover. Many studies have shown the negative impact of grasses, particularly alien grasses on the regeneration of other types of plants (Macdonald *et al.*, 1988; Richardson *et al.*, 2004), as they interfere with growth and survival of seedlings of forbs and woody plant species in most of the grassland areas (Davies, 1985 and this study). The presence of alien species may alter the usual secondary succession in old-field grasslands following grazing removal (Tremmel and Peterson, 1983; Fike and Niering, 1999), as their superior competitive ability (Clay, 1990; Bacon, 1995; Clay and Holah, 1999; Matthews and Clay, 2001) may lead to dominance of alien grasses in native and old-field grassland and thereby alter species composition (Clay and Holah, 1999) and nutrient cycling (Gay *et al.*, 1996). Treatments that reduce grass cover might thus enable recruitment of shrubby species.

The group “other species” (including forbs and geophytes) responded with an increase in cover under all disturbances. Cover of these species was highest in the herbicide treatment, followed by burning and brush cutting treatments, and was lowest in the control. This increase in cover might be due the presence of open space for colonists after burning and herbicide application (Collins, 1987), which favoured the appearance of mainly annual herbaceous species. The same has also been noted by Willson (1992). Immediately after perturbation such as burning and herbicide application, resprouting species mobilise stored carbohydrates and possibly also metabolised water in the roots (Bock and Bock, 1992). In general, annual species responded more positively to disturbances than perennial species; and short perennials responded more positively than tall perennials (Belsky, 1992). Milton (1995) documented in the Succulent Karoo that density of annual plants increased in plots cleared of shrubs, compared to surrounding undisturbed vegetation. Disturbance has been shown to reduce the

intensity of competition for limiting resources (Wilson and Tilman, 1993). The predominance of short-statured species in the disturbance plots suggests that these species were reacting as much to an absence of competition for light, as to the physical and chemical changes usually associated with disturbances (Petraitis *et al.*, 1989).

The use of fire and herbicide on old fields in Renosterveld resulted in an increased abundance of annuals, forbs, geophytes and a reduction in annual alien grass cover in the old field Renosterveld EPNR.

4.4.2 Sown species

Recruitment of the sown grass and shrub species occurred throughout the sampling period, although on rather lower levels. In general, recruitment of the shrub (*E. africanus*) was higher in all treatments than that of the grass (*E. calycina*). The species had different germination periods, and germination of both species might have been delayed due to late winter rains in 2003. *E. africanus* prefers full sun and well-drained soils, and recruits best if planted during the wet winter months so that the plants can establish themselves before the dry summer (Goldblatt and Manning, 2000).

The highest seedling recruitment and cover of *E. africanus*, was observed in the herbicide treatment. This could be related to improved moisture conditions and nutrients in herbicide plots created by the grass mulch. The herbicide killed grass species slowly, and dead grasses formed mulch that conserved moisture on the soil surface. The dead grass may also have released nutrients to the soil, resulting in high *E. africanus* seedling recruitment and cover. The second possible reason could be the low grass competition favouring the establishment and growth of the shrub *E. africanus*.

The second highest recruitment of *E. africanus* was recorded in the burning treatment, but only with a few large individuals (> 15 cm) survived until the end of the experiment. In this treatment, fire added more nutrients to the soil and also opened up space. The burn initially had low grass cover, so that there were niches for the shrubs to establish, but later on, when the grass recovered, there was again competition for the shrub seedlings, and thus the lower growth rate.

For *E. calycina*, the highest recruitment and cover was observed in the burning treatment, followed by the brush cutting treatments. Some seedlings were recorded in the control treatment, but none in herbicide treatments. After the fire, free space for germination is available (Collins *et al.*, 1998), as competition by other (grass) species is reduced, and nutrients are released after fire for at least a short period (Van Wilgen and Le Maitre, 1981; Brown and Mitchell, 1986; Stock and Lewis, 1986), facilitating the establishment of seedlings. Brush cutting also reduces competition and creates niches for seedling establishment. The higher recruitment in the brush cutting treatment might also be due to seed morphology. Seeds of *E. calycina* might come directly in contact with soil surface while seeds of *E. africanus* might be caught by grass and litter left after the cutting, thus reducing germination and seedling growth.

As expected, no *E. calycina* seedlings were recorded in the herbicide treatment, probably because of a residual effect of the selective grass herbicide. The herbicide targets grass seeds, presumably preventing germination. This might be circumvented by sowing not directly after herbicide application, but waiting until the herbicide has degraded and the effects lessened. In all treatments, all seedlings died after September, either due to the late winter rain, or due to an annual ecotype, as in some regions, *E. calycina* ecotypes are annual (Goldblatt and Manning, 2000).

