Vegetation Patterns and Dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa

By

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Φ Poem

“Colour
awash
over forelands
of fertile clay”
“When the winters’ cold and grim
the *Oxalis’s* start to brim - they open up.
The first feast for bees, in the shrubland short of trees not breeze.
Sun’s rays soon last longer in the days: *Babiana*s, *Chlorophytum*s, *Geissorhizas, Gladiolius’s,*
*Hesperanthas, Lachenalia*s, *Moraeas* and *Trachyandra*s spread their cheerful gaze.
Accompanied by annual daisies and bright gladioli filling the air with strong scents of honey -
monkey beetles waste no time as they perch upon delicate flowers, lest they are caught in the
season’s showers.
As if to suggest this is the best nature sends small midge flies to pollinate in jest, and surround
mammals to tease their bloody channels.
Another month has come and gone - not long now for the raaptol and *Micranthus* which provide
nectar for brown butterflies and painted ladies.
Then is the last sequence of bulbs - the fine white-filled fields of chinkerinchees.
Grasses’ hour is now soaking up the sun displaying beautifully crafted silhouettes till summers end.
As if heaven sent delicate geophytes are still producing their charm, when botanists avoid the
midday sun.
A brief lapse in displays until the autumn reds begin the seasonal cycles.”

Figure a: From left to right: *Moraea villosa* (Ker Gawl.) Ker Gawl. subsp. *villosa*, *Gladiolus watsonius* Thunb. and *Lampranthus elegans* (Jacq.) Schwantes

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………………………….

Dedicated to my daughter June Protea Walton

For those who cherish wild landscapes filled with wild plants and animals

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Preface

This project forms one component of a study of renosterveld in the Western Cape[1] by the Renosterveld Rehabilitation Project based at Stellenbosch University in the Department of Conservation Ecology. The Renosterveld Rehabilitation Project was partly funded by World Wide Fund/Table Mountain Fund as part of the Cape Lowlands-Renosterveld Ecology and Management project. This specific project was also supported by the National Research Foundation of South Africa under Grant number 2053674. This thesis concerns a study of renosterveld vegetation patterns and dynamics in relation to ploughing and grazing:

Chapter One is a general literature review of renosterveld vegetation.

Chapter Two is a précis of the study area characteristics applicable to both core chapters covering data analysis and synthesis.

Chapter Three focuses on vegetation patterns with a description of classified communities and ordination diagrams. This chapter is written in article format according to the South African Journal of Botany, with the aim of publishing in mind.

Chapter Four concerns the interaction of ploughing and grazing on life-form richness and cover-abundance. This chapter is written in article format according to the South African Journal of Botany, with the aim of publishing in mind.

Chapter Five is a brief summary of findings and includes management recommendations.

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[1] Erratum: note all diagrams should read “Western Cape” and not “southwestern Cape”.

Abstract

Swartland Shale Renosterveld is restricted to fertile fine-grained soils in the winter rainfall region of the Western Cape. Between 91% and 97% of this vegetation type is transformed, mostly due to agriculture. Remaining fragments have an irreplaceable conservation value due to a high richness of endemic geophytes. Information on renosterveld vegetation composition and response to disturbance is sparse. Research occurred at three sites near Wellington: Voëlvlei Provincial Nature Reserve (CapeNature), Elandsberg Private Nature Reserve (Elandsberg Farms (Pty.) Ltd.), and Krantzkop munitions factory (Armscor/Somchem) forming a contiguous fragment in the Agter-Groeneberg Conservancy. The primary research aim was to identify or ascertain patterns of plant succession in Swartland Shale Renosterveld and associated different-aged old fields (previously ploughed), with the interaction of grazing. The key research questions are: (1) What are the plant communities of unploughed renosterveld and different-aged old fields which originated in habitats of ploughed renosterveld? (2) What are the most characteristic features of the floristic and ecological relationship between the described plant communities in terms of ecological factors operating within the studied system? (3) Does total species and life-form group richness differ between natural vegetation and old fields? (4) Is life-form richness influenced by ploughing and grazing or the interaction between these disturbances? (5) Is life-form cover-abundance influenced by ploughing and grazing or the interaction between these disturbances? (6) Does alien plant species richness differ amongst seres, and with different levels of grazing intensity? A comparison of life-form richness and cover-abundance of old field vegetation was made with adjacent natural unploughed "controls". The effects of ploughing on community structure, with the inclusion of grazing was established. These life-form richness comparisons also occur across a gradient of increasing large mammalian herbivore grazing intensity. Sampling was conducted in winter and spring using nested 1000m^2 relevés.

A hierarchical classification, description and floristic interpretation of renosterveld and old field vegetation were made using TWINSPAN, SYN-TAX 2000 and CANOCO. The samples were classified with TWINSPAN and two communities were described at the association level, namely: *Ursinia anthemoides–Cynodon dactylon* Grassland Community (with two variants) and the *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland Community (with two sub-associations), respectively. The vegetation data were further hierachically classified using SYN-TAX 2000 which revealed similar clustering of sample objects to that resulting from classification and ordination. Following ordination of sample objects with CANOCO, select groups of species were used to depict their response curves in relation to seral development.

Briefly it was found that the effects of grazing *vs*. non-grazing was more pronounced on old fields than in unploughed vegetation. Overall total species and life-form richness was reduced by ploughing with old fields requiring a recovery period of 30 years to resemble unploughed vegetation.

Keywords: Swartland Shale Renosterveld, phytosociology, vegetation patterns, life-forms, succession, disturbance, ploughing, grazing, old fields.

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Chapter 1

Renosterveld: Concept, Ecology and Variability

Figure 1.1: The foothills of Elandskloof Mountains at Krantzkop (North-Eastern view) with 30-year-old fields near an uninhabited farmstead surrounded by *Eucalyptus cladocalyx*

1.1. Introduction

The aim of this thesis is to determine vegetation patterns in a remnant of renosterveld and gain an understanding of several processes operating in shaping the post-ploughed recovery and local vegetation dynamics in relation to large-herbivore grazing. A renosterveld fragment (Figure 1.1) at the Agter-Groeneberg Conservancy (hereafter denoted AGC), was studied for a description of community patterns which may have been typical of the once more widely distributed renosterveld along the West Coast foreland (Figure 1.2). This particular chapter intends to present a brief overview of the definition and ecology of renosterveld vegetation, and to outline ecosystem processes maintaining floristic richness and diversity of renosterveld in relation to disturbance.

Renosterveld is a part of the Fynbos Biome (*sensu* Kruger 1978), one of five mediterranean-type ecosystems (MTE) of the world. The five mediterranean-climate regions occupy 2.25 % of the Earth's surface (Rundel 2004), yet collectively account for almost 20% of vascular plant species (Cowling et al. 1996). These regions are renowned for citrus fruit, viticulture, olives, figs and other winter rainfall crops.

Plant communities of the Mediterranean region are highly diverse at the local and regional scale (Lavorel 1999). A multitude of vegetation types occur within these five MTE's of the world. The Mediterranean Basin contains seasonal dry forests, macchia, garrigue, and related shrublands; sclerophyllous chaparral and summer-deciduous coastal sage scrub vegetation occur in California (Keeley 2000); central Chile supports matorral (Rundel 1981) and typical Australian mediterranean-type shrublands contain mallee and kwongan (Fox 1995). Fynbos and renosterveld are MTE shrubland types in South Africa.

Fynbos and renosterveld are found within the Cape Floristic Region (*sensu* Goldblatt 1978, hereafter referred to as CFR) which was declared as one of twenty-five global biodiversity hotspots (Myers et al. 2000) due to high concentrations of endemic taxa. The CFR comprises an area of 90000 km^2 and is estimated to contain 9 030 vascular plant species (Goldblatt and Manning 2002), or a ratio of one species per 10 km^2, with 68% endemism (Bond and Goldblatt 1984). A comparative study of species richness at the 0.1 ha scale (Rice and Westoby 1983) revealed that in temperate sclerophyllous shrub-dominated vegetation on low-nutrient soils the species richness generally is in the range of 50 to 100 species. At the 1000 m^2 scale renosterveld has higher species richness than fynbos: circa 84 and 66 species, respectively (Cowling 1983a).

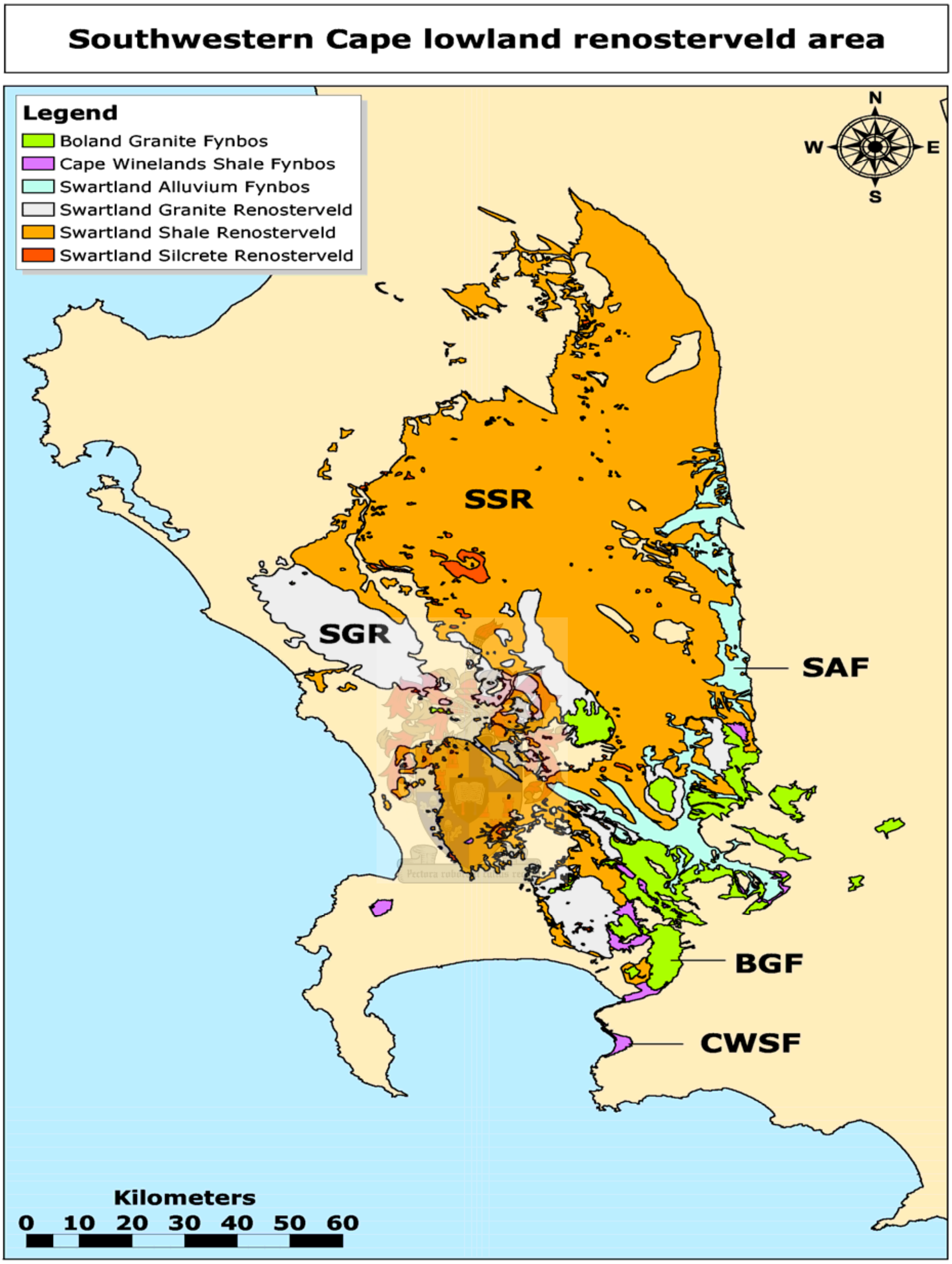

Figure 1.2: The Western Cape showing the original extent of Swartland Shale Renosterveld (SSR) (Mucina and Rutherford 2004) and adjacent vegetation types of Swartland Alluvium Fynbos (SAF), Swartland Granite Renosterveld (SGR) and Boland Granite Fynbos (BGF) with small patches of Swartland Silcrete Renosterveld and Cape Winelands Shale Fynbos (CWSF)

The common feature of all MTE's is that they occur in warm-temperate regions experiencing winter rainfall and summer drought. MTE's have often been compared with each other as there are congruencies in growth-form adaptations to local climates, but a singular robust definition for mediterranean type ecosystems is lacking. Rundel (2004) maintained that the definition of a mediterranean-climate ecosystem lacks exclusive and distinctive criteria, as MTEs are defined in rather general terms according to climate, floristics and physiognomy or a combination of these criteria, to delineate their boundaries. High species richness and endemism (Thiaw and Chouchena-Rojas 1999), frequent fires, an extensive flowering period with seasonal growth rhythms extending into summer are diagnostic of MTE's (Dodson and Kershaw 1995). Characteristic high species richness is due to spatial heterogeneity in habitat and topography, also influenced by environmental factors and moderate resource limitation (Moody and Meentemeyer 2001). Goldblatt (1978) mentioned that high species richness in the CFR is attributed to environmental heterogeneity (and edaphic diversity), different climatic regimes, and climatic fluctuations since the mid-Pliocene. Campbell and van der Meulen (1980) investigated alpha and beta species diversity in mountain fynbos vegetation along a temporal and altitudinal gradient and concluded that beta diversity was most influenced by altitude and structure (the latter related to the age of post-fire vegetation). Specifically alpha diversity (point diversity or richness) was lowest at low altitudes in mature stands of vegetation, relative to younger stands due to overtopping by emergent proteoids, whilst beta diversity (species turnover) was low at similar altitudes between different-aged stands. Cowling and Campbell (1984) studied beta diversity along coenoclines of fynbos and non-fynbos in the southeastern Cape revealing high turnover rates along an altitudinal gradient.

Huston (1994) suggests a model explaining this high diversity in terms of low competition related to nutrient-poor soils and summer drought, combined with disturbance (fire or grazing). Another model explaining higher species richness in fynbos relative to its analogues, proposed by Wisheu et al. (2000), suggests that the abundance of the seeder strategy versus the resprouter strategy, coupled with physical barriers and local isolation, could have allowed for a more rapid speciation pattern. Three factors contributing to high plant species richness and diversity in mediterranean heathlands are: oligotrophic soils allowing for either seeder or sprouter strategies upon death by fire, numeric dominance by seeders, and short generation times of seeders with high speciation rates.

Renosterveld shrubland occurs on nutrient-rich soils, thus the model proposed by Wisheu et al. (2000) would only apply for fynbos proper. Nutrient levels are then not the main determinant of species richness and diversity in this nutrient non-limited environment.

1.2. Concept of Renosterveld

Francis Masson travelled with Carl Peter Thunberg northward up the west coast and passing Kontreberg (19th February 1773) they entered "a large barren country, named the Zwart Land, owing to the renosterbossies and bakkerbossies, grey-black and pitch-black when wet" (Bradlow 1994). Masson described the area as: "the earth is a grey sand, level for many miles, and covered over with low shrubs of various sorts". Masson travelled with Thunberg again, reaching the top of Paardeberg (760 m, 6th of October 1774), where a "treasure of plants" were seen and an "extensive view of adjacent country, which is level, and has but a barren appearance; yet contains several plantations, producing abundance of corn (wheat) and wine; and the peasants live luxuriously". "Their plantations lie all around the foot of this mountain, which yields a number of fine rivulets, without which this country would be uninhabited". On the 7th of October 1774, they journeyed "northward through a level country covered with low shrubs, but it being now spring, it was everywhere decorated with flowers of the greatest beauty, every hour's march producing new charms" (Bradlow 1994).

On April 11th Burchell (1822) says the "open face of country, surface varied with smooth hills covered almost exclusively with a neat pale bushy shrub, of the height of 3 or 4 feet, called "rhinosterbosch" (rhinoceros bush), and said to have formerly been the food of the huge rhinoceros, till those animals fled before the colonists, as these gradually advanced over the country where the shrub grows." Simon van der Stel apparently named it thus because rhinoceroses (hook-lipped or Black Rhinoceros *Diceros bicornis*) inhabiting the coastal plains were camouflaged by it, and because of renosterbosses wide cover over the landscape (van der Walt 2003). In Burchell's book (1822) a "*Stoebe rhinocerotis*" vignette presents a sprig in its natural size, the leaves are very minute, and the scales, in the manner of the cypress, (the author had the same realisation in the field of an almost Lilliputian forest) the flowers are small, and, though very numerous, are neither showy nor ornamental, being of a simple herbaceous colour. Several species of *Stoebe*, which in growth resemble this one, are all, without distinction called by the colonists, "rhinoster-bosch" (says similar to tamarisk!), and perhaps in former days, been equally the favourite food of the rhinoceros. Burchell (1822) described renosterveld vegetation as "renosterbos abounds in dry hilly lands; and occupying extensive tracts, give a peculiar character to the landscape". The term renosterveld standardized by Boucher (1980) is not attributed to the most conspicuous and dominant species, namely *Elytropappus rhinocerotis* [2] (renosterbos) often forming monotypic stands, but to a vegetation in which rhinoceros previously occurred.

Contemporary descriptions and definitions of renosterveld are often ambiguous or complicated unlike those for fynbos. Consensus is lacking as to what the distinguishing features of it are, although descriptions have been adequately documented (Boucher and Moll 1981, Boucher 1983) as well as in context of the Fynbos Biome (Moll et al. 1984), there is no singular identification of underlying ecological patterns and processes especially in relation to fire. A description of renosterveld is a perception (see Krug et al. 2004; Newton and Knight 2004); much relies on the stance or view a priori one has of it. Fynbos has an adequate descriptive history, whereas renosterveld has not had an equal focus of ecological description. Descriptively maligned to either: “disclimax” (see Specht and Moll 1983), or “transitional” (scrub type Acocks 1953, fine-leaved microphyllous shrubland, Cowling 1983a, Cowling 1984, Moll et al. 1984) or a “derived” (Boucher 1987) existence or state. Perceptions of renosterveld by agriculturalists as an unwanted “quasi-state” as a result of pasturage overgrazing (du Toit and du Toit 1938) has led to a negative connotation of dominant shrubs in renosterveld. Ecotones exist in reality as boundaries between two or more vegetation types, a transition from one to another cannot exist for many square kilometres without warranting a sufficient identity as a separate ecological entity. To suggest something is transitional, in the first instance, implies there is an arrival or advance to a defined state of vegetation type at some point. The notion that renosterveld was previously a grassland, now invaded by *Elytropappus rhinocerotis* was not supported by isotopic evidence from litter and soil samples (Stock et al. 1993). Geology and soil types are the primary determinants for differences between fynbos and renosterveld vegetation types and habitats. Serotiny is a distinguishing feature of fynbos on oligotrophic soils and noticeably lacking in renosterveld. Renosterveld on eutrophic soils relies on a ground-stored seed bank, with no evidence of serotiny, and the many asteraceous species with rapid growth rates and seed formation probably invalidate the requirement that serotiny (see Enright et al. 1998) has to counteract disturbance by fires.

Moll and Jarman (1984a) identified the need for a clear definition of fynbos as different from the traditional heathland category described by Specht (1979) as these communities are not restricted to a mediterranean-climate region, but are physiognomically similar or floristically related. Thus the definition proposed by Moll and Jarman (1984a) and Moll et al. (1984) for fynbos would entail an “evergreen sclerophyllous shrubland on oligotrophic soils, comprising elements of the Cape

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[2] *Dicerothamnus rhinocerotis* is the new name for *Elytropappus rhinocerotis* but as yet is unpublished and exists in PhD format only (by M. Koekemoer). Thus the old name is given preference throughout this thesis.

Floristic Region", which "consist of either functionally isobilateral picophyllous and/or microphyllous to mesophyllous-leaved shrubs", also "associated with evergreen aphyllous and/or narrow-leaved sclerophyllous hemicryptophytes". In addition Moll and Jarman (1984b) incorporated changes to the limited definition of heathlands (as characteristically dominated by Ericaceae) for application in South Africa, as "true" ericaceous heathlands here are restricted to montane environments, as clarified by Campbell (1978). Structurally heathlands are characterised by a closed (dense) to mid-dense (or open; Moll and Jarman 1984b) assemblage of evergreen, sclerophyllous shrubs, dwarf shrubs, also including seasonal hemicryptophytes and therophytes (Specht 1979). Evergreen sclerophyllous hemicryptophytes are an important component of heathlands, as is the seasonal geophytic component and a few parasitic epiphytes. Depending on the availability of water; trees and tall shrubs may be common, especially so in the absence of fire (Armesto et al. 1995), or otherwise rare in heathland formations (Specht 1979), as is the case in South Africa (with the exception of the Cedarberg open temperate forest, Kruger 1979a, 1979b). The ericaceous presence is not ubiquitous to heathlands in the South African context, as these are often absent or replaced by other families with picophyllous shrubs, like Asteraceae, Thymelaeaceae and Rhamnaceae (Moll and Jarman 1984b). Thus fynbos "heathlands" are ecologically restricted to oligotrophic soils, also sands, limestones and laterites or highly leached soils. Moll and Jarman (1984b) consider the soils to be seasonally waterlogged but fail to explain the good drainage provided by steep slopes on which much of fynbos occurs. Thus Specht's (1979) criterion still holds true: that sclerophyllous heathland formations occur on oligotrophic soils, either well-drained or waterlogged. Heathland areas generally have both oligotrophic and eutrophic soils, with sclerophyllous plants occurring on the former and herbs and grasses flourishing on the latter (most notably in Australia). Thus with a similar climatic regime different vegetation types will occur on different soil types.

Coastal renosterveld, including both West Coast Renosterveld and South Coast Renosterveld (*sensu* Rebelo 1996, hereafter denoted WCR and SCR, respectively), comprises a mid-dense (i.e. partially open) to closed 1-2 m tall matrix of small cupressoid, leptophyllous, molliphyllous, divaricately branched (Boucher 1981) small-leaved evergreen shrubs (Moll et al. 1984, McDowell and Moll 1992), dominated by the Asteraceae family. Emergent bush-clump or thicket species of subtropical affinities (like the Celastraceae and Oleaceae families) with broad orthophyllous leaves are regularly spaced in the renosterveld matrix. Clumps of the wild olive (*Olea europaea* subsp. *africana*) occur alongside rivers, drainage lines, or in rocky outcrops as well as on termitaria (heuweltjies) (Boucher 1981). Renosterveld is hardy shrubland vegetation, enduring hot summers and desiccating winds, adapted to survival in these climes by the sclerophyllous and cupressoid leaf physiology of dominant microphyllous asteraceous shrub species or alternatively seasonal dormancy by geophytes and some hemicryptophytes.

1.3. Patterns of Functional Types

A broad functional-type pattern or physiognomy of South African shrublands is defined on the basis of floristics. Floristic affinities of renosterveld with fynbos are low in spite of their structural similarity (Boucher and Moll 1981), although Boucher (1983) found that 54% of species were shared between WCR and mountain fynbos at Jonkershoek. The presence of restioids, ericoids and proteoids are diagnostic of fynbos vegetation. The restioid component is the most diagnostic (or constant) physiognomic and floristic feature of fynbos (Kruger 1979a, Taylor 1978), followed by the ericoid growth form and the frequent proteoid growth form. Differential structural elements of sedges, non-ericaceous ericoids, and ericoid asteraceous forms occur throughout (Cowling and Holmes 1992). The presence of endemic families, for example Penaeaceae and Stilbaceae are common, as is leaf spinescence. The diagnostic fynbos plant families: Ericaceae, Proteaceae and Restionaceae are lacking in renosterveld (Taylor 1978). Some ericoid, proteoid and restioid species do occur in renosterveld at low densities (Taylor 1996), as some representatives of these families are restricted to specific habitats (in renosterveld). Coastal renosterveld is best described as a shrubland including swards of graminoids and geophytes with some open spaces allowing for an abundance of ephemeral species. By nature of the topography, patches of wetlands occur in renosterveld wherever drainage is poor, especially alongside slow-flowing rivers and in alluvial floodplains. Termitaria (heuweltjies) are a feature of the renosterveld landscape, and provide additional micro-habitats (synusia) in the shrubland matrix. A physiognomic feature of fynbos is the lack of dominance by any one species (exceptions are found in seepage areas or localized types of fynbos, and long post-fire intervals), unlike renosterveld which is usually dominated by one or more asteraceous shrub species.

The mediterranean-type vegetation of the Fynbos Biome is composed of sclerophyllous species adapted to seasonal drought by their conservative leaf size and transpiration rates. Seasonal drought periods are a common feature of mediterranean-climate regions, even though average seasonal temperatures vary. Sclerophylly in MTE’s is either a response to low nutrient environments or seasonal drought (Specht 1979). Sclerophyllous leaves have thick cuticles with sunken stomata and are varied in shape and form: leptophyllous; nanophyllous; microphyllous; cupressoid or aphyllous (Specht 1979). Sclerophyllous leaves are usually small or inwardly-rolled as in Ericaceae and/or with thick cuticles or hair to reduce evapotranspiration. Sclerophyllous shrubs and dwarf shrubs and also geophytes dominate the ground stratum of plant communities on oligotrophic soils, while grasses and herbs are rare. On eutrophic soils the ground stratum is herbaceous and composed of: annual grasses, herbs, forbs and geophytes. Specht (1973) says in the mediterranean area of southern Australia below the dominant overstorey of *Eucalyptus*, eutrophic soils support a ground stratum of perennial tussock grasses and geophytes; in contrast to a ground stratum of shrubs on oligotrophic soils. Sclerophylly is a response to conditions of water stress and an evergreen or herbaceous ground stratum is a response to soil fertility (Specht 1979). Specht (1981) mentioned that mediterranean shrublands on eutrophic (base-rich) soils produce shoot growth in spring in the upper stratum; as opposed to late spring/summer shoot growth with vegetation on oligotrophic soils (and intermediate soils like mallee with a summer-growth rhythm, Fox 1995).

Strata of Renosterveld

Mature renosterveld has many strata (Adamson 1938, Levyns 1929b, Boucher and Moll 1981) such as: an upper stratum of (often cupressoid) asteraceous shrubs, a middle stratum of dwarf shrubs, and a lower stratum of grasses, forbs, geophytes and annuals (with a large grass and geophyte component, Rebelo 1995). Levyns (1929b) and Muir (1929) correctly observed the moss and lichen flora on the surface (as well as plants festooned with lichen, B.A. Walton, personal observation), with the former most noticeable in winter when the microbial activity is highest in the pedoderm. Adamson described succession in renosterveld starting as an early sere with low life-form and floristic diversity of annuals and pioneers, advancing to another sere with dwarf shrubs and later “ericoid” dominance by a few shrubs. Renosterveld shrubland is often monotypically or co-dominated by *Elytropappus rhinocerotis* (Levyns 1929b) or *Athanasia trifurcata* with other shrub/dwarf shrub species occurring in lower densities and usually in the undergrowth (see Muir 1929). The success of *Elytropappus rhinocerotis* is attributed to an ability to grow deep tap roots (to 8 foot, Scott and van Breda 1937) after sufficient moisture to lateral roots has been provided (seedlings are initially drought intolerant, Levyns 1927). Deep roots also facilitate conditions for other plants to abstract water and other solutes. *Stoebe* is also known to have deep roots (to 5 feet, see Cohen 1935), but prefers a higher soil water content for germination (coinciding after rainfall). The lowest stratum (understorey) is mainly ephemeral and herbaceous with perennial grasses, geophytes, prostrate herbs and procumbent dwarf shrubs.

The higher proportion of grasses in SCR distinguishes it from WCR, although much grass occurs in stony places avoided by ploughing also in WCR with dense *Themeda triandra* swards (Acocks 1953). The WCR grass component is largely composed of C_3 grasses (Vogel and Fuls 1978). In

SCR communities, both grassy and shrub structural cover states exist, and Cowling et al. (1986) tentatively suggest an increased shrub component may be a result of overgrazing. Cowling (1983b, 1984), in a study of coastal shrublands, found that C_3 grasses prefer cooler south-facing slopes where the shrub stratum facilitates cooling and litter retains moisture, unlike C_4 grasses which prefer north-facing slopes. Thus radiation levels, rather than moisture, determine the patterns of C_3/C_4 grasses in SCR. The C_4 grasses overall had a higher coverage attributed to their competitive ability over C_3 grasses, and in the case of *Themeda triandra* a bimodal seasonal growth pattern (Pierce and Cowling 1983) ensured dominance. Usually grass growth is initiated in early winter to summer (Pierce 1984), with restioids from spring to summer, geophytes initiate growth in autumn until the end of spring and shrub growth is varied throughout the year but usually occurs from late winter to early summer.

1.4. Geology and Soils

The South African and Australian continents are mostly of Gondwanaland origin that in parts, are overlain by a discontinuous strip of either Tertiary or Quaternary deposits. Cowling et al. (1996) mentions that in more nutrient-rich soils, with longer fire-free intervals (like chaparral, garrigue and phrygana); the shorter-lived species are out-competed by longer-lived shrubs in seral development. Coastal renosterveld (Acocks 1953 Veld Type No. 46) is restricted to moderately fertile fine-grained soils derived from granites and shales: it occurs on a rolling topography in the coastal forelands of the Western Cape with a winter-rainfall regime (Boucher and Moll 1981), and an undulating topography in the southern Cape region with a non-seasonal rainfall regime.

Along the West Coast forelands the geology is dominated by three terranes of the Malmesbury Group from the Namibian period, namely: the Tygerberg Terrane (with the Tygerberg Formation); the Swartland Terrane (with the Franschhoek, Moorreesburg, Bridgetown, Klipplaat and Berg River Formations) and the Boland Terrane (with the Porterville and Piketberg Formations). Various Cape granite plutons have intruded into the Malmesbury Group throughout the West Coast foreland, namely: the Paarl, the Paardeberg and Darling Plutons (Anonymous 1990). The Klipheuwel Group (with the Populiersbos and Magrug Formations) from the Cambrian Period is exposed occasionally. Late Tertiary and Quaternary deposits comprise a large portion of the area as well. Some Dolerites (at Voëlvlei) and Greenstones (in the Tulbagh Valley) occur intermittently (Visser et al. 1981).

Along the South Coast forelands the geology is dominated by the Malmesbury Group from the Namibian period, with the Tygerberg Terrane (with the Tygerberg Formation) and the Boland Terrane (with the Brandwacht Formation, partially thrust over the Porterville, Moorreesburg (=Norree) and Franschhoek Formations). Various plutons from the same period occur throughout the South Coast foreland, namely: the Hermanus, Robertson and Greyton Plutons (Anonymous 1997). The Klipheuwel Group (with the Magrug Formation) from the Cambrian Period is exposed occasionally. Further inland the Malmesbury Group is composed of the Kaaimans and Kango Formations (Anonymous 1991), and the Cape Granite Suite from the Cambrian period. The Palaeozoic Period (Cambrian to Permian) produced the Cape Supergroup comprising: the Table Mountain, Bokkeveld, Witteberg, Ecca and Beaufort Groups, which support fynbos except in some formations which support renosterveld (like the Bokkeveld Group).

The South Coast Renosterveld areas (Vlakte and Ruêns and Enon Basin) are mostly ploughed up for wheat (Ellis 1973). The geology of the lowland areas is comprised of Enon (Cretaceous System), Bokkeveld Series of the Cape Supergroup and Tertiary sands and limestones. The Enon beds give rise to conglomerates and clays which are unconsolidated and alternating. Quartz veins and Bokkeveld shale or TMS inclusions are also found in the Enon beds. The higher hills of the Ruêns and well planed Vlakte areas are formed from the Bokkeveld Series consisting of shales and fine-grained phyllites. Occasionally limestone is occluded in the Bokkeveld Series.

Unlike fynbos on oligotrophic soils, renosterveld on eutrophic soils has a large biotic component of arthropods, earthworms and termites able to break down plant material and aid in decomposition, thus reducing the above-ground biomass able to burn.

1.5. Climate

Mediterranean type ecosystems are characterised by hot, dry summers and wet winters occurring in the winter rainfall regions of the World (Hobbs et al. 1995), covering 2.73 million km^2 (Thiaw and Chouchena-Rojas 1999). The mediterranean regions of the World have similar climates influenced by oceanic and atmospheric circulatory patterns. The total rainfall amount varies across these regions and typical mediterranean-like vegetation extends beyond a mediterranean climate, for example chaparral in Arizona (Keeley 2000). The five mediterranean regions of the world occur in both hemispheres: the Mediterranean Basin and California in the Northern Hemisphere; and central Chile, the southwestern and southern Cape region of South Africa and southeastern and southwestern Australia in the Southern Hemisphere. These mediterranean regions occur between the 30° and 40° latitudes either north or south (Hobbs et al. 1995).

Pleistocene glacial cycles had a more serious effect in the Northern Hemisphere and Chile than in southern Africa, contributing to higher regional diversity in the CFR (see Goldblatt and Manning 2002), which escaped most of the glaciations (and aridity) of that period, notably in the western part of the Cape flora (Cowling and Lombard 2002) and the southern Kalahari where humidity was high (Van Zinderen Bakker and Coetzee 1988). During the Quaternary period prior to the Last Glacial Maximum, cooler temperatures, especially in the southwestern and eastern Cape (Parkington et al. 2000) allowed for the spread of asteraceous shrublands (renosterveld) (Scott et al. 1997) in the Fynbos Biome, where changes in vegetation were more pronounced at lower elevations. In the Western Cape fynbos persisted as other floras descended to lower elevations in the cool period of the last glacial maximum (18 000 BP), elsewhere in southern Africa and the Mediterranean region, forest and xerophytic scrub and woods were replaced by steppe/grassland (Elenga et al. 2000).

In the Fynbos Biome, lowland renosterveld experiences a true mediterranean climate in the Western Cape whilst a non-seasonal rainfall climate exists in the southern Cape (extending into the summer rainfall region) (Wicht 1945, van Rensburg 1962, Boucher and Moll 1981). Generally the renosterveld shrubland on the coastal forelands is defined as occurring on nutrient-rich soils between a rainfall margin of 300 mm and 600 mm. At higher altitudes near foothills of mountain ranges up to 800 mm of rainfall can occur (as well as in shale bands associated with the Cape Supergroup). Thus renosterveld occurs along an edaphic and rainfall gradient between more mesic fynbos elements and arid Karoo or thicket elements. Seedling recruitment in renosterveld plant species may occur in pulses, coinciding with above average and consistent winter rains, alternating with fire-cycles. At the upper rainfall margin > 800 mm of rainfall, fynbos can exist on highly leached shale-derived soils (N Helme, personal communication), rather than forest elements in the presence of fire. Exclusion of fire does not necessarily imply forest elements would succeed renosterveld on the lowlands due to moisture limitations.

1.6. Disturbance and Vegetation Dynamics

Since the vegetation patterns and dynamics of sclerophyllous shrublands are influenced by various disturbances, it is relevant to mention disturbances, which effectively “shape” the vegetation of these regions. Renosterveld is described as a flora created and maintained by an intermediate level of disturbance(s) (Boucher 1983), both at small and large scales. Porcupine diggings (*Hystrix africaeaustralis*) and termite activity (*Microhodotermes viator*) create local habitat heterogeneity. Whilst short fire intervals (compared with fynbos) maintain habitat heterogeneity at larger scales, often creating a mosaic of vegetation patches of different ages with similar (or different) pioneer and late successional dominant species, respectively. Heydenrych (1995) stated that "renosterveld is a dynamic vegetation type, which fluctuates between a grass- and a shrub-dominated state, depending on the use of fire and brush cutting techniques". In addition grazing and browsing is an important endogenous disturbance maintaining floristic diversity.

1.6.1. Fire

Fire Regime

Exogenous disturbance of sclerophyllous vegetation by fire is an integral part of the dynamics altering, influencing and maintaining community composition and landscape patterning. Most fires occur during summer in the West Coast foreland (Kruger 1979a, 1979c). Research on the response of renosterveld vegetation following fire, and data on fuel properties is considerably lacking (van Wilgen 1987). The natural frequency of fire cycles in renosterveld vegetation is undefined but is assumed to be of a shorter fire cycle than fynbos, owing to its inherent resilience and dominant species with short maturation times (Boucher 1983). Fire is prevalent during hot dry summers and is facilitated by secondary compounds in sclerophyllous leaves (e.g. volatile oils). Levyns (1935a, 1956) confirmed "burning acts as a stimulus to germination ["sic"] compared to a brush-cut plot", by fluctuating the temperature experienced by stored seed. Equally important is the understanding of a dependency on a seed bank, with natural fluctuations in size (Cowling et al. 1987), by annuals and re-seeding forbs and shrubs. Both browsing and grazing are major selective forces in life history selection in species, similar to fire, which also influence the structure and composition of renosterveld. Fires attract grazers to new plant growth (Bond and van Wilgen 1996) and in grasslands too frequent fires disperse grazers and decrease prostrate "lawn" grasses, whilst a less frequent fire-cycle maintains grazers at "lawns" thus ensuring their persistence (Archibald et al. 2005) relative to bunch grasses. A fire-severity study on the Cape Peninsula (Euston-Brown et al. 2002) showed that vegetation diversity on granite and Quaternary sands, was worst affected by high alien plant densities, than rocky and phreatic sites. Although not strictly renosterveld this does indicate the preference of some alien plant taxa for those soil types, and an equally disturbing finding is that severe fires where alien plant densities were high pre-fire, caused a loss of major plant functional groups (Euston-Brown et al. 2002).

In contradiction to earlier studies, the historical variability of the fire regime in California is unaltered by fire suppression efforts, as large wild fires over the landscape still occur. The "natural" fire regime was considered to be small-scale fragmentary fires thus preventing landscape scale burns (Keeley 2002b, Keeley and Fotheringham 2003); however this is not the case and more large scale and widespread fires were probably important. This has implications for the concept of the natural fire regime of renosterveld, whereby both small- and landscape scale fires contribute to overall stand age heterogeneity.

Fire and Herbivory

Southern Africa has been populated by humans since at least 100 000 years ago (Deacon 1983), and probably since the Middle Stone-Age to at least the Late Stone-Age the inhabitants of the Cape region were able to make fire with stick rubbing techniques. Similarly the Californian region has experienced the use of fire by local inhabitants (Keeley 2002a), both past and present, to access resources in dense shrublands by type conversions to grasslands or a mixture thereof. Deacon (1983) made a distinction between hunter-gatherers using fire to stimulate grass growth to capture selective browsers in fynbos environments; and nomadic herders (since 2000 BP) who burnt areas to stimulate growth for heavy grazing of a short duration. The former would have occurred in smaller groups in oligotrophic environments whilst the latter were present on the nutrient-rich coastal forelands. Before the interglacial period the coastal foreland was larger in extent with large herbivore populations from which hunter-gatherers could live. The use of fire to stimulate clonal geophyte production (*Watsonia* and *Hypoxis*) was evident in archaeological remains. The use of fire contributed to the vegetation patterns on a small scale, no doubt influencing local heterogeneity and the landscape scale patterning. Deacon (1983) mentions that during the more favourable interglacial periods human density was higher and use of fire would have been more significant in influencing vegetation patterns. The use of fire was rapidly adopted by settlers farming at the Cape, and the frequency of burning increased (Botha 1924). However too frequent burning coupled with overgrazing tends to reverse the desired effect for sedentary farmers, leading to dominance by shrubs.

Since the arrival of colonists in Chile, the matorral vegetation experienced a new fire regime (exponentially increasing in frequency); consequently grazing combined with frequent fires leads to a sparsely dominated *Acacia caven* anthropogenic community (Armesto et al. 1995). Although Holmgren et al. (2000) found that fire did not influence the abundance of herbs, rather the presence of introduced plant taxa and small mammals coupled with low nutrient status (altered by anthropogenic disturbances) was the main reducing effect on native herbs which prefer the cover of shrubs in matorral.

Post-fire Succession

Renosterveld is similar to lowland fynbos in that geophyte richness does not decline with an advance of post-fire succession (B.A. Walton, personal observation). Hoffman et al. (1987) distinguished that major difference between lowland fynbos and mountain fynbos (which generally has more geophytes and annuals immediately following fire). Another difference found between lowland and mountain fynbos was that an increase in species richness occurred with an increase in vegetation cover in the former. Renosterveld diversity patterns seem to be maintained by fire to change overall tall-canopy dominance. Post-fire renosterveld vegetation is initially dominated by a ground stratum of an herbaceous flora (therophytes, geophytes and hemicryptophytes). Dwarf shrubs and shrubs (often forming two strata) follow the ground stratum.

Adamson (1938) stated that "very frequent fires result in the establishment of a low bush community which is not layered", suggesting that over-burning could reduce one or another stratum of the community (for example the dwarf shrub or forb component). Burchell (1811 sec. Boucher 1980) mentioned that renosterbos was becoming more abundant than other shrubs and grasses, due to cultivation, untimely burning and overgrazing. Many of the species occurring in WCR are resprouters (Levyns 1929b, Boucher 1981) and are stimulated to regenerate after fire, such as geophytes, graminoids and some shrubs, as well as bush-clump resprouting species of the genera: *Euclea, Olea* or *Rhus*. Clearly WCR is well adapted to fire-cycles, as 27% of species are resprouters and 22% of species are geophytes from the collected sample by Boucher (1981). Owing to the large geophytic component, the evidence of a response to fire is clear, as the below-ground perenniating organs escape natural wild fires. A small pilot study in WCR at Elandsberg Private Nature Reserve (hereafter denoted as Elandsberg) in the Wellington District, also showed most species richness at a burnt site relative to an un-burnt site (B.A. Walton, unpublished data). From many field observations it seems that fire facilitates temporal niche apportionment of species. Temporal changes in availability of a habitat by fire allows for the relatively high species richness at the scale of 1 m^2 to 0.1 ha.

Characteristically following fire, as in fynbos, the ground stratum is rapidly dominated by resprouting (or flowering, Michell 1922, Levyns 1924) geophytes and hemicryptophytes, open space allows therophytes to germinate with sufficient moisture availability. Verboom et al. (2002) measured a positive response of flowering in the geophyte *Ehrharta capensis* to the addition of nutrients and clipping (to simulate fire or grazing) without depletion of the storage organ. This post-fire persistence and immediate blooming of species is evidence that fire has influenced the Cape flora over a long ecological time period by creating this niche which is occupied by a large component of the flora (Goldblatt and Manning 2002). The availability of light (Michell 1922), free nutrients and other stimuli following fire is plausibly a causal mechanism eliciting flowering *en masse* in otherwise uneven flowering within populations. The shrub component follows either soon after a fire or a year (or few) later, for example the seeders: *Hermannia alnifolia*, *H. scabra* and *Printzia polifolia*; the resprouters: *Anthospermum decumbens*, *A. spathulatum*, *Helichrysum teretifolium*, *Phylica strigulosa* (B.A. Walton, unpublished data), *Phylica plumosa* var. *horizontalis* (with a stout rootstock from which to resprout from; Pillans 1942) and *Stoebe plumosa*.

Elytropappus rhinocerotis seed is produced in winter and germination rates are higher after a years dormancy, declining after the fourth year (Levyns 1929a), and are stimulated by fire (Levyns 1927, 1929b). Brush-cutting did not elicit the same response as fire in stimulating renosterbos germination (Levyns 1929b, 1935b), but only increased the hemicryptophyte component eventually selecting for those growth forms resulting in structural degradation (see Boucher 1995). Renosterbos produces copious numbers of seed that are extremely light with a feathery pappus easily dispersed by wind. Seedlings are moisture-sensitive (Levyns 1927), thus a protracted germination trait ensures the seedling emergence is successful (seedlings emerge for many weeks, Levyns 1935a). Levyns (1935b) intelligibly noted the difference in the more rapid return of renosterbos dominance in Stellenbosch renosterveld and a longer succession in Riversdale renosterveld - attributing the difference to damp winter months in the former. Once the renosterbos has developed a deep tap root (see Scott and van Breda 1937) it can withstand a variety of temperature and moisture fluctuations and is the prime reason for its successful dominance (although roots are shallower in shallow or moister soils). Also noteworthy is the rapid emergence either by seed or resprouting of nitrogen-fixing species from the genus *Aspalathus*. It appears that after a fire (in the absence of herbivores) a whole suite of palatable shrubs is able to germinate from seed and rapidly grow into dense stands, for example *Hermannia alnifolia* and *H. scabra* (B.A. Walton, personal observation). These species could experience the effects of overcrowding (or self-thinning) as discovered in some proteoids (Bond et al. 1995). Another possibility is that the overtopping (*sensu* Campbell and van der Meulen 1980) or an overstorey effect (see Vlok and Yeaton 1999), of dominant *Elytropappus rhinocerotis* or *Athanasia trifurcata*, influences differences in species richness between mature and post-fire stands. Quite opposite to these latter references would be the role of facilitation by mother plants of the aforementioned dominant species. Renosterbos seedlings are intolerant of shading by a dense canopy (Levyns 1927, 1929a) and will usually germinate in open spaces, also in the absence of fire.

Thus the post-fire succession of renosterveld is similar to that occurring in fynbos with an initial dominance by annuals, geophytes and hemicryptophytes, with a seral development into domination by either a few or many shrub species. Shrub domination by one or two species appears to be an interaction between this growth form only - thus all other growth forms are unaffected by it - or benefit from the canopy structure.

The "climax" stage does not imply there is an exclusion of species, rather it appears that *Elytropappus rhinocerotis* has a facilitative role as a nursery or refuge site protecting geophytes, forbs, hemicryptophytes and dwarf shrubs from exposure or grazing and trampling. This process of facilitation in renosterveld could be due to: photoperiodic requirements of other species, moisture retention (and increased infiltration) by the pedoderm (with associated worm, moss and lichen activity), protection from grazers and as structural support for lianellas. On old fields species richness seems clustered around *Elytropappus rhinocerotis*. Feral pigs (*Sus scrofa*) unfortunately take advantage of this occurrence, proceeding to scour geophytes clustered around the base of *Elytropappus rhinocerotis*, often uprooting shrubs in the process (B.A. Walton, personal observation). Thus feral pigs have revealed this facilitative process, albeit retarding recovery on to old fields!

Californian shrublands are composed of dominant sclerophyllous fire-adapted plants that are: resprouters, reseeders or a combination of these strategies (Moritz 2003). Community composition changes with topographical, edaphic and pyrogenic factors (Moritz 2003). A study of post-fire succession in Californian chaparral (Guo 2001) identified temporal changes in the species diversity, density, cover and biomass between different life-forms and plant functional types. Initially annuals (with the highest turnover rate), suffrutescent herbs and resprouters dominate the post-fire community, and then over a few years shrubs begin to dominate in cover, replacing the temporary post-fire floral diversity (Keeley 2000). Quite logically, resprouters (having the least temporal variation in species composition) are quick to recover after fire and contribute a larger total biomass relative to reseeding shrubs. Reproduction in a chaparral geophyte *Zigadenus fremontii* occurs shortly after a fire although inter-fire intervals maintain growth and carbohydrate storage (Tyler and Borchert 2002). With the increase in biomass and cover of woody shrubs a few years following fire, species richness of "fire-annuals" tends to decline noticeably (Guo 2001, Keeley 2000). This is in contrast to mountain fynbos communities which are consistently species rich throughout succession. Post-fire succession in fynbos shows a gradual decrease in species richness, but overall the species richness, immediately following fire and long after a fire, shows little difference. Thus the "initial floristic composition" model of succession proposed by Egler (1954) is applicable to fynbos as all, or most, species are present at a site following fire. Post-fire succession at a lowland fynbos site (Hoffman et al. 1987) showed highest species richness five years after a fire rather than 12-19 years after a fire, similar to chaparral.