4.4.3 Soil bioassay

To determine the long-term effect of herbicide applied to the soil, radish (*Raphanus sativus*) was used as bioassay to assess the phytotoxicity of the soil (Simone and Barry, 2003; Francisco and Wilfried, 2003). In addition, wheat grass (*Tritium aestivum*) was chosen for the bioassay, as the herbicide used targets grass species. Herbicide-treated soils had no significant effect on biomass production of either radish or wheat grass. Results of this soil bioassay therefore indicated that the use of herbicide did not affect the soil quality one year after application. Nevertheless, the test needs to be conducted shortly after herbicide application and at regular time intervals thereafter to judge the effect of the herbicide on soil quality.

4.4.4 Cost analysis

Of all treatments, burning needed the most equipment, labour and time. It was thus found to be the most expensive treatment. The second most expensive treatment was the herbicide treatment, and brush cutting was recorded as the cheapest, as the brush cutting treatment and herbicide treatment needed less labour and equipment. The costs of clearing terrestrial alien invasive plants vary widely among biomes and among species in South Africa. For example, established stands of big trees (such as wattle, pine and eucalypt) all cost Working for Water Program R6,000/ha to clear if stands are dense, whilst a low biomass cover (such as *Rubus*, *Lantana*, *Solanum*) cost around about R1,200/ha (Versfeld *et al.*, 1998). Our results are largely more expensive than the figures given by Versfeld *et al.* (1998) and also beyond the reach of the budget of nature conservation authorities (Versfeld *et al.*, 1998). This is might be due to the nature of the problem, labour costs, and methods used. Our cost results are similar to those estimated by Holmes (2002) who found that re-establishment of indigenous Renosterveld in abandoned cultivated lands by planting, was ten times more expensive than sowing (R173,690/ha and R17,646/ha).

4.4.5 Conclusion

Grass species cover (indigenous and alien) was reduced by the herbicide and burning treatments. However, the brush cutting seems to favour grass establishment. Herbicide treatment seems to increase the shrub cover and also favour significant recruitment of other species on the old field, if a herbicide that kills only grasses is used. Low recruitment was obtained for both sown species in all treatments, however, herbicide and burning treatment seems to be favourable for *E. africanus* recruitment. The recruitment of *E. calycina* was also favoured by the burning treatment. One year after application, the herbicide did not have negative effects on the soil quality. Among the four treatments the brush cutting treatment was found to be the cheapest.

The herbicide and burning treatments seem to be the best method for for promoting seedling recruitment from sown seeds and for the reduction of grass biomass. The herbicide treatment best reduces the grass competition and facilitates the establishment of shrubs, it also resulted in high species richness,

but lower species diversity. This treatment used less equipment and is also most cost effective for the farmer. Our results agreed with those from Cione *et al.*, (2002) who controlled alien grass invasion by the use of herbicide to facilitate the restoration of Californian sage scrub, a Mediterranean shrubland. Above all, we must be careful in evaluating the management technique used for restoration of natural Renosterveld vegetation, as long-term responses are not investigated in this study. Therefore, long-term monitoring of the treatment plots is necessary, as this might reveal further response to the treatment or the necessity for further management.

4.4.6 References

- Bacon, C.W. 1995. Toxic endophyte-infected tall fescue and range grasses: historic perspectives. *Journal of Animal Science* **73**: 861-870.
- Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* **3**: 187-200.
- Benwell, A.S. 1998. Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany* **46**: 75-101.
- Signal, E.M., and McCracken, D.I. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* **33**: 413-424
- Bock, J.H., and Bock, C.E. 1992. Vegetation responses to wildfire in native versus exotic Arizona grassland. *Journal of Vegetation Science* **3**: 439-446.
- Bond, W.J., and Van Wilgen, B.W. 1996. Fire and plants. Chapman and Hall, London.
- Brown, G., and Mitchell, D.T. 1986. Influence of fire on soil phosphorus status in sand plain lowland fynbos, South-western Cape. *South African Journal of Botany* **52**: 67-72.
- Cione, N.K., Padgett, P.E., and Allen, E.B. 2002. Restoration of native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology* **10**: 376-384.

- Clay, K. 1990. Comparative demography of three graminoides infected by systemic, clavicipitaceous fungi. *Ecology* **71**: 558-570.
- Clay, K., and Holah, J. 1999. Fungal endophyte symbiosis and plant diversity in successional fields. *Science* **285**: 1742-1744.
- Clemente, A.S., Werner, C., Máguas, C., Cabral, M.S., Martins-Louçao, M.A., and Correia, O. 2004. Restoration of a Limestone Quarry: Effect of soil amendments on the establishment of native Mediterranean *Sclerophyllous Shrubs*. *Restoration Ecology* **12** (1): 20-28.
- Collins, S.L. 1987. Interaction of disturbances in tallgrass prairies: a field experiment. *Ecology* **68**: 1243-1250.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., and Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tall grass prairie. *Science* **280**: 745-747.
- Davies, R.J. 1985. The importance of weed control and use of tree shelters for establishing broadleaved trees on grass-dominated sites in England. *Forestry* **58**: 167-180.
- De Bano, L.F., and Conrad, C.E. 1978. The effect of fire on nutrients in a chaparral ecosystem. *Ecology* **59**: 489-497.
- Dobson, A.P., Bradshaw, A.D., Baker, A.J.M. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**: 515-522.
- Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agriculture, Ecosystems and Environment* **62**: 81-91.
- Fairbanks D.H.K., Hughes, C.J., and Turpie, J.K. 2004. Potential impact of viticulture expansion on habitat types in the Cape Floristic Region, South Africa. *Biodiversity and Conservation* **13**:1075-1100.
- Fike, J., and Niering, W.A. 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. *Journal of Vegetation Science* **10**: 483-492.
- Francisco, J.S., and Wilfried, E.R. 2003. Maize and Raddish sequester excess cadmium and zinc in difference ways. *Plant Science* **165** (5): 1009-1022.
- Gay, D.L., Allen, E.R., Engle, D.M., and Strizke, J.F. 1996. Nitrate dynamics following brush control in a post oak-blackjack oak forest. *Agronomy Journal* **88**: 536-540.