Successional patterns may change in the presence of exotic grasses and forbs that out-compete shrub seedlings creating a “new” fire regime in fire-adapted vegetation. Fire disturbance has formed a complex mosaic within grasslands; in addition, frequent fires cause a replacement of scrub by annual grassland (Keeley 1984) effectively converting a more stable scrub or grassland state into an annual fire regime. Coastal sage scrub is recently endangered due to human development as an anthropogenically altered fire regime, can result in “type conversion” into grassland (Keeley 1990). Similarly exotic grasses and forbs are abundant when oxidant levels and nitrogen deposition is high (as in old fields), especially so if linked to an increased fire frequency (Giessow and Zedler 1996). Coastal sage scrub sites following fire in the first year are dominated by resprouting shrubs (three quarters of the shrub species) and herbs (including resprouting grasses), the latter comprising up to three quarters of total species. Post-fire seedling recruitment occurs more abundantly after the second year in coastal sage scrub, and pyrophytic endemics start to decline in abundance (as in chaparral-which share many species). Interestingly two recruitment modes occur in chaparral: one being disturbance dependent (for most species-both facultative and obligate seeders) and the other disturbance independent (a few species which are obligate-resprouters and recruit seedlings in shade of mature stands) (Keeley 1998, 2000). The major difference between coastal sage scrub and chaparral is; in the absence of fire perennial herbaceous seedlings are recruited in the former at any time-forming uneven aged stands (Keeley 1984), unlike the typical post-fire annual flora in chaparral.

Coastal sage scrub is similar to renosterveld in that species have a smaller stature with faster growth rates and light wind-dispersed seeds. The resilience of coastal sage scrub was modelled (Westman and O’Leary 1986) in relation to differing intensities and frequencies of disturbance dependent on constituent component strategies.

1.6.2. Biotic Influence

Ungulates

In the natural renosterveld plant community much grazing occurs. In the pre-colonial era, the coastal forelands supported many species of large herbivorous vertebrates (Skead 1980). This natural component of the landscape is sadly gone, hunted out by 1700 (Rebelo 1995). Presently indigenous herbivore (game) farmers are breeding certain species, and knowledge of vegetation condition and a suitable stocking density for farms is vital to sustain an ecosystem. The effect of herbivory is known to influence species composition, structure and dynamics in the CFR (Johnson 1992), whereby nitrogen-fixing plants such as *Aspalathus* possess spines amidst low leaf nitrogen levels of the majority of fynbos species. Campbell (1986) found that stem spinescence is more prevalent in non-fynbos shrublands with nutrient rich soils than in fynbos (with oligotrophic soils), attributed to larger leaf sizes and higher nutritive values of the former. Thus thicket and renosterveld ecosystems on more nutrient-rich soils show higher levels of herbivory, which suggests that nutrient availability has a pronounced effect on structure and function at all levels within the ecosystem. For the purposes of plant diversity conservation, focus is now given on the impacts of other biota and ecological processes conserved in- and outside reserves (Boshoff et al. 2001). Specifically medium and large sized mammals, which may ameliorate or inhibit certain life-forms in different seres, have been considered for effective conservation management. Herbivores are known to prefer old fields or natural (self-maintained) grazing “lawns”. Grazing on these “lawns” is easier and possibly stimulates tussock growth, whilst the common *Cynodon dactylon* sends out more stolons in response to grazing pressure.

Jones (1986) noted in a study at the Jan Briers Louw Reserve (formerly Eensaamheid Reserve and hereafter referred to as JBL) that brush-cutting, grazing (by sheep and cattle) in a reserve extension (20 ha) resulted in less *Themeda triandra* than in the reserve (8 ha, infrequently grazed by cattle, with more species than the extension). Savory (1986) noted at JBL that the grazed reserve extension area had higher cover abundances than the ungrazed reserve, noting a difference in life-form groups, whilst Scott (1986) mentioned that the species richness was higher in the grazed extension. A small project at Elandsberg (Stander 1988) measured the effects of grazing and found that species richness and community structure was not significantly different between grazed and ungrazed areas, but pointed out that grazed sites had more prostrate and bushy growth forms and higher cover-abundances, with less prostrate growth and cover on non-grazed sites. Heydenrych (1995) says "overgrazing, or grazing at the wrong time of year and habitat fragmentation for cultivation will lead to the decline of natural flora".

Shrub seedling recruitment in the absence of fire occurs in the semi-arid southern Californian coastal sage scrub-grassland mosaic (DeSimone 1999). In the northern Californian grassland the evergreen shrub *Baccharis pilularis* becomes invasive with herbivory suggesting that grazing can give shrubs a competitive advantage over grasses. In renosterveld a similar process may occur, whereby grazing pressure may facilitate shrub colonization, by reducing the cover of grasses and forbs. This process would be contrary to the popular belief that mammal-maintained grassy areas would cause a persistence of the grassy component. In the mediterranean vegetation of Israel, grazing caused a significantly greater density of geophytes than non-grazed paired sites, and this positive effect was less in low productivity sites (Noy-Meir and Oron 2001).

Other Vertebrates

The high richness and abundance of geophytes in renosterveld is apparent in the field. Geophytes such as *Micranthus junceus* show an adaptation to dispersal by mole rats (*Georychus capensis*, Lovegrove and Jarvis 1986) producing side cormlets as well as in *Gladiolus alatus* (B. A. Walton, personal observation) and leaf bulbils (*Sparaxis bulbifera*; B. A. Walton, personal observation). Aardvarks (*Orycteropus afer*) occur in renosterveld, eating both ants and termites (Taylor et al. 2002). Porcupines (*Hystrix africaeaustralis*) feed on bulbs and occur amongst (agricultural) perturbations and being resilient are able to survive through their reproductive plasticity (van Aarde 1998). Frugivorous birds are responsible for the dispersal of some bush-clump species like; *Rhus* species, *Gymnosporia buxifolia*, *Putterlickia pyracantha*, and therefore contribute to environmental heterogeneity in renosterveld Also bush-clump species often possess defence strategies for herbivory (spinescence) (Knight et al. 1989), especially so in nutrient-rich environments (Campbell 1986). Aardvarks, foxes and other insectivores in turn inhabit clumps of olive trees (*Olea europaea* subsp. *africana*) or clumps of *Maytenus acutifolia*, *Rhus* and *Salvia* species, often associated with heuweltjies.

The author has seen the following species eaten at Elandsberg by porcupines and mole rats; *Babiana angustifolia*, *Cyanella hyacinthoides*, *Micranthus tubulosus*, *Moraea lewisiae, Moraea villosa*, *Ornithogalum thyrsoides*, and *Oxalis purpurea*. *Babiana angustifolia* occurs in seasonally inundated areas and sandy soils alongside rivulets in association with *Triglochin bulbosa*. This same habitat is also favoured by feral pigs (*Sus scrofa*), rooting for geophytes, possibly competing directly with indigenous small mammals, even disturbing nesting snakes. Feral pigs forage for geophytes intensely during the wet period when the ground is soft and easy to dig, thus the wetter sites are utilized the most throughout the season until hard and dry (B. A. Walton, personal observation), similar to the behaviour of the porcupine see Bragg 2003).

WCR communities almost support the entire population of the endemic and rare geometric tortoise *Psammobates geometricus*, with outlier populations in the Berg River Valley. Small conservation reserves for *Psammobates geometricus* (Baard and Mouton 1993) have ensured the survival for some remaining patches (Baard 1993). *Psammobates geometricus* is absent from both strandveld and sand-plain fynbos with its moisture and food requirements suitably found in renosterveld (Baard 1995). Some typical food plants of *Psammobates geometricus* include *Babiana angustifolia*, *Briza maxima*, *Cyanella hyacinthoides,* *Cynodon dactylon*, *Lachenalia contaminata*, *Themeda triandra*, *Ehrharta calycina*, *Eragrostis curvula* and *Pentachistis curvifolia* (Balsamo et al. 2004). Based on personal observations it would appear that *Psammobates geometricus* actually prefers the Swartland Alluvium Fynbos habitat than Swartland Shale Renosterveld.

Insects

Activities of harvester termites (*Microhodotermes viator*) create a regular mosaic formation of vegetation within fertile soil patches known as termitaria (heuweltjies) with clear differences from the surrounding matrix. These termites inhabit ancient termitaria, new sites or occur in association with other termite species such as *Angulitermes braunsi*, foraging by day or night depending on soil surface temperature (Coaton and Sheasby 1974). Characteristically forming mounds from frass deposition, these organisms consume considerable amounts of biomass (both fresh and dry material) and bring subterranean minerals to the surface. The author has observed harvester termites (*Microhodotermes viator*) cutting fresh plant material in the field: *Athanasia trifurcata*, *Babiana odorata*, *Cynodon dactylon*, *Elytropappus rhinocerotis*, *Eragrostis curvula*, *Ficinia oligantha*, *Plantago coronopus*, *Moraea galaxia*, and *Tribolium* species. Termites mostly cut grass or sedge culms and also *Elytropappus rhinocerotis* (renosterbos) tips leaving them in the open to dry out, and later transporting them to their nest. Little "piles" of dead plant material often indicate the nearby presence of a nest! According to A. Milewski (personal communication) there could be a possible overlap with the hook-lipped Black Rhino (*Diceros bicornis*) in several of its dietary choices! Most green geophyte leaves and renosterbos are unpalatable to ruminants. The efficiency of the harvester termites in collecting fresh and dry plant material may explain why the ground is often devoid of litter! Termites perform an important role in nutrient cycling, by both collecting above ground material and concentrating it into piles and then nests, and by transporting minerals to the surface soil layers. This overall process creates heuweltjies which are more nutrient rich than the surrounding renosterveld matrix. These nutrient rich termitaria facilitate colonization by therophytes and certain geophytes (*Moraea flaccida*). There are clear and significant differences in on- and off-mound plant assemblages (both species and life-forms), with species benefiting from higher available nutrients (advantageous for exotic annual grasses and therophytes like *Avena barbata* and *Bromus pectinatus*), effective permeability and frequent disturbances. Termitaria often lack a shrub cover, or sustain certain shrub species which occur in low densities in the renosterveld matrix like *Lobostemon argenteus* or *Salvia chamelaeagnea*. Termites at a landscape scale create positive small-scale disturbances and in the process produce a dappled effect of landscape heterogeneity. Around October time termites take to wing leaving their nests in search of new homes, it is quite a site to witness as swifts or martins are ready making snatching noises in the air as they literally decimate them.

Ants occur in renosterveld and potentially collect seed of elaiosome-bearing seeds such as *Sebaea* species and Polygalaceae (N. Helme personal communication). Oil collecting bees pollinate *Diascia* species, *Hemimeris racemosa* and other oil-producing plants from the Orchidaceae (*Corycium orobanchoides*, *Pterygodium alatum*, *P. catholicum*; Pauw 2004). In short a myriad chain of interactions occur in the seemingly mundane renosterveld vegetation.

Burrowing by small and large mammals constantly breaks up the soil surface creating depressions facilitating establishment of many therophytes and geophytes. Thus the interactions by termites and small mammals contribute to local species richness by creating small scale disturbances which facilitate the establishment of pioneer species and biotically dispersed species. However feral pigs seem to hasten the spread of alien annual grasses and forbs as their digging size is larger than porcupines (B.A. Walton, personal observation).

1.6.3. Succession

The discussion here of succession relates to that following ploughing. Other types of anthropogenic disturbances such as hydrological changes to drainage catchments by dam building, soil mining; and primary succession following rainfall erosion will not be mentioned in the scope of this review.

Models of Succession

I suspect the pattern of shrub dominance in renosterveld reflects a sequence of facilitative and/or tolerant succession related to fire strategies of plants and niche apportionment by different life-forms. It might also be determined by the soil nutrient status, enabling a short span towards maturity of the component species. Guo (2001) noted that different plant groups play different roles during post-fire succession and that these groups change in terms of their biomass (resource allocation), cover and diversity with time. After much quantitative research on successionally induced community compositional changes on old fields there is still no general unified theory able to predict the pathway and outcome(s) of composition and structure (Kahmen and Poschlod 2004). In short, secondary succession is determined by local environmental site and propagules variables.

Plant communities are complex assemblages of species with an interacting web of processes, however the sum of its parts does not always equal the whole, and *vice versa*. Possibly more than one type of succession process occurs in a landscape depending on the scale of disturbance. The type of succession is habitat specific, such as in: alluvial plains, wetlands, mesic/xeric, or elevated sites. Whittaker (1974) described a “climax pattern” hypothesis where environmental gradients determine local climaxes and species are independent and “shared” by communities in a “steady state climax”, thus a departure from a climax state determined by climate alone. The sequence of arrival and initial composition of species also determine the subsequent assemblage dynamics as well as the sequence of disturbances types themselves (Fukami 2001).

Connell and Slatyer’s (1977) mechanistic models of succession, namely: facilitation, tolerance and inhibition assume that colonizing species have high seed production, an ability to germinate in disturbed environments, rapid growth and seed dormancy. These equilibrium models assume tight linkages exist amongst species (West and Yorks 2002), implying that competition and facilitation induce abiotic changes to the local environment enabling an advancement to a defined climax state of stability in relation to climate. The facilitation model assumes pioneers are the initial arrivals that improve conditions for the subsequent arrival of perennial or climax species which later out-compete them. The tolerance model assumes species are not displaced by competition but rather niche apportionment allows for co-existence. The inhibition model assumes pioneers-regardless of strategy-occupy and preclude establishment of later arrivals, i.e. a pre-emptive model without succession (bar the initial establishments). Non-equilibrium conceptual models include: the lottery model (*sensu* Chesson and Warner 1981, Dewi and Chesson 2003) which predicts that community components are randomly assembled; or the state and transition model (Westoby et al. 1989, West and Yorks 2002) of stable or unstable states that change slowly or rapidly in response to endogenous or exogenous disturbances.

Resilience

Lavorel (1999) suggests that resilience of mediterranean vegetation to disturbance is attributable to evolutionary history. Recovery from disturbances such as fire, grazing and soil disturbances are rapid and ameliorated by a change in relative abundance of species and efficient regeneration strategies. There are three ways in which ecological diversity contributes to community resilience, namely: (1) a shift in abundance of response groups following a disturbance, (2) random lottery model effects within response groups’ maintaining high species richness and (3) landscape scale variation (spatio-temporal) of different seres creates a patchy mosaic allowing dispersal between different-aged patches. Resilience is the quantitative property of the speed of recovery of an ecosystem variables' return to a stable state (implying equilibrium exists). Resilience thus varies among ecosystem components and processes, and experimental studies indicate that ecological diversity tends to increase resilience to disturbance (Lavorel 1999, Guo 2001). Understanding the recovery pathway following disturbance, is important for research and management. Armesto et al. (1995) describe causes and mechanisms that influence or determine vegetational change. The three causes of succession, namely (1) site availability due to disturbance or death, (2) differential colonization due to life history attributes and location of species (slightly different from the lottery model) and (3) differential performance of species. In South Africa research is required to contrast fire resilience strategies of serotinous fynbos shrubs with short dispersal distances ("in-situ resilience"), as opposed to well dispersed renosterveld shrubs ("resilient by migration"; Cowling et al. 1987).

Succession after Ploughing

Studies of post-ploughing succession are poorly documented in the Fynbos Biome. Ploughing of the Swartland occurred rapidly after the arrival of settlers as soon as the fertility of the region was discovered. From a farming perspective the presence of *Anthospermum aethiopicum* (Levyns 1935a), *Elytropappus rhinocerotis* (Levyns 1935a, Scott and van Breda 1937) and *Eriocephalus africanus* in stony ground indicated good quality agricultural soils (M. Gregor, personal communication), which increasingly were broken into with the advent of mechanized farming since the 1950's. Dry-land agriculture poses many problems in Australia and South Africa where salinity levels of the soil and groundwater increase due to the removal of deep-rooted natural vegetation (see Flügel 1995).

The remaining portions of WCR are comparable in size to remnants of the prairies of North America, steppes of Russia, the mallee scrub (McDowell and Moll 1992) in the wheatbelt of southwestern Australia (Dirnbock et al. 2002) - all severely reduced by agriculture. The AGC has a contiguous viable fragment of WCR forming a continuum with mountain and lowland fynbos. Dale Parker (1982) mentioned that "it is not yet established how long, if ever, it will take for the indigenous veld to take over again on abandoned agricultural lands" and stated that "a partial recovery depending on the area is perhaps possible after 25 years". Tiny fragments and patches in a "sea" of agriculture remaining on hillocks and slopes are unrepresentative of the former range of WCR on fertile flats (McDowell and Moll 1992). The presence of many Red Data species in fragments of the flats, indicate the once wider pre-agrarian distributions (McDowell and Moll 1992) and is a consequence of extensive agricultural clearance" (Hall 1987). Kemper et al. (2000) states that fragmentation increases from east to west (15% and 4% remaining vegetation respectively), as a consequence of topography where the WCR is an undulating foreland enabling total transformation unlike the more rolling SCR plain with steep hillsides. Kemper (1997, 1999) showed that small fragments contain more individuals of certain geophyte species than larger fragments (*Babiana ambigua* and *Ornithogalum thyrsoides*; B. A. Walton, personal observation of *Ornithogalum thyrsoides* and *Sparaxis bulbifera*) and no significant difference in diversity between small and large patches was found to occur. However this may be an artefact of micro-habitat preferences of local species in remaining fragments traditionally unsuitable for agriculture, as well as dense populations of "weedy" species like *Ornithogalum thyrsoides* (Kemper 1999). This could indicate that renosterveld vegetation experienced regular disturbances in the past and the floral component is pre-adapted to survive disturbances (whether fire or browsing). Certain species persist in small patches over time, in spite of edge effects and even grazing (protected by the formulation of secondary poisonous compounds like *Ornithogalum thyrsoides*, especially so if clonal or self-compatible) and some may well occur naturally in small pockets in specific microhabitats which could well be marginal habitats for agriculture (for example wetlands and hardpans). Typically in renosterveld after the destructive effect of ploughing is the colonization of bare ground by many ruderal species and grasses. *Cynodon dactylon* rapidly forms a closed mat creating an old field, and usually occurs on deep rich soils where its roots can penetrate the water table surviving the summer drought period (Galiano 1985). In addition *Cynodon dactylon* is a C_4 grass able to utilize maximum solar radiation and grow during summer (shade inhibits growth: Guglielmini and Satorre 2004), and withstand grazing pressures.

Fish (1988) compared ploughed and unploughed renosterveld vegetation at Elandsberg and concluded that there was no significant difference in species richness between the two treatments. Some areas were dominated either by *Athanasia trifurcata* or *Elytropappus rhinocerotis*, and that this "switch in dominance may be related to chance factors such as the season of ploughing (or burning!). *Athanasia trifurcata*, *Elytropappus rhinocerotis*, *Hermannia* species, *Lobostemon argenteus*, *Phylica* species and a grass taxon were observed as being constant in the field (Fish 1988). McDowell and Moll (1992) mentioned that disturbance by chemical insecticide application, herbicide application, fertilizer addition and tilling all have an impact on diversity, and their example of an old field adjacent to the 20 ha Kalabaskraal Nature Reserve (near Malmesbury) has "been re-colonized by just under one dozen indigenous species", after 15 years of recovery. The surrounding land-use (fertilizers and herbicides) affects soil chemistry, possibly excluding some indigenous species, leading to dominance by alien species (McLaughlin and Mineau 1995). As early as Thunberg's time (no doubt earlier) European taxa were observed, transported via wheat seed, for example: *Hordeum murinum*, *Lolium temulentum*, *Phalaris canariensis*, *Polygonum aviculare* and *Urtica urens* as far north as the Karoo (Asbestos Mountains).

Colonization on old fields in Europe follows a certain pattern of continuing species replacement (Wilcox 1998), also with added disturbances (Debussche et al. 1996). In contrast shrub recovery on to old fields from natural vegetation is dependent on the location of the propagule source (Lavorel 1999, Degn 2001). Interestingly Wilcox (1998) found that later-colonizing species accelerate succession, whilst increasing the abundance of annuals will not retard succession. Warren (2000) experimented with clover (*Trifolium repens*), a nitrogen-fixer, and suggested that the increase in nitrogen may facilitate grasses but retard the succession of forbs (grazing was also found to increase the cover of clover). European annual grasses now dominate Californian prairies that had common indigenous perennial grasses (Brown and Rice 2000), where *Vulpia myuros* (zorro fescue) exhibited a plastic growth response to density and decreased the above ground biomass of perennial grasses and their survival with an increase in its density. A similar pattern has occurred in western United States where nutrient additions have converted ecosystems into “old fields” of *Centaurea* forbs from the original nitrogen-limited grasslands (LeJeune and Seastedt 2001). Lavorel (1999) suggests that disturbed sites favour species with high fecundity with associated large soil seed banks. This biased lottery draw of species frequencies proportional to seed bank frequencies and a potential to achieve positive growth rates results in species diversity (Lavorel 1999) evidenced in South African shrublands. In the case of restoration of Californian grasslands or prairies, one has to evaluate potential sites so that further type-conversions are avoided, i.e. sites dominated by alien annual grass species may have been former indigenous grasslands or shrublands. Site evaluation of the substrate in this regard is important, as the perennial bunchgrasses are physiologically limited to deep soils sustaining their rootstocks. Whereas the persistence through summer as seed by alien annual grasses can occur on shallow soils (< 25cm) which can be rocky, porous and slightly alkaline (Keeley 1993).

To summarize briefly it seems that in the absence of an upper stratum component in the vegetation, species richness is considerably lower. This can be attributed to frequent disturbances by fire (savanna fire regime simulation) or overgrazing/selective grazing of palatable shrubs. After ploughing the consequent removal of the seed bank and geophyte bank causes secondary succession to become a lengthy process relative to natural post-fire succession. Grazing does not seem to be destructive in unploughed vegetation compared with old fields which are more sensitive to grazing.

1.7. Distribution, Typology and Floristics of Renosterveld

Renosterveld has five different variations determined by geographical location occurring on the coastal forelands, lower slopes and the upland interior (included by Moll and Bossi 1984) in the southwestern and eastern Cape in the CFR. Included here are the escarpment renosterveld and outliers in the north western province (Kamiesberg, see Acocks 1953, Rutherford and Westfall 1994, Low and Rebelo 1996), thus broader than the Capensis Region as defined by Taylor (1978) or Kruger (1978). Contemporary mapping efforts have further included newly delineated renosterveld vegetation types (Mucina and Rutherford 2004), in these five broad renosterveld types.

Coastal Renosterveld described by Acocks (1953, Veld Type No. 46), comprises two coastal foreland portions: one western (known as the Swartland) and one eastern (known as the Ruêns) and an elevated smaller portion at Elgin. The vegetation type formerly referred to as WCR (Rebelo 1996) comprises two Broad Habitat Units defined by Cowling and Heijnis (1999), which are Boland Renosterveld (BHU 32) and Swartland Renosterveld (BHU 31), and is now (for the most part) referred to as Swartland Shale Renosterveld (Mucina and Rutherford 2004). Newly described vegetation types of Swartland Silcrete Renosterveld occur as isolated patches on the West Coast forelands. Western Silcretes (Mucina and Rutherford 2004) occur on the South Coast forelands. The small elevated portion originally included by Acocks in Coastal Renosterveld, then included into South and South West Coast Renosterveld by Rebelo (1996), is now delimited as Elgin Shale Fynbos (Mucina and Rutherford 2004). South Coast Renosterveld (Rebelo 1996) was assigned to Central and Eastern Overberg Renosterveld, and Western Overberg Renosterveld BHU's (Cowling and Heijnis 1999).

Acocks (1953) Veld Type No. 43 comprises all the elevated inland renosterveld vegetation as Mountain Renosterveld. Rebelo (1996) split this into three different vegetation types based on locality: Central Mountain Renosterveld, Escarpment Mountain Renosterveld and North-western Mountain Renosterveld. Thus Central Mountain Renosterveld is upland renosterveld which occurs on the Great and Little Karoo basin fringes and westward towards Worcester. The vegetation has an open to medium-dense canopy, either low or high of *Elytropappus rhinocerotis* and *Pteronia incana*, with scattered emergent trees and large shrubs such as: *Acacia karroo*, *Aloe ferox*, *Euclea undulata*, and *Rhus* species. Grazing depresses the grass component; there is also a forb and succulent component. It is grazed and ploughed for pastures, cereals, fruit orchards and vines. Rainfall is between 250-400 mm p.a., falling in winter mainly. Escarpment Mountain Renosterveld (Low and Rebelo 1996) occurs on the Escarpment foothills from Calvinia to Sutherland, then to

Beaufort West and the Roggeveld, Koms and Nuweveld Mountains. It is dominated by *Elytropappus* species and *Relhania genistifolia*, and used for stock farming (sheep). Mean annual precipitation is between 200-300 mm and it falls mainly in winter. North-western Mountain Renosterveld (Low and Rebelo 1996) occurs in the Kamiesberge Mountains near Leliefontein in Namaqualand, zonal between fynbos and Succulent Karoo along an aridity gradient. Dominant species are *Elytropappus rhinocerotis*, *Eriocephalus africanus*, *Euryops lateriflorus* and *Nylandtia spinosa*. It is ploughed and grazed, with stock farming, none is formally conserved. Mean annual precipitation is 250 mm, mostly in winter (with some mists in summer and winter).

Renosterveld communities are exceptionally rich in geophytes (Duthie 1930, Cowling 1983a, Paterson-Jones 1998) adapted to seasonally dry climates, notably of the families: Asparagaceae, Iridaceae, Hyacinthaceae, Asphodelaceae, Oxalidaceae (Boucher 1981) as well as Amaryllidaceae, Geraniaceae and Orchidaceae (Goldblatt and Manning 2002) as well as Anthericaceae and Colchicaceae. The frequency and diversity of geophytes, according to Kruger (1979), increases with that of soil fertility, aridity and fire frequency. Geophytic species richness is most pronounced in WCR extending northward into the succulent Karoo (Procheş et al. 2006), compared with the lower geophytic richness in SCR where the understorey is predominantly grassy (Paterson-Jones 1998). Goldblatt (1976) defined an area corresponding to the winter rainfall region of the Fynbos Biome (and including the Succulent Karoo), which constitute the core of diversity and endemism for the genus *Moraea*. Many of these *Moraea* species are nearing extinction (or are extinct) due to the plough. Other genera with species near to extinction are *Gladiolus watsonius* and *Oxalis natans*. The flora of the CFR has a low proportion of annuals (6.8%) for a largely semi-arid climate compared with California (30%) and Chile (16%). This could indicate that the CFR is more resilient than other mediterranean vegetation types with a predisposition to shrub cover (annuals are most abundant following disturbance by fires or grazing). Annuals persist in time by producing large seed outputs and contribute to a seed bank, whereas geophytes invest energy in below ground organs to retreat from “unfavourable growth periods” (Goldblatt and Manning 2002). Other speciose plant families that occur in renosterveld are: Asteraceae, Boraginaceae, Fabaceae, Rhamnaceae, Rosaceae, Rubiaceae and Thymelaeaceae (Goldblatt and Manning 2002). Genera such as: *Gnidia*, *Helichrysum*, *Hermannia*, *Lobostemon*, *Muraltia*, *Otholobium* and *Phylica* commonly occur in the renosterveld matrix.

Goldblatt and Manning (2000) noted that renosterveld shares few species with the adjacent fynbos vegetation, and consists of many microphyllous asteraceous plants with a dense shrubland and rich herbaceous flora. Renosterveld shrublands support many grass species (207 species occur in the

Fynbos Biome according to Goldblatt and Manning 2000), but is neither a grassland nor a woody savanna, rather a shrubby continuum from mountainous fynbos shrublands on to nutrient-rich lowlands, opening wide in places near wetlands or hardpans, alternating with lowland fynbos or strandveld on oligotrophic and tertiary sands, respectively. SCR has a higher proportion of grasses than WCR (Acocks 1953). Temperate grass subfamilies are most dominant in renosterveld compared with tropical grass subfamilies in the Fynbos Biome, and some C_4 grasses from the latter subfamily, like *Hyparrhenia hirta* and *Themeda triandra*, can dominate disturbed vegetation of road verges on shale or granitic soils (Linder 1989). The C_3 grasses of the WCR are from the Arundinoid and Pooid subfamilies (Linder 1989) of the genera: *Ehrharta*, *Eragrostis*, *Merxmuellera*, *Pentachistis* and *Tribolium* with some C_4 grasses, such as *Cymbopogon marginatus* and *Themeda triandra*. The Arundinoid subfamily has been further subdivided into the subfamilies: Arundinoideae and Danthonioideae with the genus *Eragrostis* in the tribe Eragrostideae of the subfamily Chloridoideae (Grass Phylogeny Working Group 2001), and *Ehrharta* in the Ehrhartoideae (Verboom et al. 2004).

The different and newly described renosterveld vegetation types (Mucina and Rutherford 2004) are defined according to their particular geology, structure and characteristic species. They are too numerous to mention here. In short Swartland Shale Renosterveld is typically shrubby whilst Swartland Alluvium Renosterveld has more open spaces and dominated by dwarf shrubs or hydrophilic grasses. Swartland Silcrete Renosterveld often has open hard-pan areas with unique decumbent or dwarf succulents. However even within a vegetation type structural variation exists between the amount and size of shrubs (and thicket or bush-clump elements) and the grass and herbaceous (including geophytes) components.

1.8. Conservation Implications

Little remains today of the once vast stretch of natural renosterveld vegetation which occurred on the West Coast forelands, (known as the Swartland; Meadows 2003), from Somerset West in the south to Piketberg in the north. Presently there is focus on the last remaining portions of WCR and SCR of the Fynbos Biome. With the aim to establish and understand the general vegetation patterns and processes maintaining species richness and abundance, with a view to conserving these threatened natural ecosystems.

High soil fertility and agricultural potential of coastal renosterveld regions (*sensu* Acocks 1953) resulted in severe transformation by agriculture for crops like: canola, vines, olives, *Eucalyptus* (for bee farming, windrows and woodlots) and grain (barley, rye, oat and wheat) and some forestry practices as well as artificial pastures (of grasses and herbs). Only 18 000 isolated fragments of coastal renosterveld remain (von Hase et al. 2003) of varying levels of ecological integrity. Within-fragment dynamics will ultimately be related to the surrounding matrix types (Jules and Shahani 2003). First Boucher (1981) estimated only 5.76% of WCR remains, then McDowell (1988) estimated that 3% remains of the original extent of WCR, and only 0.46% is conserved (6648 km^2) (Wood and Low 1998). Reyers et al. (2001) proposed that 9% remains, although Newton and Knight (2005) identified 6.5% as remaining, similar to the CCU (von Hase et al. 2003) estimate of 5% remaining for Boland, Swartland and Elgin Renosterveld Broad Habitat Units. Similarly the SCR region is also severely fragmented and first McDowell (1988) mentioned only 18% remains, then Kemper (1997) mentioned 15% remains, whilst the CCU (von Hase et al. 2003) calculated that 12% remains of Overberg Renosterveld, whereas Reyers et al. (2001) suggests 39% remains of south and south-west (i.e. including Elgin Renosterveld BHU) coast renosterveld. Mountain renosterveld is less transformed occurring in distinct portions unfortunately lacking phytosociological surveys with concomitant descriptions of community types. Reyers et al. (l.c.), using vegetation types of Low and Rebelo (1996), suggest that mountain renosterveld is almost entirely intact, where North-Western Mountain Renosterveld has 94%, Escarpment Mountain Renosterveld has 99% and Central Mountain Renosterveld has 80% remaining, respectively. Remaining fragments have an irreplaceable conservation value (*sensu* Pressey et al. 1994, Ferrier et al. 2000) as mapped by CAPE (Cowling et al. 1999, Young and Fowkes 2003) to achieve conservation targets (Cowling and Heijnis 2001, Cowling et al. 2003) and a high richness of endemic geophytes (Goldblatt and Manning 2002). Preceding agriculture, the pastoral Khoe-Kheon grazed their cattle and sheep in lowland vegetation (renosterveld) (Deacon 1983), and herbivores are still grazing renosterveld as additional feed on some farms. South Africa’s demand for housing, road widening/alteration, occasional brick-making and surface sand mining (B. A. Walton, personal observation) and alien plant invasions further threaten remaining fragments. As a consequence of fragmentation (or severe attrition in the case of coastal renosterveld), a simple rule of geometry applies: that the perimeter length of a patch changes as a linear function, whilst the area changes as a square function (Hunter 1996). The smaller a patch becomes the more area is exposed as an edge, and corresponding edge effects are more prevalent. Fragment size and degree of isolation from the “mainland” determine species diversity and ultimately the population viability (Donaldson 2002).

The challenge for conservation is that there is scant baseline information on renosterveld vegetation composition and responses to disturbances, to enable effective management decisions concerning land use. The cessation of ploughing on set-aside schemes, nature reserves or fallow land allowed for this study of old field succession. The Departments of Botany and Zoology, and Conservation Ecology at Stellenbosch University undertook research projects into various ecological aspects of renosterveld. For example at Elandsberg: Shiponeni (2003) studied seed dispersal syndromes, van Rooyen (2003) studied the extent of alien grass penetration into renosterveld, Midoko-Iponga (2004) studied competition by *Cynodon dactylon* and herbivory on selected shrub species, with disturbance treatments, Farley (in prep.) studied habitat preferences of herbivores at Elandsberg (all in WCR) and Raitt (2005) studied renosterveld in relation to management and grazing in the Heidelberg District. Luyt (2005) studied the habitat preference of bontebok in the Bontebok National Park in the Swellendam District, while Winter (2003) investigated land user willingness to conserve SCR fragments in the Overberg. Similarly, studies by Conservation Farming (SANBI) investigated renosterveld in the Nieuwoudtville area (Bragg 2003).

A concerted effort was made by the Botanical Society's Cape Conservation Unit (CCU) to compile a map of remaining fragments of WCR and SCR, with species checklists. This included all lowlying areas instead of only the higher slopes surrounding hills and mountains (see Tansley 1982). GIS data were prepared by Ian Newton (UWC) and the CCU in conjunction with ground surveying by Nick Helme to ascertain fragment condition, i.e. whether agricultural fields, old fields or renosterveld. Another objective of the CCU was to designate priority pilot areas to implement conservation partnerships with land users via the CapeNature (formerly Western Cape Nature Conservation Board) conservation stewardship project. The study area of this project coincided within the Agter-Groeneberg pilot site. Contemporary conservators and land users are therefore able to apply research guidelines within their daily operational activities. Understanding and interpreting ecosystem patterns operating in renosterveld, at a local and landscape scale are important to conservation. Information on vegetation dynamics at a fine scale in relation to disturbances such as fire, grazing or ploughing are necessary for an holistic overview of renosterveld ecosystem patterns and processes. This project interprets small-scale vegetation patterns in nature to facilitate conservation of this highly fragmented vegetation type. Finally implementation of relevant environmental policies coupled with empirical findings and adaptive management will be the key and litmus-test in deciding the future fate of renosterveld.

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Chapter 2

Agter-Groeneberg Conservancy: Description of the Study Area

Figure 2.1: North-East view from Slangkop ridge overlooking the Elandsberg flats with current- and old fields, as well as patches of Swartland Shale Renosterveld and Swartland Alluvium Fynbos (Mucina and Rutherford 2004) remnants leading up to the foothills

2.1. The Study Area

The study area (Figure 2.1) is a contiguous portion of the Agter-Groeneberg Conservancy (hereafter referred to as AGC), north of Wellington near Hermon in the Western Cape (Figure 2.2), at 19°00’–19°02’ E, 33°36’–33°50’ S, at altitudes ranging from 60 to 120 m. This area includes the Voëlvlei Provincial Nature Reserve (861.86 ha, hereafter denoted Voëlvlei), Elandsberg Private Nature Reserve (3800 ha, hereafter denoted Elandsberg) and Krantzkop munitions and rocket fuel factory (2500 ha, hereafter denoted Krantzkop). The eastern side of these properties are unfenced along the upper foothills as they meet the mountain slopes. Other properties in the AGC, not included in this study area include Rooshoek (1251.65 ha), Limietrivier (662.29 ha), Foxenburg (110.16 ha), Boplaas (78.63 ha), Palmiet Valley (349.34 ha), Lupinvale (161.146 ha), Kruishof (255.69 ha), Bool Smuts (23.498 ha), and Countess Labia (23.919 ha). Voëlvlei (Vogel Vallij, erf no. 253), managed by CapeNature (formerly Western Cape Nature Conservation Board), incorporates some unplanted Department of Water Affairs and Forestry property (Kasteels Kloof, erf no. 255). The AGC surrounds the Voëlvlei Dam and water treatment plant (managed by the Cape Metropolitan Council). Voëlvlei is a medium-use utilization zone characterized by previous user impacts, infrastructure and degradation (Anonymous 2000). Elandsberg is owned at present by Elandsberg Farms (Pty.) Ltd. and includes the erven Elandskloof (15), Langehoogte (14), and Bartholomiews Klip (17 and 19) with farmsteads. A brief history of Elandsberg is in Appendix 1. Additionally old fields at the Droogepan (6) and Tweespruit (8) erven have been set-aside and are included in the Elandsberg Private Nature Reserve. Krantzkop is the property of Armscor with Somchem a division of the Denel (Pty) Ltd. company on site, bordering Elandsberg from the south and including the farm Welbedagt (20), previously owned by Elandsberg prior to expropriation by Armscor. Krantzkop has a total area of 3000 ha, of which an exclusion zone of 200 ha incorporates the factory establishments, whilst another private area of 300 ha is on lease to a neighbouring farm for wheat production.

The area utilized by large herbivores at Krantzkop is 2500 ha (excluding herbivores inside the 200 ha exclusion zone). The three sites are contiguous from north to south with differences in large mammalian herbivore densities. Voëlvlei contains no intentionally stocked large mammalian herbivores except for occasional Grey Rhebuck (*Pelea capreolus*), thus serving as a control for the impact or influence of grazing on vegetation patterns. Elandsberg and Krantzkop are stocked with wild animals for the purpose of ecotourism, occasional game trophy hunting, and breeding programmes for the Plains Zebra (*Equus burchelli*, locally called the “quagga”) and TB-free Cape Buffalo (*Syncerus caffer caffer*). Krantzkop has double the biomass (kilograms per hectare of Large

Animal Unit's) compared with Elandsberg, thus forming a gradient from north to south of increasing grazing intensity. These sites were selected for research as they contain a portion of the last remaining Swartland Shale Renosterveld (Mucina and Rutherford 2004) and are all afforded protection status. Recently (2004) these three sites have been officially incorporated into the AGC due to efforts by the conservation stewardship programme of CapeNature, thus fulfilling a conservation objective of CapeNature.

2.2. Major Vegetation Patterns

The study area is located within Coastal Renosterveld (*sensu* Acocks 1953) of the Fynbos Biome (*sensu* Kruger 1978, Rutherford and Westfall 1994), classified later as West Coast Renosterveld (Low and Rebelo 1998) as well, in part, as the Boland Renosterveld BHU (Broad Habitat Unit *sensu* Cowling and Heijnis 1999). The vegetation of the study area (Figure 2.3) has recently been classified as Swartland Shale Renosterveld (Mucina and Rutherford 2004), a unit roughly encompassing Boland Renosterveld and Swartland Renosterveld BHU's (Cowling and Heijnis 2001). The Swartland Shale Renosterveld occurring at this portion of the AGC is found in the form of discrete patches, representing one of seven fragments larger than 1000 ha (Von Hase et al. 2003). The undulating topography of the West Coast foreland allows for a natural drainage system towards the Atlantic Ocean where the vegetation experiences wide differences in moisture availability. The Berg River (with its primary catchment area starting in Franschoek) drains the major portion of the West Coast forelands. The remaining renosterveld occurs in a narrow strip running south to north prior to the foothills of the Elandskloof Mountains, dissected by seasonal rivulets and rivers. Swartland Alluvium Fynbos and Swartland Shale Renosterveld (Mucina and Rutherford 2004) mostly occur on lower lying areas (Figure 2.3), often seasonally inundated due to the gentle undulating topography. Discrete stands of Swartland Shale Renosterveld also occur on west-facing slopes (like Blourug at Elandsberg), ridges and flats in clumps or isolated patches. Wetlands occur where drainage is poor or along the fringes of rivulets and rivers experiencing seasonal inundation. Thicket-like vegetation occurs often on ridge crests of Klipheuwel (for example Slangkop ridge on Elandsberg Farm); in addition unusual ferricrete outcrop (hardpan) associated communities occur in more sparsely vegetated patches.

Figure 2.2: Study area locality near Hermon in the Western Cape of South Africa

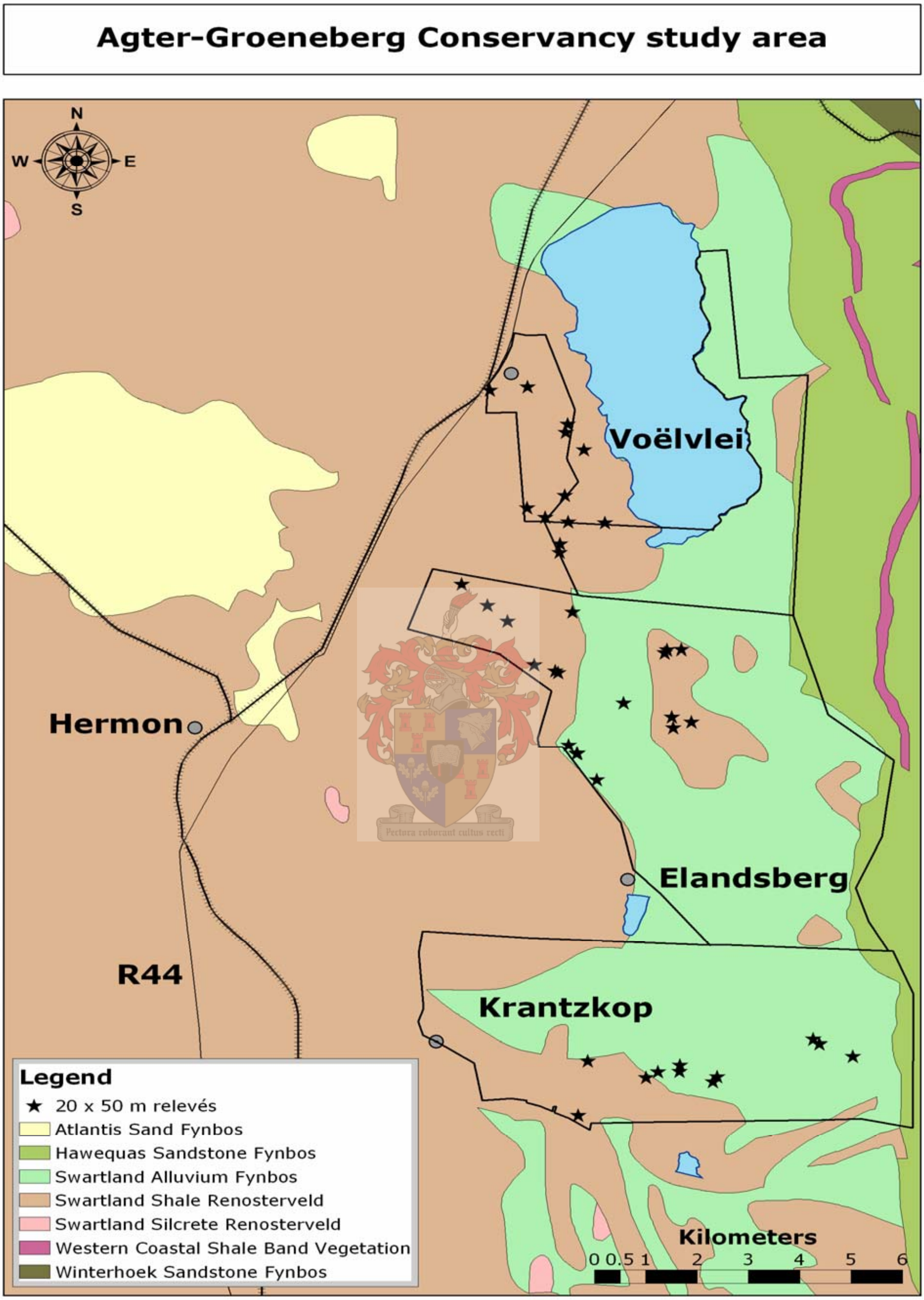

Figure 2.3: Study area showing the study sites (Voëlvlei, Elandsberg and Krantzkop), near Hermon. Asterisks indicate the relevé positions

2.3. Rainfall and Temperature Patterns

Winter rainfall is predominant in the study area, with dry summers typical of a mediterranean type climate. The renosterveld along the West Coast forelands receives between 250 and 600 mm of rain annually, with at least 30% falling in winter (Moll et al. 1984), most of it in form of cyclonic rain from cold fronts (Talbot 1947). The hot dry summers are conducive to fires, as are föhn-like berg winds, which decrease humidity (Wicht 1945) and sometimes precede winter anti-cyclones (Kruger 1979a).

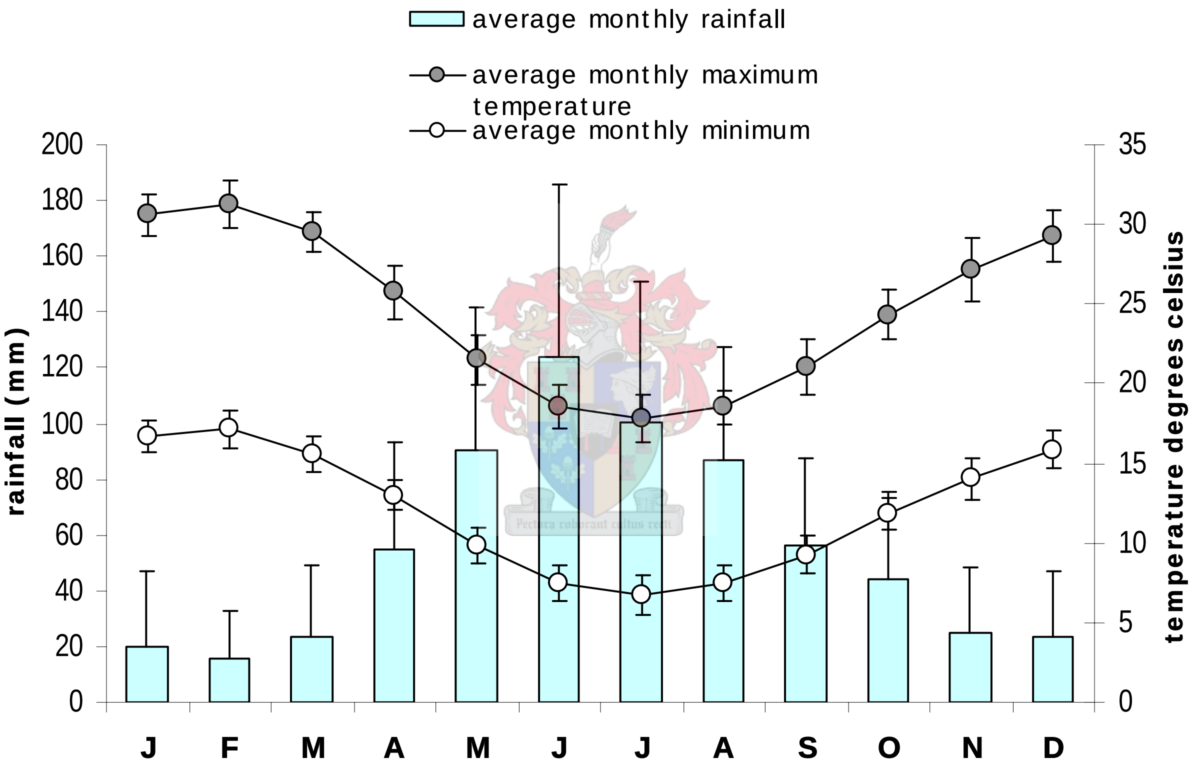

Figure 2.4: Average monthly rainfall (72 years) and temperature (39 years) data for Wellington (by courtesy of the South African Weather Service, G. Swart personal communication). The vertical bars denote standard deviation

Climate data for the study area is based on data collected from the Wellington station (25 km south of Elandsberg) supplied by Swart (2005) by courtesy of the South African Weather Service. A calculated monthly average for rainfall and temperature contained only years with full monthly recordings (from 1882-1927 and 1965-2004 for rainfall, and from 1965-2004 for temperature) (Figure 2.4.). The month of maximum rainfall is during the winter month of June (72 year average of 123.68 mm) and the month of minimum rainfall coincides during the peak of summer in February (72 year average of 15.58 mm), with an annual rainfall average of 663.5 mm (in 2001 851.9 mm was recorded and in 2002, 780.5 mm). The coldest temperatures occur in the month of July (average temperature for 39 years is 6.68°C) whilst the warmest temperatures occur in the month of February, (average temperature for 39 years is 31.26°C). Wind is strongly seasonal with south-easterly winds in summer (Fuggle and Ashton 1979) whereas in winter the north-western winds precede frontal low pressure cells, originating from the circum-polar westerly winds, bringing rainfall (Kruger 1979b).