- Goedmakers, A. 1989. Ecological perspectives of changing agriculture land use in European community. *Agriculture, ecosystems and environment* **27**: 99-106.
- Goldblatt, P., and Manning, J.C. 2000. Cape Plants. National Botanical Institute, Cape Town.
- Henderson, P.A. and Seaby, R.M.H. 2001. Species Diversity and Richness version 2.65. PISCES conservation Ltd, Lymington, UK.
- Hobbs, R.J., and Harris, J.A. 2000. Restoration ecology: repairing the Earth's ecosystems in the new millennium. *Restoration Ecology* **9**: 239-246.
- Hobbs, R.J., and Norton, D.A. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* **4**: 93-110.
- Holmes, P.M. 2002. Renosterveld Restoration on Cultivated Lands at Eerste River, Western Cape: Preliminary Findings of Pilot Study. Report to large quarries, Cape Ecological Services, 23 Dreyersdal Road, Bergvliet, 7945.
- Holmes, P.M., and Richardson, D.M. 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African Fynbos. *Restoration Ecology* **7**(3): 215-230.
- Irene, C.W., Michael, L.R., Linda, O., and Avi, S. 2000. *Evolutionary Ecology Research* **2**: 935-955.
- Klotzli, F., and Grootjans, A.P. 2001. Restoration of natural and semi-natural wetland systems in Central Europe: progress and predictability of developments. *Restoration Ecology* **9**: 209-219.
- Krebs, C.J. 1989. Ecological methodology. Harper and Row publishers, New York.
- Kutiel, P., and Kutiel, H. 1989. Effects of a wildlife on soil nutrients and vegetation in Aleppo pine forest on Mount Carmel. Israel. *Pirineos* **134**: 59-74.
- Low, A.B., and Rebelo, A.G. 1998. Vegetation of South Africa, Lesotho and Swaziland. Pretoria: Department of Environmental Affairs and Tourism, Pretoria.
- Macdonald, I.A.W., Graber, D.M., DeBeneditti, S., Groves, R.H., and Fuenles, E.R. 1988. Introduced species in nature reserves in Mediterranean climatic regions of the world. *Biological Conservation* **44**: 37-66.

- Magurran, A.E. 1988. Ecological diversity and its measurement. London, Croom Helm.
- Matthews, J.W., and Clay, K. 2001. Influence of fungal endointeractions. *Ecology* **82**: 500-509.
- Mike, G. (pers.comm.). Elandsberg Farm, PO Box 38, Hermon.
- Milton, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karro shrubland. *Journal of Applied Ecology* **32**: 145-156.
- Petraitis, P.S., Latham, R.E., and Niesenbaum, R.A. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64**: 393-418.
- Richardson, D.M., Rouget, M., Henderson, L., Nel, J.L. 2004. Invasive alien plants in South Africa: macroecological patterns, with special emphasis on the Cape Floristic Region. *Proceedings of the 10th international conference on Mediterranean Climate Ecosystems, MEDECOS*, Rhodes, Greece, pp:132.
- Scott, J.M. 1986. The effects of grazing on the alpha diversity of West Coast Renosterveld at the farm Eensaamheid. Botany Department, University of Cape Town, South Africa.
- Simone, J.L., and Barry, R.T. 2003. Effect of pulp mill solids and three composts on early growth tomatoes. *Bioresource Technology* **89** (3): 297-305.
- Solow, A.R. 1993. A simple test for change in community structure. *Journal of Animal Ecology* **62**: 191-193.
- StatSoft, Inc. (2003). STATISTICA (data analysis software system), version 6. www.statsoft.com.
- Stock, W.D., and Lewis, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralising agent in a South African coastal fynbos ecosystem. *Journal of Ecology* **74**: 317-328.
- Thanos, C.A., and Rundel, P.W. 1995. Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* **83**: 207-216.
- Tremmel, D.C., and Peterson, K.M. 1983. Competitive subordination of a Piedmont old field successional dominant by an introduced species. *American Journal of Botany* **70**: 1125-1132.