2.4. Geology and Soils

Primary focus here is on the Coastal Foreland physiographic zone (Wellington 1955) between the coast and the Cape Fold Belt. The geology of the West Coast foreland supporting renosterveld is predominantly built by metamorphosed shales of the Pre-Cambrian Malmesbury Group, unlike the fine sandstones of marine origin (Tankard et al. 1982) of the Table Mountain Group (Ordovician and Silurian), flooded by the sea until the late Tertiary (Flügel 1995). The West Coast forelands are bordered eastward by the Olifants River and Elandskloof Mountains built mainly of sandstones of the Table Mountain Group (Cape Supergroup) and westward, flanking the sea, the shales are overlain by Tertiary aeolian sand deposits, some 30 km wide in places, on the low lightly dissected peneplain (< 200 m). This undulating inland plateau the orogenic Saldania Belt (Rozendaal et al. 1999), flanks the Kalahari Craton, has as its main exposure the Malmesbury Group, with three terranes subdivided by north-west fault and sear zones. The Colenso (Saldanha-Stellenbosch) fault divides the Tygerberg terrane (west) from the Swartland terrane, whilst the Piketberg-Wellington fault zone divides the Swartland from the Boland terrane (east). The Swartland terrane is composed of the Berg River, Klipplaat and Moorreesburg Formations (Pre-Cambrian/Namibian), with the latter formation being most dominant (Rozendaal et al. 1999). The Berg River Formation contains chlorite schist, greywacke, cherty limestone lenses and quartz schist on top; it is overlain by the Klipplaat Formation composed of quartz-sericite-chlorites schist with phyllite and limestone interbeds. The Moorreesburg Formation has a basal arenite with adjacent chlorite-muscovite schist and is composed largely of inter-layered greywacke and phyllite. Near the study site the Porterville Formation (Pre-Cambrian/Namibian) from the Boland terrane of the Malmesbury Group is also present. The Klipheuwel beds (Cambrian) are exposed in a few areas (like Heuningberg, Visser et al. 1981) composed mostly of sandstone and conglomerates, with minor shale bands. In general the Klipheuwel Group form a flatter landscape than the Malmesbury Group and are harder containing less salts (Merryweather 1965). In places, there are granitic intruded masses of the Cape Granite Suite (Kruger 1979a) from the early Cambrian (for example Paarl Mountain, Paardeberg and granite plutons near Darling) which break the even surface, and some younger (Ordovician) inselbergs of the Table Mountain Group (for example Piketberg and Riebeek Kasteel). Overlaying portions of the Moorreesburg Formation is a more recent gravely alluvium from the early Quaternary period, typically occurring alongside the Elandskloof mountain range at the study site. At Voëlvlei there are igneous greenstones and epidiorite dykes about 5 km long (now submerged in part) parallel to the Malmesbury Formation (Visser et al. 1981). The greenstone here is associated with carbonate rocks (with chert) either pure dolomitic limestone or a mixture of greenstone and dolomite (like pyroclasts).

Along the foothill zone of the Cape Folded Belt red apedal soils occur unlike the residual and duplex soils found on the peneplain surfaces (Lambrechts 1983). The rocks of the Malmesbury Group give rise to shallow, brownish sandy soils that are susceptible to erosion and sheet wash (especially on slopes) following heavy rains (Talbot 1947). These nutrient-rich soils derived from the shales are fine-grained clays and silts. The soils are acid, loams to sandy loams with moderate amounts of exchangeable bases and total nitrogen, with low levels of available phosphorous (Cowling et al. 1986). The Swartland soils have similar phosphorus content to mountain fynbos on granite-derived soils (Witkowski and Mitchell 1987). According to Ellis (1973), soils derived from granite and shale of the coastal forelands are base-saturated with a corresponding high pH value, and are relatively fertile. These fine-textured soils impede drainage (Kruger 1979a) and consequently affect infiltration properties. The natural biotic pedoderm of bacteria, lichens, mosses, liverworts and fungi as well as earthworm activity facilitate infiltration and the supply of nutrients to plants. Infiltration rates are greatly reduced after tillage and destruction of the pedoderm where the biological crust is transformed into a mineral (or physical) crust (Mills and Fey 2003), if otherwise not of local substrate origin. The four specific soil units (Görgens and de Clercq 2002) (Figure 2.5) occurring at the study area where relevés were sampled are listed in order of most occurrence, and abbreviated as K, Av + Cv, Cv + C, C + Cv. These soil units are all a mixture of soil forms (Anonymous 1991) and a description of soil form composition follows.

The most abundant substrate in the study area are the terrace gravels (K), which are deep, very stony, grey to yellow sandy loams; with dominant (> 60%) Fernwood, Vilafontes, Kroonstad, Lamotte and Wasbank soil forms, and subdominant (< 40%) Witfontein and Kroonstad soil forms. The next most abundant soil forms are a combination of two soil units (Av + Cv), both shallow gravelly loam (mostly ploughed). The dominant composite soil unit on either rock or hardpan (Av)

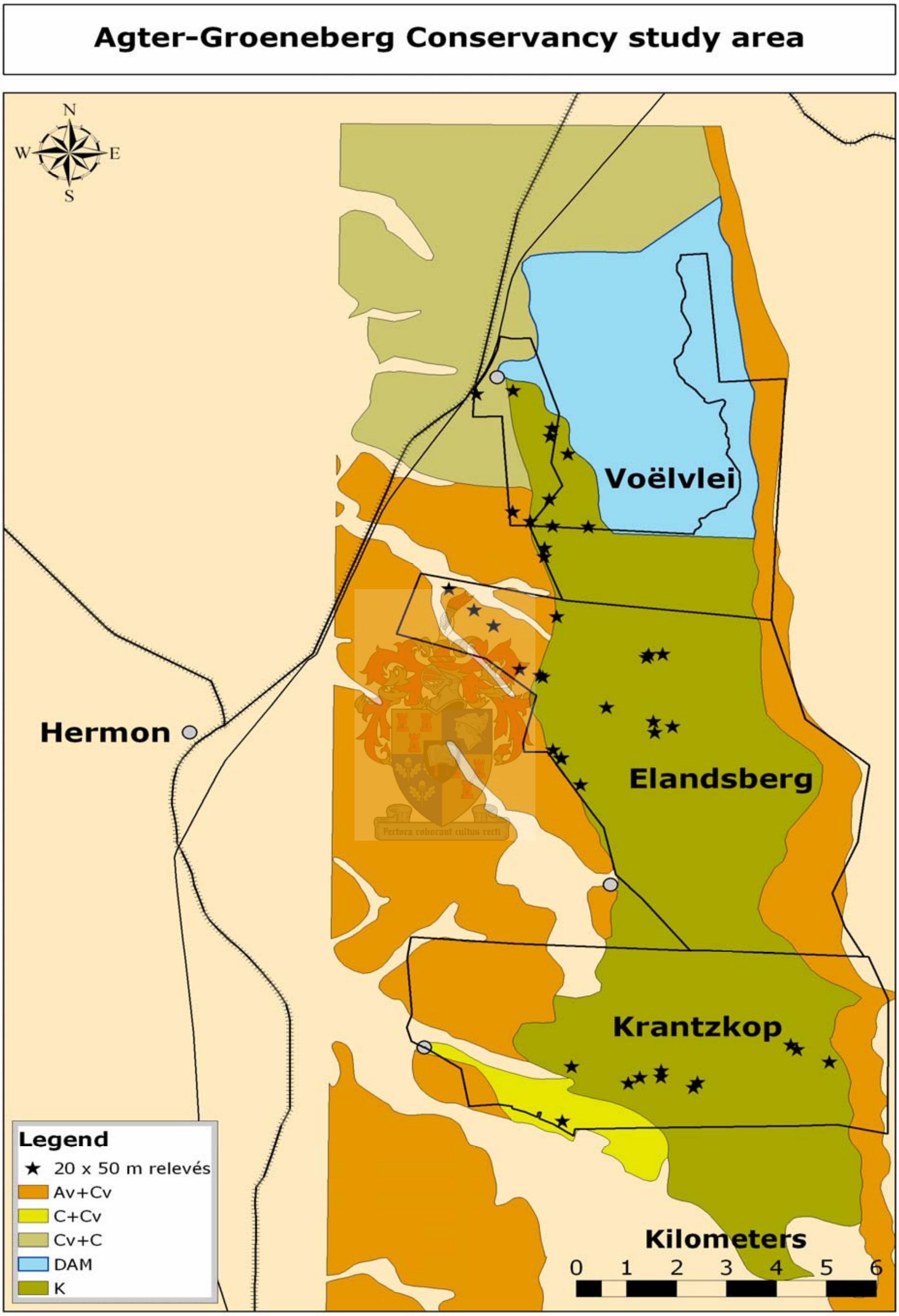

Figure 2.5: Study area showing the soil units (Görgens and de Clercq 2002) of the study sites (Voëlvlei, Elandsberg and Krantzkop). Asterisks indicate the relevé positions

has dominant Glenrosa and Mispah soil forms and rock, and subdominant Swartland and Klapmuts soil forms. The subdominant composite soil unit is a dry grey-coloured duplex soil (Cv) with dominant Swartland, Glenrosa, Cartref, Tukulu and Klapmuts soil forms, with subdominant Estcourt, Sterkspruit and Kroonstad soil forms. Then follows a combination of two soil units Cv + C, both dry grey-coloured gravelly loamy duplex soils, and occur on the boundary of Voëlvlei (mostly ploughed). They are the dominant shallow duplex composite soil unit (Cv, as described above) and the subdominant moderately-deep duplex composite soil unit (C) with the dominant Swartland, Klapmuts, Tukulu, Cartref and Glenrosa soil forms with the subdominant Estcourt, Sterkspruit, Vilafontes, Kroonstad and Valsrivier soil forms. The least abundant soils are also a combination of two soil units C + Cv occuring at the south west end of the Krantzkop old fields only in a small area. It has the same components as described above except the soil unit dominance is reversed.

Heuweltjies occur throughout the area and are richer in organic material, finer in texture and higher in pH than surrounding soils (Merryweather 1965). Termite activity results in the accumulation of calcium salts and organic matter, thoroughly mixed in the soil, with channels lined with fine particles (and fungus gardens in active mounds). Heuweltjies in sandier soils (overlaying shales) are more different to the surrounding soil surface horizon than those in shale alone, as fine particles are mined deeper from below to line channels.

2.5. Disturbance

The environmental disturbance factors primarily incorporated in this study are grazing and ploughing. Both a grazing gradient (of three different stocking rates) and a ploughing gradient (of four seral stages in a chronosequence including a control) were major foci of this study.

2.5.1. Fire History

Fires usually occur in the summer dry season in the Western Cape (Kruger 1979c), often due to lightning strikes in the mountains (Wicht 1945, personal observation) or by humans. “Fire-stick farming” was practiced since the Holocene to maintain productive geophytes like *Watsonia borbonica*, as well as in conjunction with hunting herbivores (Deacon 1983).

At Krantzkop fire-breaks are regularly burnt every three years, which are extremely wide (> 200 m) to prevent the rocket fuel and munitions factory from igniting and exploding. The entire property, excluding the wild olive ridge and the flats below it surrounding the factory establishment, burnt in 1993. Much of the area had also burnt three years earlier. Prior to this, most of the vegetation (both fynbos and renosterveld) was approximately 25 years old (S. Mitchell, personal communication). Similarly, many wild fires have occurred at Elandsberg and Voëlvlei, during 1982, 1988, 1989 and 1999. Elandsberg, Voëlvlei and Krantzkop have frequently burned, often in patches (the most recent in long "tongues" descending from the mountain range to the foothills and forelands or plains below) which has created a mosaic of different stand ages of varying sizes. GIS data (by courtesy of P. Viljoen at Waterval, CapeNature) were used to identify the current stand ages in which relevés were sampled and a list is included in Appendix 2.

2.5.2. Grazing Intensity

Three levels of grazing intensity occur across the three contiguous study sites, forming a grazing gradient of increasing intensity from North to South. Voëlvlei is not intentionally stocked with large mammalian herbivores, except for a few wild Grey Rhebok (*Pelea capreolus*), Grysbok (*Raphicerus melanotis*) and probably Duiker (*Sylvicapra grimmii*), and serves as a control site for grazing. Elandsberg and Krantzkop are purposely stocked with large mammalian herbivores, the latter having double the amount of herbivores than the former. An adequate census count of all species at Elandsberg is available for 1996 and 2003 only, whilst a repeated census count is available for Krantzkop since 1985. Information about herbivore densities at Krantzkop was obtained from S. Mitchell who is responsible for their management and conservation.

For this study, only the herbivore census count of 2003 was used to quantify the stocking rate for the two sites. Elandsberg has only two reliable census counts from 1996 and 2003, whereas Krantzkop has 14 census counts from 1985. At Elandsberg, the introduced browsers and grazers include Black Wildebeest (*Connochaetes gnou*), Bontebok (*Damaliscus pyrgargus*), Eland (*Taurotragus oryx*), Gemsbok (*Oryx gazella*), Ostrich (*Struthio camelus australis*), Plains Zebra (*Equus burchelli*, locally called "quagga's"), Red Hartebeest (*Alcelaphus buselaphus*) and Springbok (*Antidorcas marsupialis*). Cape Buffalo (*Syncerus caffer caffer*) are kept in a separate camp outside the reserve, and are therefore excluded from this study. In 2002, the Blue Wildebeest (*Connochaetes taurinus*) were removed from Elandsberg. Occasionally Eland jump the fences at Krantzkop and Elandsberg, and Grey Rhebok (*Pelea capreolus*) have been observed in Elandsberg farmlands and at Voëlvlei (B. Walton, unpublished observations). A sole Mountain Zebra (*Equus zebra zebra*) seen at Elandsberg probably arrived along the foothills from Krantzkop.

Densities of introduced large mammalian herbivores at Krantzkop have remained stable over the last five years (S. Mitchell, personal communication). Krantzkop has a large fenced internal no-access zone that splits the herbivore populations in an otherwise open tract of shrubland, riverine terrace/wetland and scattered old fields. The Eland move freely between areas, Bontebok and Black Wildebeest stay on the old fields. Oryx and Red Hartebeest utilize renosterveld for browsing, whilst Blue Wildebeest stay at the foothills with adjacent old fields (S. Mitchell, personal communication).

Potential consumption of plants by other herbivores was excluded from this study. The geometric tortoise (*Psammobates geometricus*) is known to browse *Briza maxima*, *Babiana angustifolia*, *Cyanella hyacinthoides*, *Cynodon dactylon*, *Ehrharta calycina*, *Eragrostis curvula*, *Lachenalia contaminata*, *Pentachistis curvifolia* and *Themeda triandra* (Balsamo et al. 2004). Similarly browsing by harvester termites on: *Athanasia trifurcata*, *Babiana odorata*, *Cynodon dactylon*, *Elytropappus rhinocerotis*, *Eragrostis curvula*; feeding of feral pigs on *Babiana angustifolia*, *Cyanella hyacinthoides* and uprooting, as well as by large herbivores, of *Elytropappus rhinocerotis*, *Eriocephalus africanus* subsp. *paniculatus*, *Relhania fruticosa* were observed (B. Walton, unpublished observations). Porcupines were not incorporated in the scope of this study, and their impacts were assumed to be similar across the study area. Feral pigs (*Sus scrofa*) occur at all sites and were introduced into state forests in the 1920's (Bigalke and Pepler 1991) as a biocontrol agent for the pine emperor moth (*Imbrasia cytherea*). Their disturbance due to their foraging activity especially in loamy seasonally waterlogged areas is worrying and they consume and destroy local patches of geophytes (B. Walton, unpublished observations). The disturbance caused by Feral Pigs is assumed to be similar at all sites, but their true densities are unknown. The Elandsberg Farms (Pty.) Ltd. hunt approximately 100 Feral Pigs a year in post-harvested wheat fields (B. Wooding, personal communication).

2.5.3. Ploughing

Since the initial arrival of colonists in the 17th century in South Africa, the Swartland has endured transformation by agriculture that intensified during the 20th century. The once extensive stock farming was replaced by an intensive wheat production system especially since the 1940's (Meadows 2003) and which accelerated by mechanized farming during the 1950's.

Voëlvlei and Krantzkop were last ploughed in the 1970's, prior to the expropriation of agricultural land by CapeNature and Armscor, respectively. Krantzkop was last ploughed in 1975. Thus, Voëlvlei and Krantzkop only have 30-year-old fields and unploughed renosterveld available for a study of post-ploughed secondary succession. Elandsberg has a chronosequence of three different-aged old fields and unploughed renosterveld, namely last ploughed in the 1960's, 1987, and in 1997. The different-aged old fields at Elandsberg have different ploughing histories (Appendix 2). Both the 5- and 15-year-old fields were intensely cultivated, unlike the 30-year-old fields surrounded by renosterveld. Those latter fields were briefly ploughed for oats, grazed by sheep and then abandoned (M. Gregor personal communication). The 30-year-old fields at Voëlvlei and Krantzkop were intensely cultivated until expropriation and cessation of ploughing.

2.5.4. Invasive Alien Plant Species

As "alien", we consider here those species that are not native to the Cape flora. Agricultural practices have facilitated the spread and existence of mostly ruderal species. In the Swartland, annual (as well as some perennial forbs and hemicryptophytes) alien taxa comprise most of the alien component in terms of richness and abundance, specifically mediterranean grasses that have entered the area since the advent of agriculture. Burchell (1967) collected *Briza maxima* at Cape Town in 1810 and a species of *Bromus* and *Lolium* in the interior. Alien annual grasses were transported with oat and wheat seeds or other pasture plants (like *Medicago*) from Europe. The alien annuals are a feature of the agriculturally transformed landscapes, and are either used as pasture feed (like *Lolium perenne*) or inhabit fallow or old fields, along with many ruderal herbaceous alien species. Consequently, they are also found in natural vegetation either spread via wind from adjacent agricultural fields or dispersed in herbivore dung.

Large trees such as acacias consequently spread into and from areas neglected by farming or other non-irrigable areas in the agricultural matrix alongside drainage lines (*Acacia mearnsii*) or deep sands typical of sandplain fynbos (*Acacia cyclops* and *A. saligna*; Merryweather 1965). *Eucalyptus cladocalyx* and other species generally radiate outward from woodlots or around the fringes of waterways and dams where planted. *Pinus* species descend from mountainside plantations and are common in places amongst granitic outcrops often with *Hakea sericea*. Fire increases the spread of these alien trees with concomitant problems of increased fire severity due to higher fuel loads.

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Chapter 3

Vegetation Community Patterns in Renosterveld and Old-fields at Agter-Groeneberg Conservancy near Wellington, Western Cape, South Africa

Figure 3.1: A South-East view of a 15-year-old field at Slangkop (Elandsberg) adjacent to a narrow stand of unploughed Swartland Shale Renosterveld (Mucina and Rutherford 2004), with Swartland Alluvium Fynbos flats in background. Note the advance of flowering *Relhania fruticosa* (L.) Bremer on to the old field

3.1. Introduction

The renosterveld is a unique species-rich ecosystem (Levyns 1929, Duthie 1930, Taylor 1978), acknowledged as having a 100% irreplaceability value (von Hase et al. 2003) due to natural habitat demise and transformation (Figure 3.1). The decline of renosterveld vegetation has not occurred without recommendations for formal protection by researchers and conservation agencies, however targets have not been met (see Tansley 1982, Jarman 1986, McDowell 1988) and many valuable tracts have been continuously transformed since then. In order to define effective measures aimed at conservation of a natural ecosystem, the basic vegetation and ecological patterns have to be thoroughly surveyed and described. Vegetation classification, description and mapping in the Fynbos Biome traditionally concentrated on fynbos (see Werger 1972, Glyphis et al. 1978, Laidler et al. 1978, Campbell 1983, 1985, McDonald 1985, Taylor 1996, Cowling 1992, Simmons 1996, Cowling et al. 1997, Hoare et al. 2000). Some studies investigated various issues of patterns in the renosterveld (Levyns 1929, 1935, Muir 1929, Grobler and Marais 1967, Linder 1976, van der Merwe 1976, 1977, Cowling 1983, Pierce and Cowling 1983, Cowling 1984, Cowling et al. 1988, Rebelo et al. 1991, Euston-Brown 1995) or drew valuable comparisons with fynbos (see Cowling 1983, Kruger and Taylor 1979). Still, the renosterveld vegetation of the Fynbos Biome of South Africa is lacking adequate coverage by empirical baseline studies involving classification, description, and (until recently) mapping of vegetation. A holistic correlation of these patterns with intrinsic ecological patterns and processes is also incomplete. Studies for example by Michell (1922), Taylor (1978), Cowling et al. (1986), Wood and Low (1993) usually only involved compilations of checklists (see Heydenrych and Littlewort 1995); but see Boucher (1987).

Levyns (1935) noted that renosterveld is often dominated by *Elytropappus rhinocerotis*, and has a conspicuous shrub synusia and speciose herbaceous component (graminoids, geophytes and annuals). Acocks (1953) ascribed the differences in grass abundance between West Coast renosterveld and South Coast renosterveld to seasonal versus non-seasonal rainfall patterns, respectively. Acocks (l.c.) described the species-rich coastal renosterveld vegetation in terms of the absence of (or relationship to) thicket vegetation elements. Merryweather (1965) mentioned that heuweltjies on the West Coast forelands are formed by termite activity, and are absent on the South Coast foreland (Boucher and Moll 1981). Taylor (1978) described coastal renosterveld on the elevated coastal plain, as being dominated by renosterbos (*Elytropappus rhinocerotis*) with co-dominant shrub species like *Relhania genistifolia* (widespread, see Bremer 1976) or *R. fruticosa* (mostly West Coast renosterveld), and many grass species of low cover. A lucid point mentioned from research conducted by Levyns (1927), was that renosterbos seedlings are moisture sensitive, perhaps implying grassier conditions when drought persists. Kruger (1979) described coastal renosterveld as a complex successional gradient from a shrubland to shrubby grassland.

A major contentious issue still clouding the enigmatic renosterveld is an accurate and stable definition of renosterveld. Generally the renosterveld shrubland on the West Coast foreland is defined as occurring on nutrient-rich soils (unlike fynbos on oligotrophic soils) between a rainfall margin of 300 mm and 600 mm. Renosterveld occurs along an edaphic and rainfall gradient between more mesic fynbos elements and thicket elements along both the West and South Coast forelands, unlike the zonations of the interior renosterveld between xeric fynbos and Karoo elements. Coastal renosterveld usually has three strata (Adamson 1938, Levyns 1929, Boucher and Moll 1981), such as (1) the upper layer 1.0 to 1.5 m tall, (2) the lower layer of 0.1 to 0.5 m tall), and rarely (3) a taller shrub layer (up to 3.0 m tall) occurring on heuweltjies or alongside drainage lines.

In an attempt to document vegetation community patterns in renosterveld, this chapter embarks on the classification and description of the renosterveld (and associated) vegetation in a limited, but representative area**.** This vegetation description will serve as a baseline study for further ecological studies aimed at formulation of efficient and sensible management guidelines, decisions and practices to be implemented in context of actual biodiversity.

Our study object is the Agter-Groeneberg Conservancy (hereafter referred to as AGC), formally established in 2004 via the conservation stewardship programme of CapeNature. AGC (including both renosterveld and fynbos) contains at least 950 plant taxa, nearly 10% of the Fynbos Biome’s flora. AGC contains some local endemics, such as *Brunsvigia elandsmontana* and *Moraea villosa* subsp. *elandsmontana* as well as a large number of threatened taxa.

The following questions are being addressed in this Chapter:

1. What are the plant communities of unploughed renosterveld and different-aged old fields which originated in habitats of ploughed renosterveld?

2. What are the most characteristic features of the floristic and ecological relationship between the described plant communities in terms of ecological factors operating within the studied system?

3.2. Materials and Methods

3.2.1. Vegetation Data

A phytosociological survey was conducted to gather vegetation data on presence and relative-abundance of taxa in relevés. Vegetation was sampled on both old fields (presumed to have previously supported renosterveld vegetation) as well as in unploughed renosterveld. A nested quadrat sampling method of 1000 m^2 relevés was used. The relevé layout design used here is shown in Figure 3.2. The adopted sampling scale of 0.1 ha was chosen for comparative purposes with previous vegetation surveys in mediterranean type ecosystems (Rice and Westoby 1983). Relevés were placed at sites with similar habitat conditions, either unploughed renosterveld or different-aged old fields with a low (5- and 15-year-old fields) or high shrub cover (30-year-old fields). Vegetation stands never ploughed were used as the baseline reference (controls) from which to infer community compositional changes caused by previous ploughing and contemporary grazing disturbances.

The different-aged old fields and controls were assigned to a seral stage class; 5-year-old fields (Sere 1), 15-year-old fields (Sere 2), 30-year-old fields (Sere 3) and unploughed renosterveld (Sere 4). Not all seral stages occurred at Voëlvlei or Krantzkop as those two sites were last ploughed in the 1970's, prior to the expropriation of agricultural land by CapeNature and Armscor, respectively (Krantzkop was last ploughed in 1975). Thus only unploughed renosterveld and 30-year-old fields existed at Voëlvlei and Krantzkop, making an unbalanced design. Elandsberg has old fields of different set-aside ages, namely last ploughed in the 1960's, 1987, and in 1997. A sequence of aerial photographs (1938, 1949, 1967, 1973, 1987 and 1997) was used to select suitable sites for relevés in vegetation of the four seral stages within the study area. The aerial photographs give an indication of the decline in extent of untransformed vegetation since 1934 to 1996, especially after the introduction of mechanized farming in the 1950's (M. Gregor, personal communication).

All taxa present were recorded (with the exception of unidentifiable or rare seedlings) on field data sheets (Appendix 3.1), and the height of common species was measured (an average of three individuals). Species (in relevés and nested quadrats) were assigned to a life-form class (Raunkiaer 1934, Mueller-Dombois and Ellenberg 1974) in the field and later verified in the literature (Goldblatt and Manning 2000) or by expert botanical knowledge (Appendix 3.2). Raunkiaer's life-form classification was slightly altered for relevance to the preponderance of shrub species short in stature.

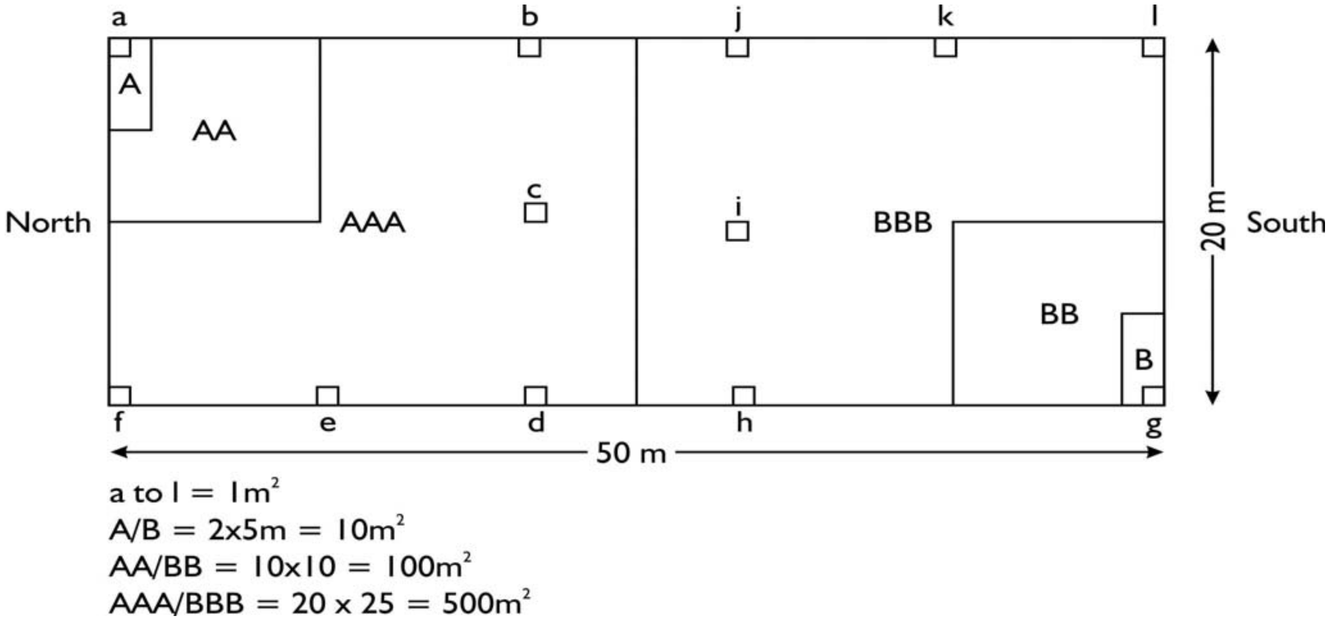

Figure 3.2: Diagram of the 1000 m^2 (20 m by 50 m) relevé layout used in this study

In total 36 relevés (1000 m^2) were sampled, of which nine relevés were sampled at Voëlvlei, 16 relevés were sampled at Elandsberg, and 11 relevés were sampled at Krantzkop, respectively. All taxa present were recorded for calculation of alpha (point) species richness only. In each relevé habitat data were recorded on field data sheets (Appendix 3.3) and an overview of the relevé physiognomy was noted with estimates of percentage canopy cover for the shrub, herb and graminoid synusia. All 1000 m^2 relevés were oriented from north to south and GPS waypoint coordinates were taken at the north-east corner of the relevé as a marker (Appendix 3.4). Relevé coordinates were converted into a point layer and were superimposed in GIS programs (Mapinfo 5 and ArcMap 8) to show their position in the field (Figure 2.4b). Different data layers were used to obtain relevé disturbance history such as a LANDSAT^{TM} 7 image (TM bands 548 (RGB), orthorectified mosaic summer 2000-2001, by courtesy of CapeNature), a chronology of composite aerial photographs (by courtesy of IP Newton), an untransformed lowland vegetation layer of both extant lowland fynbos and renosterveld by von Hase et al. (2003) as well as by Newton and Knight (2005). A list of the disturbance history for each relevé is given in Appendix 2.

Two 10 m^2 quadrats per 1000 m^2 relevé (72 in total) were sampled at alternate ends of the relevé (see Figure 3.2.). Cover-abundance was recorded with the refined Braun-Blanquet scale (Barkman et al. 1964) (Table 3.1, Appendix 3.5).

Table 3.1: Quadrat scales and measurements within each relevé

10 m^2	All species identified and their cover-abundance recorded
1000 m^2	All species identified and a percentage estimate of total shrub/graminoid/herb canopy cover recorded

3.2.2. Environmental Data

Grazing intensity increased along a gradient at the three sites (see Chapter Two: Study area) and were assigned to classes of; low intensity (LI), moderate intensity (MI) and high intensity (HI), respectively, as a nominal scale and recoded and binarized as pseudo-variables for gradient analyses. A total stocking density per site for large herbivores was calculated (Table 3.2). To obtain this figure the number of individuals per species was multiplied by their metabolic equivalent (a fraction of a standard Large Animal Unit (LAU) with a mass of 450 kg, Bothma 2002). Dividing the sum of the LAU's per site by the area in hectares (Σ (n *LAU)/ha) gives the value of 0.05 LAU/ha for Elandsberg and 0.11 LAU/ha for Krantzkop respectively. Thus the stocking rate at Krantzkop is precisely 2.2 times that of Elandsberg. No calculation of a sustainable stocking capacity was attempted, only a direct measurement of existing stock. Table 3.3, depicts the amount of relevés sampled at the AGC with corresponding ploughing and grazing disturbance factors.

The post-fire age of stands (fire-age) was determined on site with the aid of mental records (M. Gregor and B. Wooding for Elandsberg), GIS data (with a record of the extent of each fire for the area by courtesy of CapeNature, P. Viljoen, Tulbagh) and a sequence of orthophotos as described above for seral stage determination, for use in multivariate analyses. The different fire-ages of stands were not evenly replicated across other factor levels, as it proved difficult to obtain in the field due to the patchy and random distribution of fires across the study sites. Relevés were assigned to a fire-age class burnt last either in: 1982 (F1), 1988 (F2) and/or 1999 (F3), as a nominal scale and recoded as pseudo-variables for gradient analyses.

Vegetation and environmental data were stored and managed in the TURBOVEG databank program (Hennekens and Schaminée 2001).

Table 3.2: Large herbivore census (for 2003) at Elandsberg (3800 ha) and Krantzkop (2500 ha), with Large Animal Unit (LAU) fraction equivalents (sensu Bothma 2002). n = number of individuals

Species	Elandsberg 2003	Krantzkop 2003	LAU equivalent	Elandsberg (n*LAU)	Krantzkop (n*LAU)
Black Wildebeest	40	22	0.46	18.4	10.12
Blue Wildebeest	0	28	0.50	0	14.00
Bontebok	100	47	0.22	22.00	10.34
Eland	90	87	1.02	91.80	88.74
Gemsbok	11	67	0.56	6.16	37.52
Hartebeest	12	50	0.37	4.44	18.50
Kudu	0	5	0.42	0	2.10
Mountain Zebra	0	20	0.62	0	12.40
Ostrich	45	0	0.25	11.25	0
Plains Zebra	30	5	0.66	19.80	3.30
Springbok	120	480	0.15	18.00	72.00
Grey Rhebok	0	30	0.10	0	3.00
Total n	448	841			
Total LAU's				191.85	272.02
LAU/ha				0.05	0.11
ha/LAU				19.81	9.19

Table 3.3: Details of ploughing and grazing disturbance factors (and respective levels) for the 36 relevés surveyed in this study

Factor	State	Relevés	Voëlvlei	Elandsberg	Krantzkop
Grazing intensity			low: 1	moderate: 2	high: 3
Seral stage	sere 1: 5-year-old field	3	0	3	0
Seral stage	sere 2: 15-year-old field	6	0	6	0
Seral stage	sere 3: 30-year-old field	17	5	4	8
Seral stage	sere 4: unploughed renosterveld	10	4	3	3

3.2.3. Soil Sampling and Analysis

Soil samples (500 grams) were taken in twenty-four 1000 m^2 relevés only with a hand core borer at five random points and mixed together. The samples were not evenly replicated for all factor levels (seral stage and grazing intensity). Soil analyses (Table 3.4) were conducted by BemLab cc in Somerset West. The following soil characteristics were measured: texture, pH (KCl; see McLean 1982), electrical resistance (Ohms; see Richards 1954), hydrogen ($cmol^{(+)}/kg$), organic carbon (%, see Nelson and Sommers 1982), nitrogen (%), phosphorus (mg/kg; see Bray and Kurtz 1945), potassium (mg/kg), exchangeable cations; Na, K, Ca, Mg ($cmol^{(+)}/kg$; see Chapman 1965) and base saturation (Table 3.5). Carbon, nitrogen and potassium content (a measure of organic material) could be limiting (or not freely-available) in shale and one can expect a difference in amount with ploughed versus unploughed land. Univariate tests of significance (ANOVA) were employed (StatSoft, Inc. 2004) for establishing differences in the content of the measured soil variables amongst the seral stages, and distribution of normality was checked as well.

Table 3.4: Variables and methods of the soil analyses (performed by BemLab cc, Somerset West). Data types: I: interval scale, R: ratio-scale

Variable name	Data type	Unit of measurement	Method of unit of measurement
Soil reaction	I	pH	10 g soil + 25 ml 1M KCl, read after 1 hour
Electrical resistance of soil	R	ohms	Soil sample is saturated with de-ionized water and resistance is measured in a USDA cup
Extractable cations: Na, K, Ca and Mg (Ammonium acetate - 1M, pH 7)	R	$cmol^{(+)}/kg$ and mg/kg (K)	5 g soil + 50 ml ammonium acetate solution, shaken for 30 minutes and filtered. Analyzed for Na, K, Ca and Mg with the ICP
Extractable phosphorus	R	mg/kg	Bray 2
Organic carbon	R	%	Walkley Black
Total nitrogen	R	%	Digestion with a Leco FP528 nitrogen analyzer

Table 3.5: Environmental variables of 24 relevés (1000 m^2) used in gradient analyses. Relevé code (first column) with corresponding nominal scale variables: seral stage (four classes), grazing intensity (GI; three classes), post-fire age (FA; three classes) and estimated soil texture (third column); and measured (ratio-scale/interval scale) soil variables in following columns. Note species richness added as a passive co-variable in constrained ordination. Total exchangeable cations are the sum for H^+, Na^+, K^+, Ca^{2+} and Mg^{2+}. For geographic coordinates of relevés see Appendix 3.5

Relevé	Sere	Texture	pH (KCl)	H+ (cmol/kg)	P Bray II mg/kg	K mg/kg	N %	C %	Total cmol/kg-exchangeable cations	C/N ratio	FA	GI	Richness
E9	4	Loam	4.6	1.7	13	238	0.30	4.4	15.18	14.49	1	2	65
E17	4	Sand	4.0	1.3	2	64	0.10	1.3	3.02	13.13	1	2	111
K7	4	Sand	3.8	1.7	9	74	0.09	1.4	3.47	16.32	2	3	69
V10	4	Loam	5.0	1.2	7	142	0.21	2.9	8.08	14.05	1	1	56
V11	4	Sand	5.0	1.0	15	127	0.12	2.1	5.97	18.02	3	1	63
E6	3	Sand	4.1	1.3	7	77	0.10	1.3	3.70	13.75	1	2	68
E7	3	Loam	4.7	1.1	11	147	0.16	2.1	8.18	12.86	1	2	55
E8	3	Loam	4.9	1.0	5	178	0.18	2.6	11.20	14.20	1	2	68
E10	3	Sand	4.0	1.1	3	73	0.09	1.2	3.41	14.12	1	2	86
K3	3	Sand	4.3	1.2	12	125	0.16	2.3	4.71	14.01	2	3	63
K4	3	Sand	4.3	1.8	13	116	0.22	3.3	7.11	14.87	2	3	51
K5	3	Sand	4.6	1.2	10	73	0.13	2.0	5.24	15.07	2	3	38
K8	3	Sand	4.2	1.2	7	88	0.10	1.5	3.06	15.25	1	3	51
K9	3	Sand	4.2	1.3	29	99	0.11	1.8	4.20	16.30	1	3	32
K10	3	Sand	4.4	1.3	8	98	0.13	2.1	4.90	16.05	1	3	59
V7	3	Sand	5.3	0.7	7	64	0.12	1.6	5.81	13.14	3	1	60
V8	3	Sand	4.7	1.4	15	83	0.15	3.3	6.07	22.65	2	1	72
V9	3	Sand	5.4	0.6	4	44	0.05	0.7	3.31	13.47	3	1	57
V12	3	Sand	6.0	0.5	9	73	0.08	0.9	4.87	10.36	1	1	33
E11	2	Sand	3.8	1.1	6	61	0.05	0.7	2.86	13.77	1	2	35
E12	2	Sand	5.0	0.9	6	112	0.14	1.9	5.49	12.92	1	2	33
E13	2	Sand	4.3	1.1	9	100	0.09	1.4	3.95	14.67	1	2	54
E19	2	Sand	5.0	0.0	25	149	0.23	2.4	4.70	10.80	1	2	49
E18	1	Sand	5.4	0.6	32	58	0.08	1.1	5.53	13.21	1	2	38

3.2.4. Methods of Vegetation Classification

The 10 m^2 scale quadrats (72 in total, two quadrats per 1000 m^2 relevés) with 244 species cover-abundance measurements were used in vegetation classification. The 72 quadrats with cover-abundance and environmental data were exported from TURBOVEG in a Cornell condensed file format used in MEGATAB (Hennekens and Schaminée 2001). Prior to export the differentiated alpha-numerical Braun-Blanquet cover-abundance values were code-replaced using an ordinal scale (van der Maarel 1979). All species layers (i.e. seedling, juvenile or adult) were exported to allow for better matrix table sorting, but were later merged when appropriate in MEGATAB. The data were classified using TWINSPAN (Hill 1979) in MEGATAB. The raw matrix table was further manually sorted to optimize the species-group versus relevé-group coincidence.

Manual sorting of species was done in the full matrix table as well as the synoptic table to arrange species by order of most to least frequent. Differential species were diagnosed on the basis of fidelity (see Schaminée et al. 1995): as either exclusive differential species (de; purely in one phytocoenon) or selective differential species (ds; if overlapping division boundaries), at this syntaxonomic scale. Diagnostic species were assigned to a phytocoenon on the basis of their frequency of occurrence: a strictly dichotomic numerical approach using a 40% difference in frequency between divisions as the criterion-otherwise relegated to the common species group at the top of the table. This dichotomic approach was repeated between subordinate divisions within phytocoena to distinguish species faithful to certain sub-communities or variants as well. Similarly species not differential to subordinate divisions were relegated as diagnostic for phytocoena only.

The communities were described to the level of association and sub-association or as variants. All common species showing no fidelity to any phytocoena or divisions were re-arranged in order of occurrence with most frequent ranked at the top (except for the group of common alien species placed after the lowest occurring indigenous taxon). Species occurring once or twice only were relegated to Appendix 3.5.

SYN-TAX 2000 (Podani 2001) was used to perform Complete Linkage Clustering (with Chord Distance as a measure of resemblance) to classify 72 quadrat data (10 m^2). For theory of clustering and resemblance methodologies see Podani (1994).

3.2.5. Nomenclature of Plants and Plant Communities

Specimens were collected and either identified on site or in Herbaria (for the complete plant checklist see Appendix 4.2). The nomenclature of taxa follows Goldblatt and Manning (2000) and Goldblatt et al. (2005).

The naming of associations and sub-associations follows the principles of the syntaxonomic nomenclature as depicted in the 3rd ed. of the Code of Phytosociological Nomenclature (Weber et al. 2000). The communities were also named by a combination of major dominants and structural terms.

3.2.6. Multivariate Analyses

Ordination at 10 m^2 Scale

The 10 m^2 quadrats were also subjected to ordination. The aim here was to identify possible coenoclines (gradients of vegetation composition) and to compare those to environmental variables. The nominal-scale environmental variables of quadrats included in the ordination analyses were seral stage (four classes), grazing intensity (three classes) and fire-age (three classes), (as described above in 3.2.1). These explanatory variables were re-coded and binarized as pseudo-variables. No further data transformation was done prior to any ordination.

The vegetation samples were analyzed using Principle Components Analysis (PCA). The program package CANOCO (ter Braak and Šmilauer 2002, Lepš and Šmilauer 2003) was used to perform the linear model of indirect gradient analysis (PCA). Scaling was focussed on inter-species correlations with species scores divided by their standard deviation, and the data were untransformed with centring by species (not samples). Quadrat field names were re-coded with their corresponding classified community unit code to reflect whether patterns of similarity found with TWINSPAN vegetation classification were similar in multivariate ordination space.

The 72 quadrat data with corresponding nominal-scale environmental variables were analyzed using Canonical Correspondence Analysis (CCA). The program package CANOCO was used to perform the CCA. Bi-plot scaling was focussed on inter-species distances, and the data were untransformed with no forward selection. Another CCA ordination was performed with the addition of quadrat species richness included as a passive co-variable-enabling better separation of sample scores (as they were agglomerated). The scaling was as above for the first CCA ordination with no data transformation or forward selection.

Ordination of samples and soils variables (1000 m^2 scale)

Twenty-four relevés at the 1000 m^2 scale (with species presence-absence data) were analyzed using Canonical Correspondence Analysis (CCA) to determine vegetation patterns in relation to soil properties. The list of environmental variables measured and used in ordination is in Table 3.4 and 3.5. A CCA ordination was used to illustrate whether ploughing had altered the soil properties relative to unploughed renosterveld. As the sample scores were agglomerated in an initial ordination species richness of relevés was included as a passive co-variable in a bi-plot. Bi-plot scaling was focussed on inter-species distances, and the data were untransformed with no forward selection.

3.3. Results

3.3.1. Classification of Vegetation

The first division of the 72 quadrats with TWINSPAN yielded a distinct separation between the different-aged old fields dominated by *Cynodon dactylon*, and renosterveld vegetation with a medium (60 cm) to high (> 75 cm) shrub stratum. Thus there are two major plant associations or communities identified (Table 3.6): the *Ursinia anthemoides-Cynodon dactylon* Grassland (1) and the *Pterygodium catholicum–Elytropappus rhinocerotis* Shrubland (2). Further secondary divisions yielded two variants of the old-field *Ursinia anthemoides–Cynodon dactylon* Grassland and two sub-associations or sub-communities of the *Pterygodium catholicum–Elytropappus rhinocerotis* Shrubland, respectively.

Community 1: *Ursinia anthemoides–Cynodon dactylon* Grassland Community
Table 3.6, relevés 1-34
Scientific name: *Ursinio anthemoidis–Cynodontetum dactyli* ass. nova hoc loco
Holotypus: Table 3.6, relevé 9

The *Ursinio anthemoidis–Cynodontetum dactyli* Community was described on the basis of 34 relevés with ten diagnostic species. It is dominated by stoloniferous grass *Cynodon dactylon* with the emergent annual *Ursinia anthemoides* (present from mid-winter to late spring). The community is characterized also by the presence of many alien annual grasses and forbs such as *Bromus rigidus* (de), *Echium plantagineum* (de), *Erodium botrys*, *Lolium perenne* (de), *Medicago sativa* (de), *Trifolium angustifolium* and *T. repens* (de). This phytocoenon is composed of different-aged old fields, in various stages of secondary succession following the abstention of ploughing. Recovery has allowed for the arrival of pioneering species such as some geophytes, dwarf shrubs and shrubs, on to these fields in the chronosequence mirroring secondary successional states of a previously ploughed renosterveld community. The propagule sources here are both endogenous and exogenous: from adjacent agricultural fields (alternatively with grain or pasture crops and ruderal species) and nearby stands of either; Swartland Shale Renosterveld or Swartland Alluvium Fynbos (Mucina and Rutherford 2004), and more rocky ridges (possibly laterites) as well as taxa which have escaped tillage. Advancing or pioneering palatable shrub species are usually browsed by large herbivores: for example *Anthospermum spathulatum*, *Hermannia alnifolia*, *H. scabra*, *Muraltia heisteria* and *Thesium funale*). The bulbous geophyte *Lachenalia contaminata* (de) is present here as it prefers open areas alongside rivulets or seasonally inundated, often growing *en masse*.