- Tyler, C.M. 1995. Factors contributing to post-fire seeding establishment in chaparral: direct and indirect effect of fire. *Journal of Ecology* **83**: 1009-1020.
- Van Wilgen, B.W., and Le Maitre, D.C. 1981. Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *South Africa Forestry Journal* **119**: 24-28.
- Van der Putten, W.H., Mortimer, S.R., Hedlund, K., Van Dijk, C., Brown, V.K., Leps, J., Rodriguez-Barrueco, C., Roy, J., Len, T.A.D., Gormsen, D. Korthals, G.W., Lavorel, S., Regina, I.S., and Smilauer, P. 2000. Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* **124**: 91-99.
- Versfeld, B.D., le Maitre, D.C., and Chapman, R.A. 1998. Alien plant species and water resources in South Africa – a preliminary assessment. WRC report TT99/98, CSIR, Pretoria.
- Von Hase, A., Rouget, M., Maze, K., Helme, N., 2003. A Fine-Scale Conservation Plan for the Cape Lowlands Renosterveld: Technical Report. Cape Conservation Unit, Botanical Society, Cape Town.
- Willson, M.F. 1992. The ecology of seed dispersal. In: Fenner, M. (ed), seeds: *The ecology of regeneration in plant communities*. CAB International, Oxford, UK, PP: 61-85.
- Wilson, S.D., and Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* **74**: 599-611.
- Wooding, B. (pers.comm.) Elandsberg Farms, PO Box 38, Hermon.
- Zar, J.H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, London, UK.
- Zedler, J.B. 2000. Progress in wetland restoration ecology. *Trends Ecology and Evolution*. **15** 402-407.

Chapter 5: Discussion and Conclusion

5.1 General discussion

Changes in land use, habitat fragmentation, nutrient enrichment, and environmental stress often affect species richness and diversity in many ecosystems (Chapin *et al.*, 1997; Vitousek *et al.*, 1997). There is increasing interest in developing better predictive tools and a broader conceptual framework to guide the restoration of degraded lands. Traditionally, restoration efforts have focused on re-establishing historical disturbance regimes or abiotic conditions (physical and climatic environments), relying on successional processes to guide the recovery of biotic communities. However, strong feedbacks between biotic factors and the physical environment can alter the efficacy of these successional-based management efforts. Successful restoration can be a slow and difficult process, particularly in landscapes where competition from non-native invasive plants or mammalian herbivory produces high seedling mortality (Parker and Salzman, 1985; Bonser and Reader, 1995; Parmesan, 2000; Van der Wal *et al.*, 2000). Our aim was to determine which ecological factors and processes influence shrub establishment on old lands in Renosterveld, and to evaluate some technologies to help the farmers who wish to facilitate the restoration of their transformed areas.

An abandoned old-field in West Coast Renosterveld was chosen for restoration. West Coast Renosterveld is one of the three forms of Mediterranean shrublands found in South Africa (Di Castri, 1981). With the arrival of European settlers in 17th century, the rate of transformation of the landscape increased, as the influence of the European settlers was different to that of the Khoekhoen herders in several regards (Fairbanks *et al.*, 2004). This transformation led to radical fragmentation of the remaining natural vegetation up today where only about 5% of the original West Coast Renosterveld remains (Low and Rebelo, 1998), of which 1.72 % is formally conserved (Low and Rebelo, 1998). Today the main threat to the remaining vegetation is agricultural expansion, transforming most of the remaining patches of relatively pristine veld into farm land, mainly for wheat,

vines and olives (Fairbanks *et al.*, 2004). Other threats are increases in urbanization and related infrastructure (e.g. roads).

The aims of this study, which forms part of the Renosterveld Restoration Project, were to investigate the effect of grazing and alien pastoral grasses on the establishment of indigenous shrub species and compared methods to facilitate the return of indigenous vegetation to previously transformed areas.

Duelli (1997) stated that intensive agricultural management has led to an alarming level of ecological degradation and that less intensive land use could have different effects. Reduction of land use intensity enriches regional species diversity by counteracting the loss of species.

Observations made at Elandsberg Private Nature Reserve show that natural vegetation does not return into old fields even after years, and even if they are adjacent to natural vegetation (Shiponeni, 2003). Bakker and Berendse (1999) showed that the development of species-rich vegetation on abandoned arable land is often constrained, even when natural abiotic conditions have been restored. They argue that the reasons for this constraint include a depleted seed bank, the poor seed dispersal of late succession species as well as the fact that the first established competitive weedy species, which are already present in the seed bank of agricultural sites, prevent vegetation development for many years (Hansson and Fogelfors, 1998). Shiponeni (2003), in contrast, found that seeds are either newly deposited into the old field, or are present in the seed bank. Therefore, other factors may limit the natural return of the vegetation. A possible explanation is that seedlings of indigenous plants can not establish on the old fields due to the competition from lawn grasses and annuals that dominate the old fields.

Furthermore, the large herds of game once found in the Western Cape have diminished drastically, and it is therefore nearly impossible to determine which role these herbivores have played in Renosterveld ecology. Indigenous game species were reintroduced at Elandsberg and grazing by these herbivores might also have an influence on the establishment of indigenous shrub species and the maintenance of plant communities. Large herbivores continually influence vegetation structure and community composition through defoliation and

trampling (Knapp *et al.*, 1986; Roovers *et al.*, 2004). My prediction was that establishment of indigenous Renosterveld plant seedlings was inhibited by grass competition, grazing, or a combination of the two factors.

My results, along with others (Ponder, 2000; West *et al.*, 1999), showed that there were significant differences in overall survival and growth between species, and each species responded differently to the negative effects of herbivory and plant competition. However, grass competition had a stronger effect on seedling establishment than grazing by large herbivores and only light grazing pressure was used. Survival and growth of seedlings were reduced under grass competition supporting the view that grass competition is a detrimental factor affecting seedling establishment (du Toit, 1967; Brown and Booysen, 1967; Goldberg, 1987; Miller and Werner, 1987; Bush and VanAuken, 1995).

The results indicate that most of the target plants competed for resources with the grass species, and competition affected the seedlings throughout the growing season, but mortality was higher, and growth was reduced, for seedlings exposed to grass competition from emergence through to the end of the experiment. Herbivory only had no significant impact on the target species, but it appeared to reduce seedling growth and survival in *O. europaea spp.africana*. No interaction effect of competition and herbivory was found for the species investigated. Competition and grazing therefore seem to influence the seedlings independently.

The comparison of different management methods (control, brush cutting, burning and the use of herbicide) to control annual alien grasses indicated that treatments did not differ significantly in their effects on species richness. Nevertheless species richness declined with disturbance intensity from the controls through mowing and burning to herbicide treatment, probably because burning reduced the biomass of competitive annual and perennial grasses without eliminating grass species from the treatment. Renosterveld seedlings may have benefited from less grass competition for belowground resources, and above the ground competition (Wilson, 1988; Van Auken and Bush, 1991).

My findings on the influence of herbicide on cover of alien grasses match the results of Cione *et al.*, (2002) who controlled alien grass invasion with herbicide to facilitate the restoration of Californian sage scrub. The greatest shrub cover was

recorded in the herbicide and brush cutting treatments. This can be explained by the competition release due to the low grass cover, which might increase the shrub cover. Herbaceous species responded with an increase in cover in all treatments, with the highest cover recorded in the herbicide treatment. This supports the hypothesis that disturbance reduces the intensity of competition for a limiting resource (Wilson and Tilman, 1993).

In the re-seeding experiment, the highest recruitment and cover of the shrub *E. africanus* was found in the herbicide treatment. This confirms the observation that reduced competition due to grass biomass reduction benefits Renosterveld shrub species. The species might have also benefited from the moisture retained by the dead grass layer. In contrast, the indigenous grass *E. calycina* responded best to the burning treatment. In tall grass prairie, burning before planting or interseeding tall grass prairie it is recommended to reduce excessive shading for the emerging seedlings (Packard and Mutel, 1997). No *E. calycina* seedlings were recorded in herbicide treatment due to the toxicity effect of herbicide after two weeks of application. Therefore, an appropriate time period after application of a grass-specific herbicide needs to be determined before sowing of indigenous grasses for restoration purposes.

However, after one year the herbicide application did not have a negative effect on the soil quality as indicated by the results of the bioassay. In the light of the above results, and as the herbicide application had an intermediate cost for the farmer, this treatment is recommended to facilitate the return of natural vegetation on abandoned farm land.

5.2 Conclusion and recommendations

The emerging link between theoretical models of alternative ecosystem patterns and restoration of degraded area is an exciting development. It has the potential to advance both the practice of restoration and our understanding of the dynamics of degraded systems (Katharine *et al.*, 2004). In most restoration studies the identified or reference aims are clearly described but are rarely supplemented by monitoring, which is necessary for site managers and scientists (Bakker *et al.*, 2000; D' Antonio and Meyerson, 2002). In this study it is difficult to draw clear recommendations for landowners. More small-scale mechanistic and

large-scale landscape manipulations are needed to test which aspects of the theory are important, what system characteristics indicate the presence or absence of alternative ecosystems, how to determine whether thresholds exist, and the relative strengths of different factors affecting resilience in degraded systems. Addressing these questions involves testing the effectiveness of different restoration methods across the degraded system by increasing the sample size (Pywell *et al.*, 2002) and quantitatively synthesizing results from a range of projects to determine environmental contingencies (D' Antonio and Meyerson, 2002).

Experiments conducted over smaller scales, such as this one, are therefore a necessary first step for generating and testing general principles about how grass competition and herbivory affect seedling establishment, survival and growth on abandoned agricultural lands in West Coast Renosterveld. The results obtained in this study are specific; the influence of grass competition on seedling establishment and survival was greater than that of herbivory. The grass competition influenced seedling growth and survival, whilst herbivory did not. Although seedlings in weeded plots were more visible and more accessible to herbivores than seedlings in non-weeded plots, survival and growth was better in weeded plots irrespective of protection from herbivory. Unprotected seedlings in weeded plots fared better than protected seedlings in non-weeded plots.