Variant 1: *Arctotheca calendula* Variant
Table 3.6, relevés 1-6

This variant comprises a small cluster of six relevés with two diagnostic species only (selective differentials), possibly distinguished on the basis of high nutrient levels corresponding to fields of a recent set-aside age of five years only. These fields have thus had recent applications of lime, which were used to homogenize the soil properties. The presence of the rosette annual *Arctotheca calendula* typifies this variant as does the occurrence of the alien forb *Erodium moschatum*.

Variant 2: *Petrorhagia prolifera* Variant
Table 3.6, relevés 7-34

The second variant comprises 28 relevés and seven diagnostic species with *Petrorhagia prolifera* being most dominant. The other frequently occurring species are indigenous geophytes such as *Disa bracteata* (de), *Romulea flava* (de) and *Trachyandra flexifolia* (de). The annuals *Cerastium capense* (de) and *Monopsis debilis* (de) are also present. These species no doubt tolerate or thrive in poorly-shaded conditions, where seasonal moisture (and even inundation) allows them to persist.

Community 2: *Pterygodium catholicum–Elytropappus rhinocerotis* Shrubland Community

Table 3.6, relevés 35-72

Scientific name: *Pterygodio catholici–Elytropappetum rhinocerotis* ass. nova hoc loco

Holotypus: Table 3.6, relevé 49

This community was described on the basis of 38 relevés and has 26 diagnostic species. Both unploughed renosterveld and some 30-year-old fields comprise the *Pterygodio catholici–Elytropappetum rhinocerotis* Community. It is dominated by *Elytropappus rhinocerotis* and other co-dominant shrub species: *Anthospermum galioides* (de), *Eriocephalus africanus* subsp. *paniculatus* (kapokbos) and *Lobostemon argenteus* (de). The emergent proteoid *Leucadendron lanigerum* var. *lanigerum* (de) is occasional. These shrubs often reach a height of 1.2 m (even 1.5 m) in unploughed renosterveld and 30-year-old fields. These 30-year-old fields have differing disturbance histories-some were ploughed often and utilized extensively for agriculture, whilst others were briefly ploughed and abandoned when deemed unsuitable for crops due to the rockiness of the substrate. These 30-year-old fields are either surrounded by unploughed renosterveld or in close proximity to unploughed renosterveld. Propagules are dispersed on to old fields by wind as well as by animals (ecto- or endozoochory), where they are kept at a height of 30 to 70 cm due to browsing by herbivores. Dwarf shrubs like *Aspalathus ciliaris* (de), *Erica coarctata* (de), *Pelargonium myrrhifolium* (de) and *Phylica strigulosa* (de) - a resprouter often partially browsed - are interspersed amongst shrubs or open spaces. The small suffrutescent *Polygala scabra* (de) is hairy and cryptic usually occurring in the shade of bushes. One can often distinguish three vegetation strata, with the first being that of the tall shrubs, the second of low-grown prostrate and dwarf shrubs, and the third one comprising graminoids, rosette perennials, geophytes and annuals. The ground stratum is often partially covered by lichens and mosses, the latter especially from early winter to late spring, however these were not sampled. *Anthospermum galioides* is indifferent to disturbance by fire, either killed or able to resprout from the base (personal observation; Puff 1986) and often browsed short, otherwise rambling. The orchid *Pterygodium catholicum* (de), diagnostic for this community, is usually encountered in leaf during its growing season from mid winter (June) to late spring (October) until flowering. It is a clonal geophyte forming large clumps under bushes or near them, in moss and annual covered clayey soils often broken up by earthworm activity. An interaction with an oil collecting bee (*Rediviva peringueyi*) determines whether seed is set for *Pterygodium catholicum* (likewise for the annual *Hemimeris racemosa*), whereby the bee pollinator requires an ample sized stand of vegetation for a solitary nesting site in which to burrow into the soil (Pauw 2004). Typically, following fire annuals and graminoids dominate the ground stratum and geophytes are stimulated to flower *en masse* (Goldblatt and Manning 2002; personal observation; A. Pauw, personal communication; B. Bytebier, personal communication). The erect *Gladiolus watsonius* (de) typical of heavy clay soils (Delpierre and du Plessis 1974) and endemic (Goldblatt and Manning 1998) to West Coast Renosterveld, could be considered a flagship species here as it mostly has been observed in unploughed renosterveld (occasionally in 30-year-old fields) and is a sheer delight to the eye and nose and no doubt to its pollinator (s). Other geophytes occurring in this community are; *Cyphia volubilis* (de) (intricately intertwined in the protection afforded by bushes from browsing) is striking when in bloom, the prostrate *Cyphia phyteuma* (de) nestles under or amongst bush cover or in small spaces, *Moraea gawleri* (de) often up to 60 cm, is abundant in places in spring as are many unidentified taxa of *Drimia* s.l. (de) and of *Eriospermum* (de). Annuals begin to germinate in early winter and mostly flower during or before spring. These include *Adenogramma lichtensteiniana* (de), *Diascia elongata* (de), *Hemimeris racemosa* (de), *Phyllopodium cordatum* (de), *Sebaea albens* (de) and *Vellereophytum dealbatum* (de). The graminoids here are the short perennial grasses: *Tribolium hispidum* and *T. uniolae*; and the weakly perennial or annual *Pentachistis airoides* subsp. *airoides* The latter species is common in renosterveld "forming a thick mat between the bushes" (Linder and Ellis 1990). The grasses do considerably well amongst bushes or interstitial open spaces, in the absence or presence of grazers, and flourish shortly after fire.

Sub-community 1: *Oxalis pes-caprae–Hermannia alnifolia* Sub-community

(Table 3.6, relevés 35-58)

Scientific name: *Pterygodio catholici-Elytropappetum rhinocerotosi oxalidetosum pedis-capraeae* subass. nova

Holotypus: Table 3.6, relevé 49

This sub-community was described on the basis of 24 relevés; it has 12 diagnostic species, and it is often dominated by the shrub *Hermannia alnifolia* (de) also by the decumbent palatable pea *Indigofera psoraloides* (de) and occasionally *Otholobium decumbens* (de). It contains many geophytes such as *Androcymbium capense* (de), *Babiana odorata* (de), *Cyanella lutea* (de), *Hesperantha falcata* (de), *Oxalis pes-caprae*, *O. tomentosa* and *Sparaxis villosa* (de). The fern *Mohria caffrorum* (de) occurs here with the succulent annual plant *Carpanthea pomeridiana* (de), the former occurring most abundantly in unploughed stands representing a rich green or thick stratum over the soil surface pedoderm during winter. This community is influenced by herbivory since many species are palatable (see van Breda and Barnard 1991) and *Hermannia alnifolia*, having an endo-zoorochorous mode of dispersal (Shiponeni 2003) is typically browsed to 50 cm here, even amongst dense shrub cover. *Hermannia alnifolia* and *H. scabra* are usually reseeders and form dense stands a short period following fire (especially in the absence of browsers at Voëlvlei) and flower in the next season. Their abundance declines as more dominant and less palatable shrubs mature, like *Elytropappus rhinocerotis* and *Athanasia trifurcata*.

Sub-community 2: *Ischyrolepis capensis-Anthospermum spathulatum* Sub-community
(Table 3.6, relevés 59-72)
Scientific name: *Pterygodio catholici-Elytropappetum rhinocerotis ischyrolepidetosum capensis* subass. nova hoc. loco
Holotypus: Table 3.6, relevé 62

This sub-community is based on 14 relevés and 19 diagnostic species. It is dominated by the restio *Ischyrolepis capensis*, which occurs in dry habitats and disturbed places at low elevations (Haaksma and Linder 2000), the shrub *Anthospermum spathulatum* (de) (often stunted by browsing) and the dwarf shrub *Aspalathus ciliaris*. *A. spathulatum* is usually killed by fire, but occasionally resprouts from the base as well (Puff 1986; B. A. Walton, personal observation). The resprouting habit is probably dependant on moisture availability. The plant often forms a stunted rounded bush here from browsing, unlike its usual erect habit. *Ehrharta longifolia*, *Ficinia indica* and *Ischyrolepis gaudichaudianus* (de) are other graminoids occurring in this vegetation type. *Ischyrolepis capensis*, *I. gaudichaudianus* and *Ficinia indica* are all resprouters rejuvenated after fire; *Ficinia indica* is usually browsed either by termites or mammalian herbivores. *Ehrharta longifolia* is an annual or pauciennial found under cover of shrubs as a respite from direct sunshine and grazers. The rosette hemicryptophyte *Berkheya armata* (de) is common, while *Gazania serrata* occurs occasionally on the flats especially in more open areas, and *Lotononis prostrata* (de) rambles throughout in places. *Aristea africana* (de), *Empodium plicatum*, *Eriospermum capense* (de), *Lachenalia pallida*, *Lapeirousia azurea* (de), *Oxalis livida*, *Spiloxene capensis* (de) and *Wachendorfia brachyandra* are the most common geophytes here. The wealth of geophytes, in particular the presence of wetland type taxa like *Empodium* and *Spiloxene*, suggest a less well-drained habitat than Sub-community 1. The latter taxa grow along verges of rivulets or seasonal rivers and often occur in drainage lines of old fields. The succulent *Lampranthus elegans* with an erect, prostrate or spreading habit occurs often in seasonally inundated flats and is a marvel to the eye, as well as the mat-forming *Lampranthus tegens* (de).

The hierarchical clustering (complete linkage with chord distance) corroborated the vegetation classification of quadrats found using TWINSPAN quite well (Figure 3.3). The first split showed that the Community 1 was discrete from Community 2. However, the sub-communities of Community 2 were indiscernible.

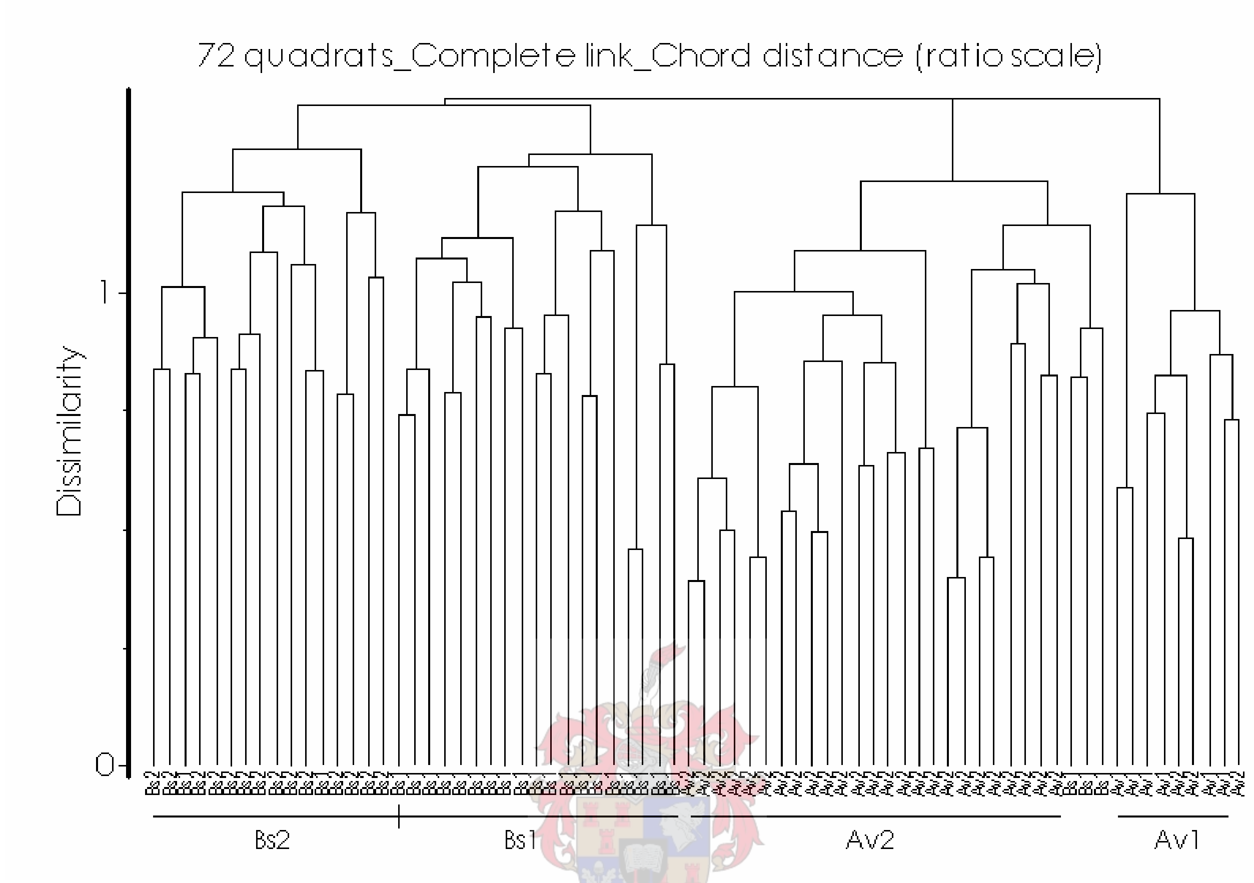

Figure 3.3: Hierarchical tree of 72 quadrats (as used in classification; see Tab. 3.6) at 10 m^2 scale. Complete linkage clustering with Chord distance (as resemblance function) was used. Av1 = Variant 1, Av2 = Variant 2, Bs1 = Sub-community 1 and Bs2 = Sub-community 2

3.3.2. Ordination

Ordination at 10 m^2 Scale

The PCA ordination of samples at the 10 m^2 scale (Figure 3.4.a) revealed that along the ordination axis 1 samples from both unploughed renosterveld and 30-year-old fields are dissimilar to younger old fields (15- and 5-year-old fields), hence recovering a general sequence of succession. The samples from unploughed renosterveld were similar to 30-year-old fields (both classified as the renosterveld sub-communities) in terms of abundance of their constituent species, as they overlapped in multivariate space.

Table 3.6: Structured full relevé table of 10 m^2 quadrats of renosterveld and old fields at the Agter-Groeneberg Conservancy. HL = herb layer, SL = shrub layer; grazing code is the level of intensity (1 = none, 2 = moderate and 3 = high); seral code is the seral stage (1 = 5-year-old fields, 2 = 15-year-old fields, 3 = 30-year-old fields and 4 = unploughed renosterveld); fire age code is the post-fire age of vegetation (1 = 20-29 years ago, 2 = 10-19 years ago, and 4 = < 5 years ago). Alien taxa are in italics. See Appendix 3.6 for a list of infrequently occurring taxa, omitted in this table. The column "Diag." indicates the diagnostic value of a taxon as a composite code; c = common species in this table, de = exclusive differential species, ds = selective differential species.

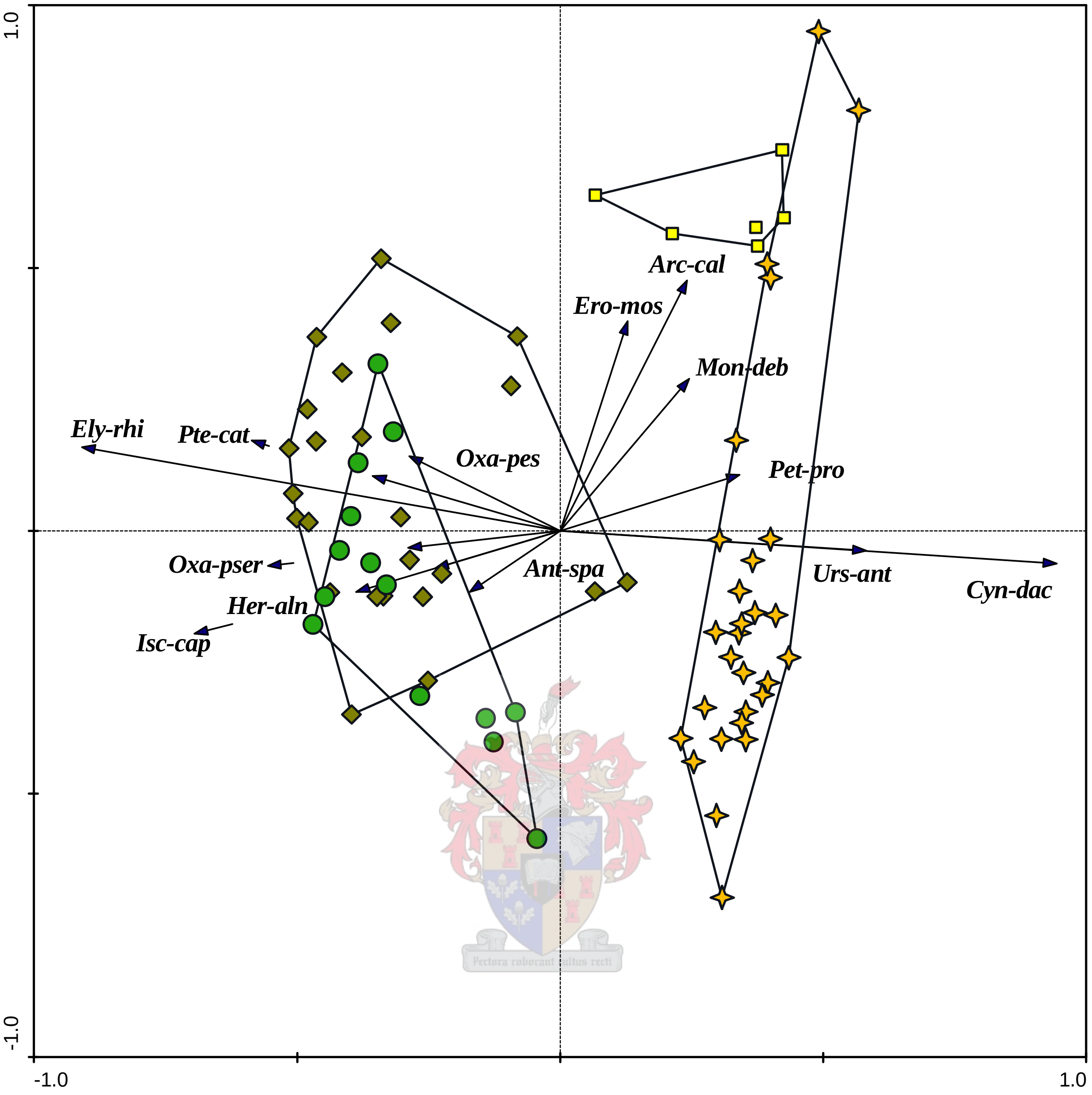

Figure 3.4a: PCA ordination diagram of the first two axes of 72 quadrat samples (10 m^2). The polygons recover the communities (in the form of an envelope enclosing all samples of related class, as featured in Tab. 3.6). Yellow squares represent the Variant 1 of the old field community, orange stars represent the Variant 2 of the old field community, brown diamonds represent Sub-community 1 of the renosterveld community and green circles represent the Sub-community 2 of the renosterveld community. Species are: Urs-ant = *Ursinia anthemoides*, Cyn-dac = *Cynodon dactylon*, Ero-mos = *Erodium moschatum*, Arc-cal = *Arctotheca calendula*, Pet-pro = *Petrorhagia prolifera*, Mon-deb = *Monopsis debilis*, Pte-cat = *Pterygodium catholicum*, Ely-rhi = *Elytropappus rhinocerotis*, Oxa-pes = *Oxalis pes-caprae*, Oxa-pser = *Oxalis pes-caprae* var. *sericea*, Her-aln = *Hermannia alnifolia*, Isc-cap = *Ischyrolepis capensis*, Ant-spa = *Anthospermum spathulatum*

Along axis 2 the 5-year-old fields were well separated from the 15-year-old fields, again recovering the sampled chronosequence. The ordination thus recovered a gradient of secondary succession.

The CCA bi-plot revealed discrete groups of samples along the ordination axis 1, effectively recovering the chronosequence. The sequence of these groups corresponds to their seral stage (Figure 3.5a). It appears here that only after 30 years will vegetation on old fields resemble that of unploughed renosterveld. The samples were agglomerated into only 13 samples from the set of 72, suggesting that the samples were highly constrained by the nominal variables used in the analysis. Nevertheless the unploughed renosterveld samples and 30-year-old fields were dissimilar to each other, and clustered around their respective centroid of seral stage environmental pseudo-variable. Both the sample set of 15- and 5-year-old fields were agglomerated and had identical coordinates to their respective seral stage environmental pseudo-variable centroid score.

Along ordination axis 2 the gradient of grazing intensity was recovered as was the sample fire history age (in slightly opposing directions). However these two explanatory pseudo-variables and their recovered gradients may be an artefact of specific site or habitat differences related to other confounding factors like soil type. Seral stages were not evenly replicated, as only Elandsberg had the full chronosequence (whilst the other two sites had only the later two seres), possibly distorting the gradient of grazing intensity. Due to the unevenness of sample replication for the post-fire age factor the gradient of stand age is perhaps not reliable for interpretation. Figures 3.5b and 3.5c depict the first and third, and, second and third ordination axes, respectively. Figure 3.5b is similar to Figure 3.5a in that the ordination recovers the chronosequence along axis 1, but without a linear recovery of the grazing gradient along axis 3. Figure 3.5c shows a similarity amongst the second, third and fourth sere and the grazing and fire history gradients rotate clockwise about the axes. In addition species richness of the quadrats was assigned as a passive co-variable in a fourth CCA ordination bi-plot (Figure 3.5d) which was able to tease out the sample agglomeration. This ordination showed that the unploughed renosterveld was similar to the 30-year-old fields (probably due to similar species richness and not species cover-abundances).