Removal of neighbouring plants are widely used to test for competition release (Parker and Salzman, 1985; Reader *et al.*, 1994; Bonser and Reader, 1995; Van der wal *et al.*, 2000; Friedli and Bacher, 2001). Plant competition has been shown to have a strong effect on aboveground plant performance in many studies (Donald, 1994; Reader *et al.*, 1994; Bonser and Reader, 1995; Ang *et al.*, 1995; Friedli and Bocher, 2001). Our results are consistent with previous work on the combined effect of herbivory and competition on plant performance (Ang *et al.*, 1995; Bacher and Schwab, 2000). As Renosterveld shrub seedlings fare better under reduced grass competition, grass removal on old fields is the recommended management option in West Coast Renosterveld. Restoration of old-field Renosterveld should focus less on herbivory control and more on strategies for eradication of grass biomass.

Often a degraded system is characterized by species that respond differently (or not at all) to the historical disturbance regime that once maintained the structure and composition of the system in its former state (Chapin *et al.*, 1997). The new species (native or alien) that comprise the degraded community often have distinctive traits that can change the ecosystem characteristics of the system, such as rates of resource turnover, nutrient distribution and disturbance regimes (D' Antonio and Meyerson, 2002).

As noted by Granger (1999), the cost of rehabilitation using seedlings rather than seeds is high. The need for some form of pre-planting treatment to facilitate establishment adds further expenses. Full removal of existing vegetation before planting, although providing ideal conditions for seedling establishment, survival and growth, is not a practical means of rehabilitating degraded grassland because of the high mechanical and labour inputs required (Holmes, 2002).

Burning as a management strategy reduces shrub cover and increases overall species richness and diversity. Burning also reduces grass biomass, and increases recruitment of indigenous seedlings. The use of herbicide may resolve the problem of grass biomass invasion and increases not only shrub cover but also species richness. This treatment also increases the cover of geophytes, forbs and other herbaceous species, but probably reduces overall species diversity. Brush cutting increases overall species richness and diversity, with an increase in shrub and grass cover. This method is not suitable to remove grass biomass on the old field. Our recommendation for the restoration of old fields in West Coast Renosterveld is therefore to apply herbicide to remove grass competition, thus facilitating the establishment of indigenous shrub and herbaceous species. In addition, after a suitable waiting period, the field can be oversown with seeds of indigenous shrub and grass species of early successional stages to increase overall species diversity.

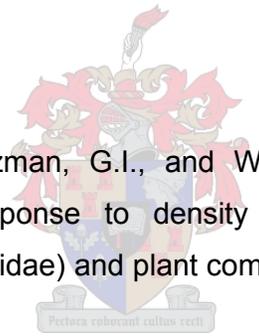
For successful restoration of old fields in West Coast Renosterveld, further studies are needed on the use of the herbicide and burning as management techniques. The selection of the herbicide and application thereof must be considered carefully, especially when indigenous grasses are to be sown. In addition, native seeds should be taken from local sources to minimize genetic contamination. Seeds should also be sown in the most suitable seasons for

germination and seedling survival. This can be done by either by monitoring soil moisture or through repeated seeding trials in the nursery or field.

Recommendations

- Remove grass biomass by using grass specific herbicide
- After suitable waiting period (at least one month after herbicide application) oversow with indigenous seedlings of early successional stages, e.g. *Aristida congesta*, *Ehrharta calycina*, *E. capensis*, *Eragrostis capensis*, *E. curvula*, *Heteropogon contortus*, *Pentaschistis airoides*, *P. pallida* and *Tribolium uniolae* (all Poaceae), and, as shrubs species: *Athanasia trifurcata*, *Eriocephalus africanus*, *Helichrysum asperum*, *Hermannia scabra*, *Leysera gnaphalodes* and *Relhania fruticosa*.
- Repeat herbicide application and seed broadcasting, if necessary.

5.3 References

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- Ang, B.N., Kok, L.T., Holtzman, G.I., and Wolf, D.D. 1995. Canada thistle (*Cirsium arvense*) response to density of *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae) and plant competition. *Biological Control* **5**: 31-38.
- Bacher, S., and Schwab, F. 2000. Effect of herbivore density, timing of attack, and plant community on performance of creeping thistle, *Cirsium arvense* (L.) Scop. (Asteraceae). *Biological Control Science and Technology* **10**: 343-352.
- Bakker, J.P., Grootjans, A.P., Hermy, M., and Poschlod, P. 2000. How to define targets for ecological restoration? Introduction. *Applied Vegetation Science* **3**: 3-6.
- Bakker, J.P., Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* **14**: 63-68.
- Bonser, S.P., and Reader, R.J. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* **76**: 2176-2183.

- Brown, N.A.C., and Booyesen, P. 1967. Seed germination and seedling growth of two *Acacia* species under field conditions in grassveld. *South African Journal of Agricultural Science* **10**: 666-695.
- Bush, J.K., and Van Auken, O.W. 1995. Woody plant growth related to planting time and clipping of C₄ grass. *Ecology* **76**: 1603-1609.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., and Tilman, D. 1997. Biotic control over the functioning of ecosystems. *Science* **277**: 500-504.
- Cione, N.K., Padgett, P.E., and Allen, E.B. 2002. Restoration of native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology* **10**: 376-384.
- D' Antonio, C., and Meyerson, L.A. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* **10**: 703-713.
- Di Castri, F. 1981. Mediterranean-Type shrublands of the world. *Mediterranean-Type shrublands* vol.11. Elsevier Scientific Pub.Co, New York, pp: 1-52.
- Donald, W.W. 1994. The biology of Canada thistle (*Cirsium arvense*). *Reviews of Weed Science* **6**: 77-101.
- Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. *Agriculture, Ecosystems and Environment* **62**: 81-91.
- du Toit, P.F. 1967. An autecological study of the seedling of *Acacia karroo*. *Proceedings of the Grassland Society of South Africa* **2**: 119-126.
- Fairbanks, D.H.K., Hughes, C.J., and Turpie, J.K. 2004. Potential impact of viticulture expansion on habitat types in the Cape Floristic Region, South Africa. *Biodiversity and Conservation* **13**:1075-1100.
- Friedli, J., and Bacher, S. 2001. Direct and indirect effects of a shoot-base boring weevil and plant competition on the performance of creeping thistle, *Cirsium arvense*. *Biological control* **22**: 219-226.
- Goldberg, D.E. 1987. Neighborhood competition in old field plant community. *Ecology* **68**: 1211-1223.
- Granger, J.E. 1999. Artificial establishment of indigenous bunch grasses from plugs. In: Eldridge, D., Freudenberger, D. (eds). *People and Rangelands*:

- Proceedings of the 6th International Rangelands Congress. International Rangeland Congress Inc., Aithkenvale, Qld, pp: 317-319.
- Hansson, M., and Fogelfors, H. 1998. Management of permanent set-aside on arable land in Sweden. *Journal of Applied Ecology* **35**: 758-771.
- Holmes, P.M. 2002. Renosterveld Restoration on Cultivated Lands at Eerste River, Western Cape: Preliminary Findings of Pilot Study. Report to large quarries, Cape Ecological Services, 23 Dreyersdal Road, Bergvliet, 7945.
- Katharine, N.S., Katherine, L.G., and Gregory, R.H. 2004. Alternative feedbacks in restoration ecology. *Trends in Ecology and Evolution* **19** (1): 46-53.
- Knapp, A.K., and Seastedt, T.R. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* **36**: 662-668.
- Low, A.B., and Rebelo, A.G. 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism. Pretoria, South Africa.
- Miller, T.E., and Werner, P.A. 1987. Competition effects and responses between plant species in a first –year old field community. *Ecology* **68**: 1201-1223.
- Packard, S., and Mutel, C.F. 1997. The Tallgrass Restoration Handbook: Four Prairies Savannas and Woodlands. Island Press, Washington DC, USA.
- Parker, M.A., and Salzman, A.G. 1985. Herbivore exclosure and competitor removal: effect on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. *Journal of Ecology* **73**: 903-913.
- Parnesan, C. 2000. Unexpected density-dependent effects of herbivory in a wild population of the annual *Collinsia torreyi*. *Journal of Ecology* **88**: 392-400.
- Ponder, F. 2000. Survival and growth of planted hardwoods in harvested openings with first-order lateral root differences, root-dipping, and tree shelters. *New Zealand Journal of Applied Forestry* **17** (2): 45-50.
- Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., and Peel, S. 2002. Restoration of species-rich grassland on arable land: assessing the timing processes using a multi-site experiment. *Journal of Applied Ecology* **39** (2): 294.
- Reader, R.J., Wilson, S.D., belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olf, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., Grigulis, R., and Beisner, B.E. 1994. Plant

- competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* **75**: 1753-1760.
- Roovers, P., Veheyen, K., Hermy, M., and Gulinck, H. 2004. Experimental trampling and vegetation recovery in some forest and heathland communities. *Applied Vegetation Science* **7**: 111-118.
- Shiponeni, N.N. 2003. Dispersal of seeds as a constraint in revegetation of old field in Renosterveld vegetation in the Western Cape, South Africa. M.Sc. thesis, University of Stellenbosch, South Africa.
- Vitousek, P.M., Mooney, H.A., Melillo, J.M. 1997. Human domination of earth's ecosystems. *Science* **277**: 494-499.
- Van Auken. O.W., and Bush, J.K. 1991. Influence of shade and herbaceous competition on the seedling growth of two woody species. *Madrono* **38**: 149-157.
- Van der Wal, R., Egas, M., Van der Veen, A., and Bakker, J. 2000. Effects of competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* **88**: 317-330.
- West, D.H., Chappelka, A.H., Tilt, K.M., Ponder, H.G., and Williams, J.D. 1999. Effect of tree shelters on survival, growth, and wood quality of 11 tree species commonly planted in Southern United States. *Journal of Arboriculture* **5** (2): 69-75.
- Wilson, J.B. 1998. Shoot competition and root competition. *Journal of Applied Ecology* **25**: 279-296.
- Wilson, S.D., and Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* **74**: 599-611.

Appendix A. List of all species found in the old field at Elandsberg Private Nature Reserve (*Walton, B., and Milton, S.J. pers.comm.*).

Species or Genus name	Family	Species group
<i>Avena barbata</i> Brot.	Poaceae	alien grass
<i>Briza maxima</i> L.	Poaceae	alien grass
<i>Bromus pectinatus</i> Thunb.	Poaceae	alien grass
<i>Lolium perenne</i> L.	Poaceae	alien grass
<i>Vulpia myuros</i> (L.) C.C. Gmel.	Poaceae	alien grass
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	indigenous grass
<i>Ehrharta calycina</i> J.E. Sm.	Poaceae	indigenous grass
<i>Heteropogon contortus</i> (L.) P.Beauv.ex Roem. & Schult.	Poaceae	indigenous grass
<i>Pentstemon densifolia</i> (Nees) H.P. Linder	Poaceae	indigenous grass
<i>Stipagrostis zeyheri</i> subsp. <i>Zeyheri</i> (Nees) De Winter	Poaceae	indigenous grass
<i>Tribolium echinatum</i> (Thunb.) Renvoize	Poaceae	indigenous grass
<i>Tribolium</i> sp.	Poaceae	indigenous grass
<i>Arctotheca calendula</i> (L.) Levyns	Asteraceae	other
<i>Cotula turbinata</i> (L.) Pers.	Asteraceae	other
<i>Sonchus</i> sp	Asteraceae	other
<i>Crassula glomerata</i> Berg.	Crassulaceae	other
<i>Ficinia indica</i> (Lam.) Pfeiffer	Cyperaceae	other
<i>Eriospermum</i> sp	Eriospermaceae	other
<i>Erodium</i> sp	Geraniaceae	other
<i>Pelargonium</i> sp	Geraniaceae	other
<i>Wachendorfia</i> sp	Haemodoraceae	other
<i>Wachendorfia</i> sp	Haemodoraceae	other
<i>Ornithogalum thyrsoides</i> Jacq.	Hyacinthaceae	other
<i>Spiloxene capensis</i> (L.) Garside	Hypoxidaceae	other
<i>Geissorhiza aspera</i>	Iridaceae	other
<i>Gladiolus</i> sp	Iridaceae	other
<i>Moraea lugubris</i> (Salisb.) Goldblatt	Iridaceae	other
<i>Moraea</i> sp	Iridaceae	other
<i>Moraea umbellata</i> Thunb.	Iridaceae	other
<i>Romulea flava</i> (Lam.) M.P.de Vos	Iridaceae	other
<i>Cyphia incisa</i> (Thunb.) Willd.	Lobeliaceae	other
<i>Oxalis polyphylla</i> Jacq.	Oxalidaceae	other
<i>Oxalis flava</i> L.	Oxalidaceae	other
<i>Oxalis glabra</i> Thunb.	Oxalidaceae	other
<i>Oxalis</i> sp	Oxalidaceae	other
<i>Oxalis purpurea</i> L.	Oxalidaceae	other
<i>Oxalis</i> sp	Oxalidaceae	other
<i>Rumex cordatus</i> Desf.	Polygonaceae	other
<i>Ischyrolepis capensis</i> (L.) H.P. Linder	Restionaceae	other
<i>Thesium funale</i> L.	Santalaceae	other
<i>Thesium</i> sp	Santalaceae	other
<i>Cyanella hyacinthoides</i> L.	Tecophilaceae	other
Unidentified		other



Appendix A (continued). List of all species found in the old field at Elandsberg Private Nature Reserve (*Walton, B., and Milton, S.J. pers.comm.*).

<i>Elytropappus rhinocerotis</i> (L.f) Less.	Asteraceae	shrub
<i>Eriocephalus africanus</i> L.	Asteraceae	shrub
<i>Helichrysum asperum</i> (Thunb.) Hilliard & B.L.Burt	Asteraceae	shrub
<i>Leysera gnaphalodes</i> (L.) L.	Asteraceae	shrub
<i>Relhania fruticosa</i> (L.) Bremer	Asteraceae	shrub
<i>Stoebe plumosa</i> (L.) Thunb.	Asteraceae	shrub
<i>Ursinia anthemoides</i> (L.) Poir.	Asteraceae	shrub
<i>Phyllica strigulosa</i> Sond.	Rhamnaceae	shrub
<i>Hermannia scabra</i> Cav.	Sterculiaceae	shrub
<i>Athanasia trifurcata</i> (L.) L.	Asteraceae	shrub
<i>Aspalathus ciliaris</i> L.	Fabaceae	shrub