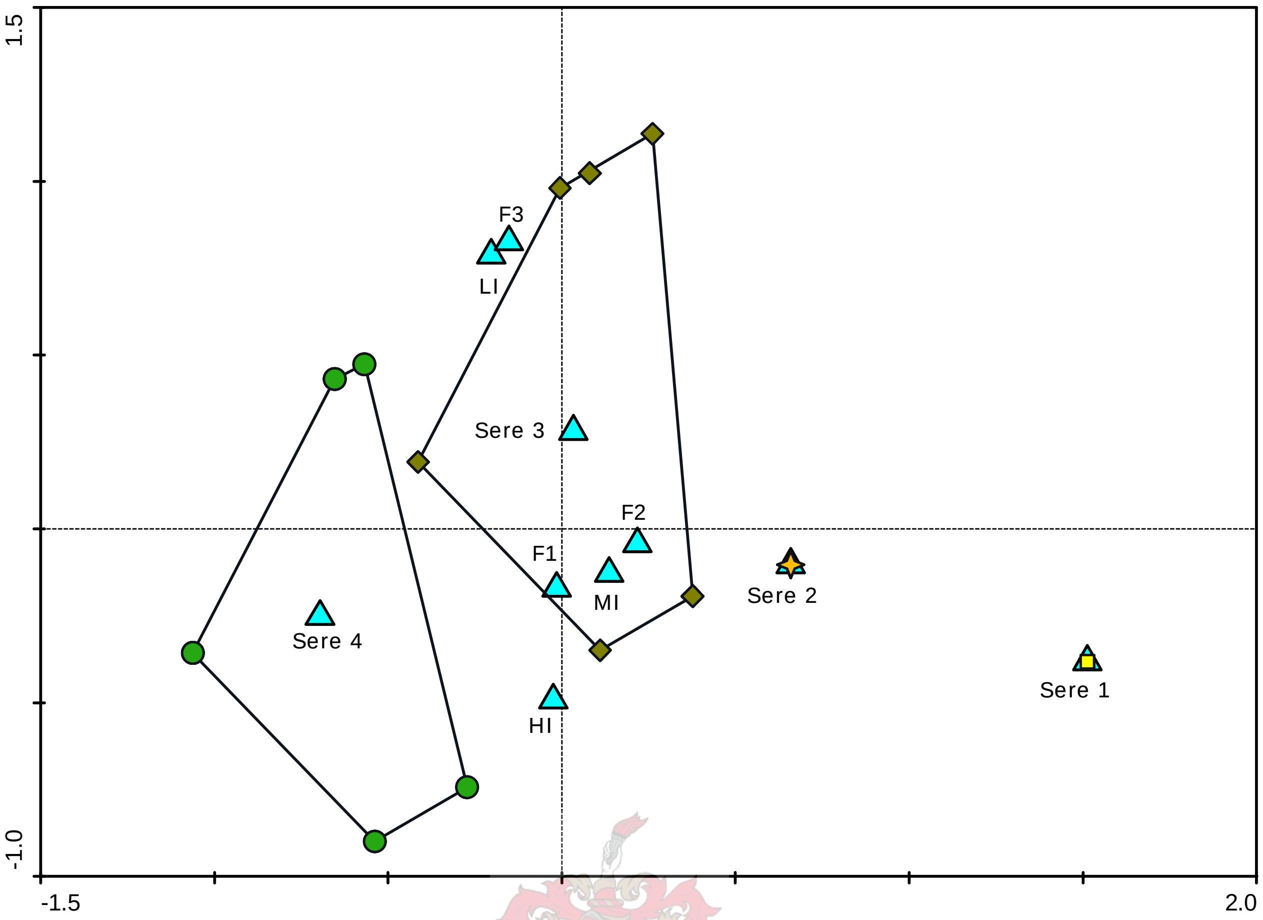

Figure 3.5a: CCA ordination diagram of the first two axes of 72 quadrat samples (10 m^2). The polygons recover the seral stages (in the form of an envelope enclosing all samples of related sere). Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old fields; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity; MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982; F2 = 1988; F3 = 1999). Sample objects are: yellow squares for Sere 1, orange stars for Sere 2, brown diamonds for Sere 3 and green circles for Sere 4

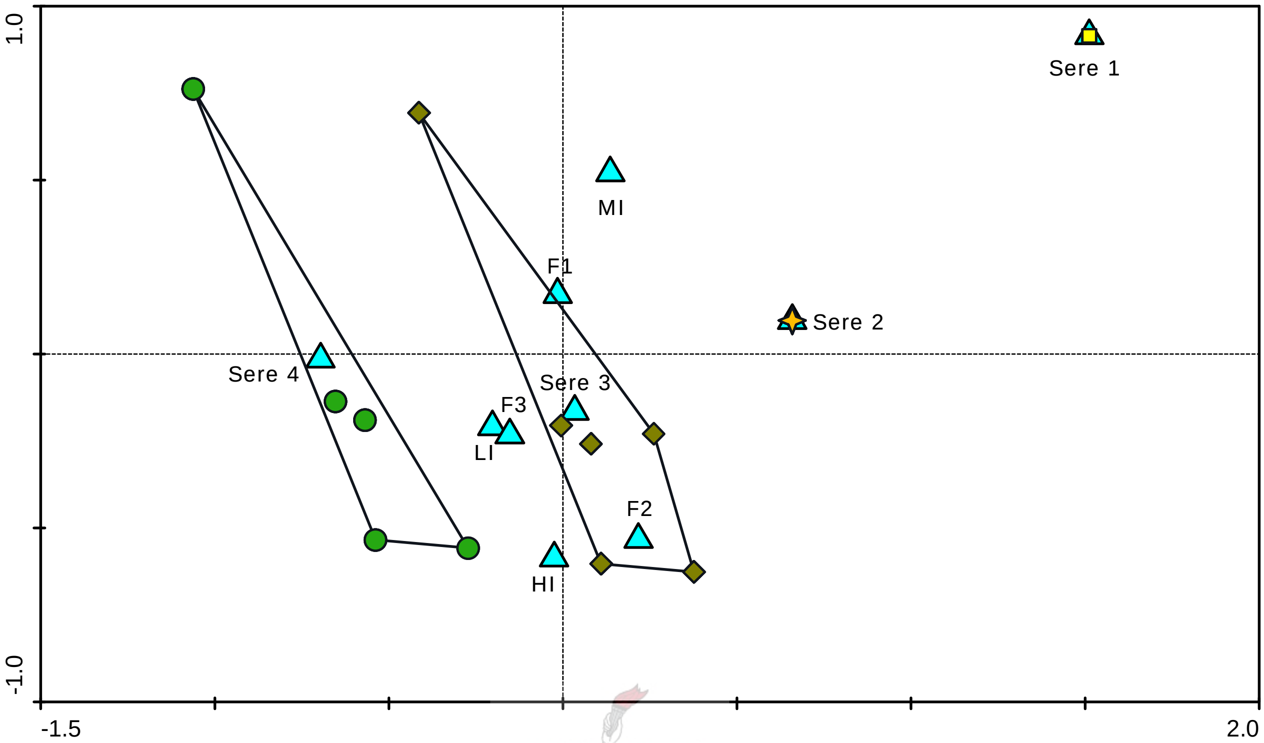

Figure 3.5b: CCA ordination diagram of the first and third axes of 72 quadrat samples (10 m^2). The polygons recover the seral stages (in the form of an envelope enclosing all samples of related sere). Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old fields; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity; MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982; F2 = 1988; F3 = 1999). Sample objects are: yellow squares for Sere 1, orange stars for Sere 2, brown diamonds for Sere 3 and green circles for Sere 4

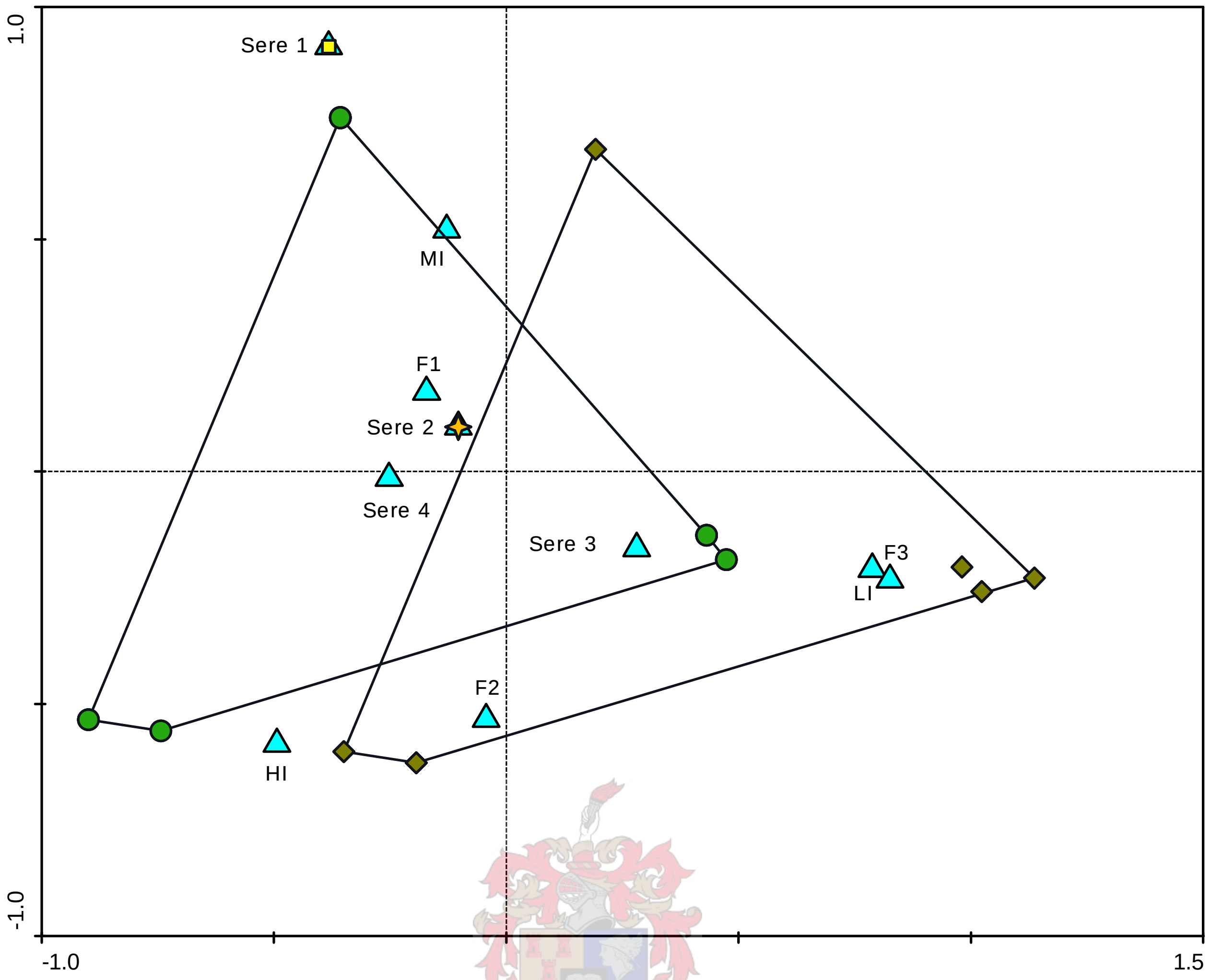

Figure 3.5c: CCA ordination diagram of the second and third axes of 72 quadrat samples (10 m^2). The polygons recover the seral stages (in the form of an envelope enclosing all samples of related sere). Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old fields; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity; MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982; F2 = 1988; F3 = 1999). Sample objects are: yellow squares for Sere 1, orange stars for Sere 2, brown diamonds for Sere 3 and green circles for Sere 4

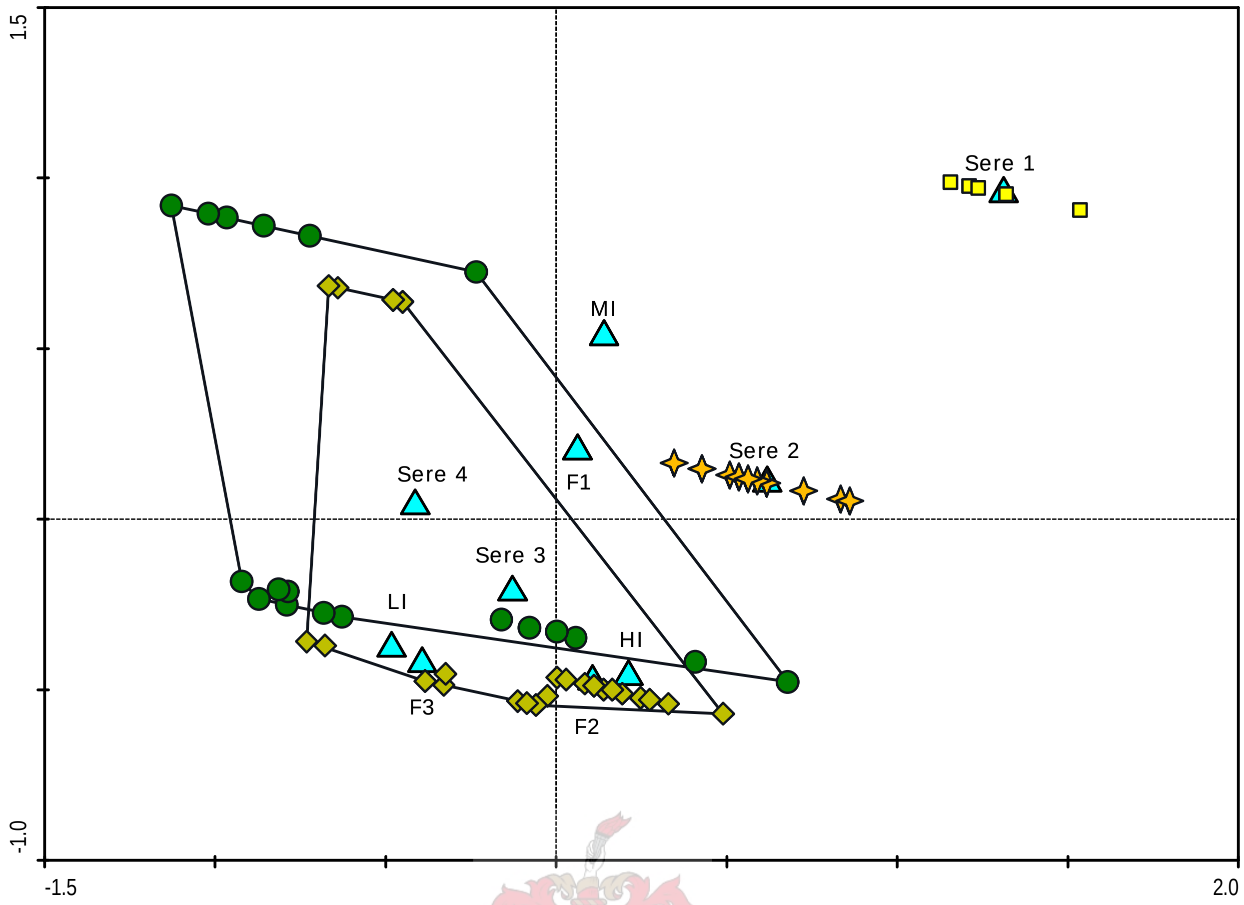

Figure 3.5d: CCA ordination diagram of the first two axes of 72 quadrat samples (10 m^2). The polygons recover the seral stages (in the form of an envelope enclosing all samples of related sere). Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old fields; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity; MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982, F2 = 1988, F3 = 1999). Species richness of relevés was entered as a passive numerical co-variable. Sample objects are: yellow squares for Sere 1, orange stars for Sere 2, brown diamonds for Sere 3 and green circles for Sere 4

Ordination at 1000 m^2 Scale

The unploughed relevés appeared to have the highest carbon and nitrogen status relative to the different aged-old fields with values above 3% organic matter content (A Rozanov, personal comment), although these were not significantly different with univariate tests of significance (ANOVA). The only soil variable that was significantly different amongst the seral stages was phosphorus content, specifically between the single sample from the first sere and the other seral stages (Figure 3.6). The 30-year-old fields and a 5-year-old field have a very low electrical resistance with corresponding high Na^+ content and conductivity. They have a high salinity and conductivity, probably due to fertilizer applications, specifically lime during tillage to homogenize the fields, and low acidity relative to other stands. In ordination the cluster of 15- and the single 5-year-old field samples are low in carbon, nitrogen, potassium, CEC and carbon-nitrogen ratio relative to the 30-year-old fields and unploughed renosterveld (Figure 3.7a) suggesting depletion due to tillage.

Overall there is a good phosphorus and potassium content (fertility), except for some old fields. The CCA ordination bi-plot diagram shows the samples are all different from each other without a discrete or tight grouping of any, thus the chronosequence was not recovered here. The single sample from sere 1 behaved as an outlier corresponding to low CEC values with the highest phosphorus value. The samples from Sere 2 (15-year-old fields) were clustered close to each other, thus similar in terms of their phosphorus content and carbon-nitrogen ratio. Clearly samples from the later seres (3 and 4) varied in terms of pH, CEC, carbon, potassium, nitrogen, carbon-nitrogen ratio and phosphorus content. Another CCA bi-plot was made with the exclusion of the seral stage explanatory variable in an attempt to factor out the effect of the chronosequence (ploughed versus unploughed) on the sample relationships. No different patterns emerged with or without the seral stage explanatory variable in the CCA ordination suggesting that this factor was not informative regarding soil patterns. Here again the unploughed renosterveld and 30-year-old fields similarly displayed a wide variation in soil properties related to differences in micro habitat or site variation of the study area. The second sere was dissimilar from the later two seres and the single sample from sere 1 was an outlier, showing the highest levels of phosphorus content of the soil. The addition of species richness as a co-variable showed the same pattern of orientation (relationships) of explanatory variables and was thus used here. Another CCA ordination was performed with samples classed according to similar habitats (Figure 3.7b)

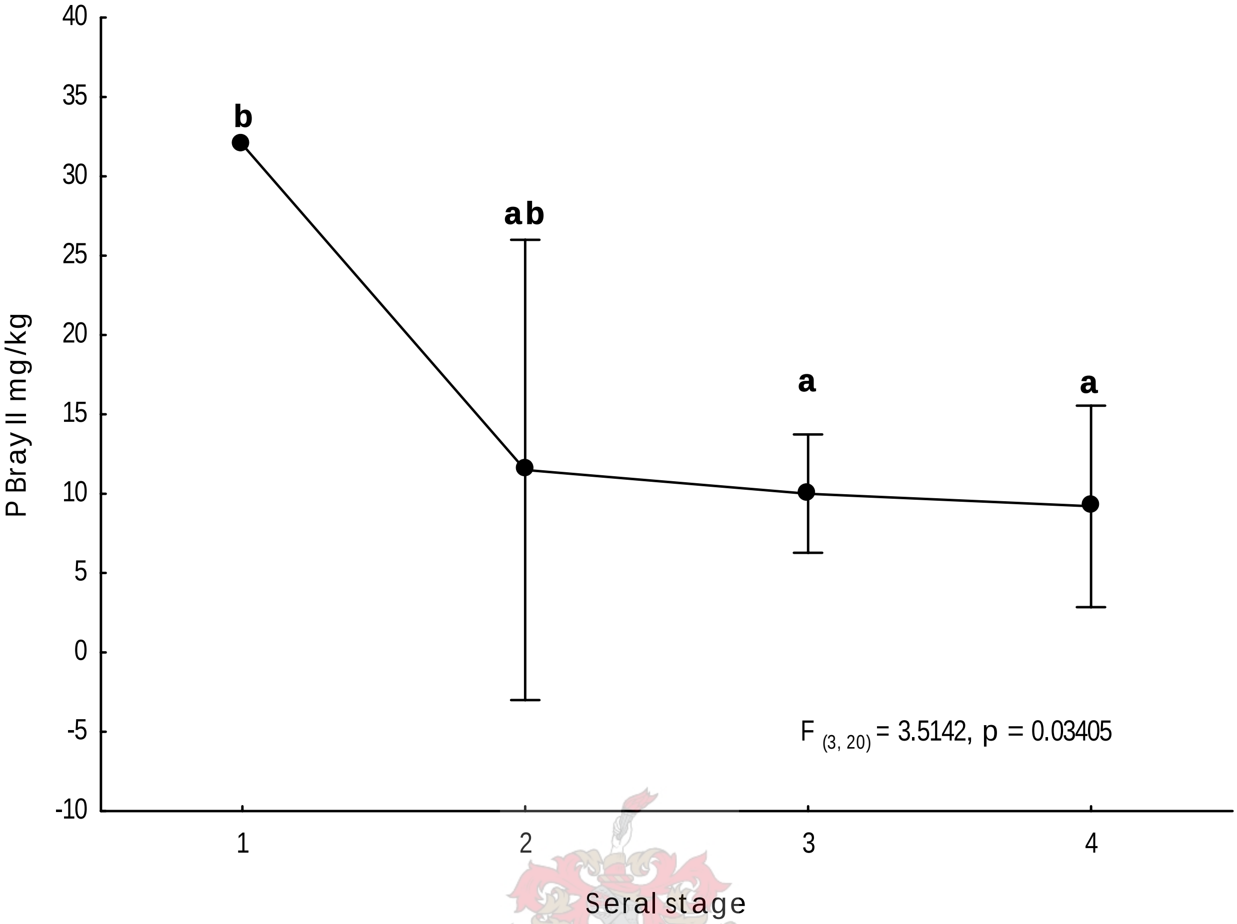

Figure 3.6: A one-way ANOVA test of phosphorus content (y-axis, weighted means) per sere. 1 = a single 5-year-old field (Sere 1), 2 = 15-year-old fields (Sere 2, n = 4), 3 = 30-year-old fields (Sere 3, n = 14) and 4 = unploughed renosterveld (Sere 4, n = 5). Vertical bars denote 0.95 confidence intervals; characters depict Bonferroni degree of similarity

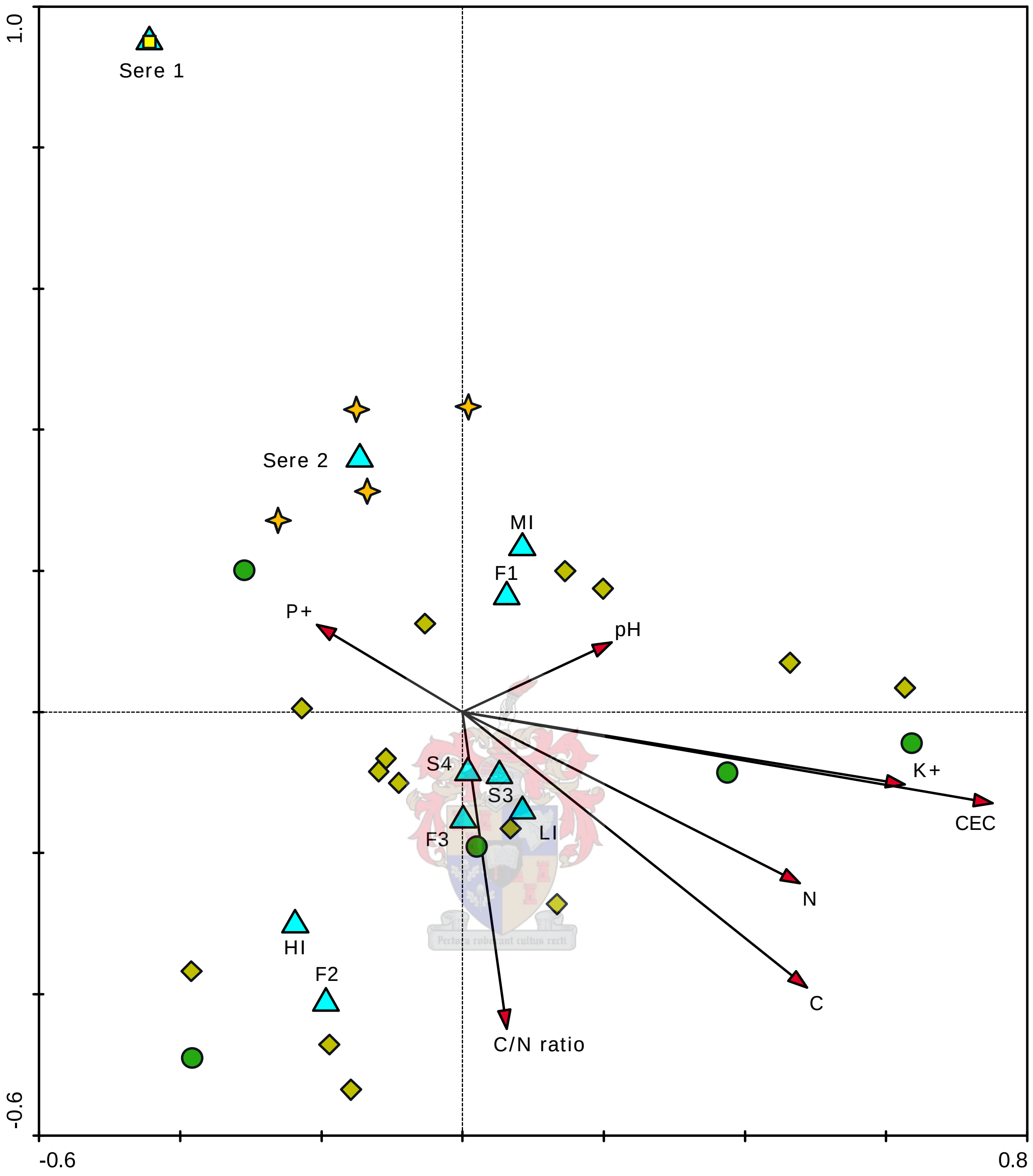

Figure 3.7a: CCA ordination diagram of the first two axes of 24 relevés (1000 m^2) with environmental variables. Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old field; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity, MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982; F2 = 1988; F3 = 1999). Numerical variables are: C/N ratio, C = carbon, N = nitrogen, K+ = Potassium, P+ = phosphorus and CEC = total sum of exchangeable cations, with pH measured in an interval scale. Species richness of relevés was entered as a passive numerical co-variable. Sample objects are: a yellow square for Sere 1, orange stars for Sere 2, brown diamonds for Sere 3 and green circles for Sere 4

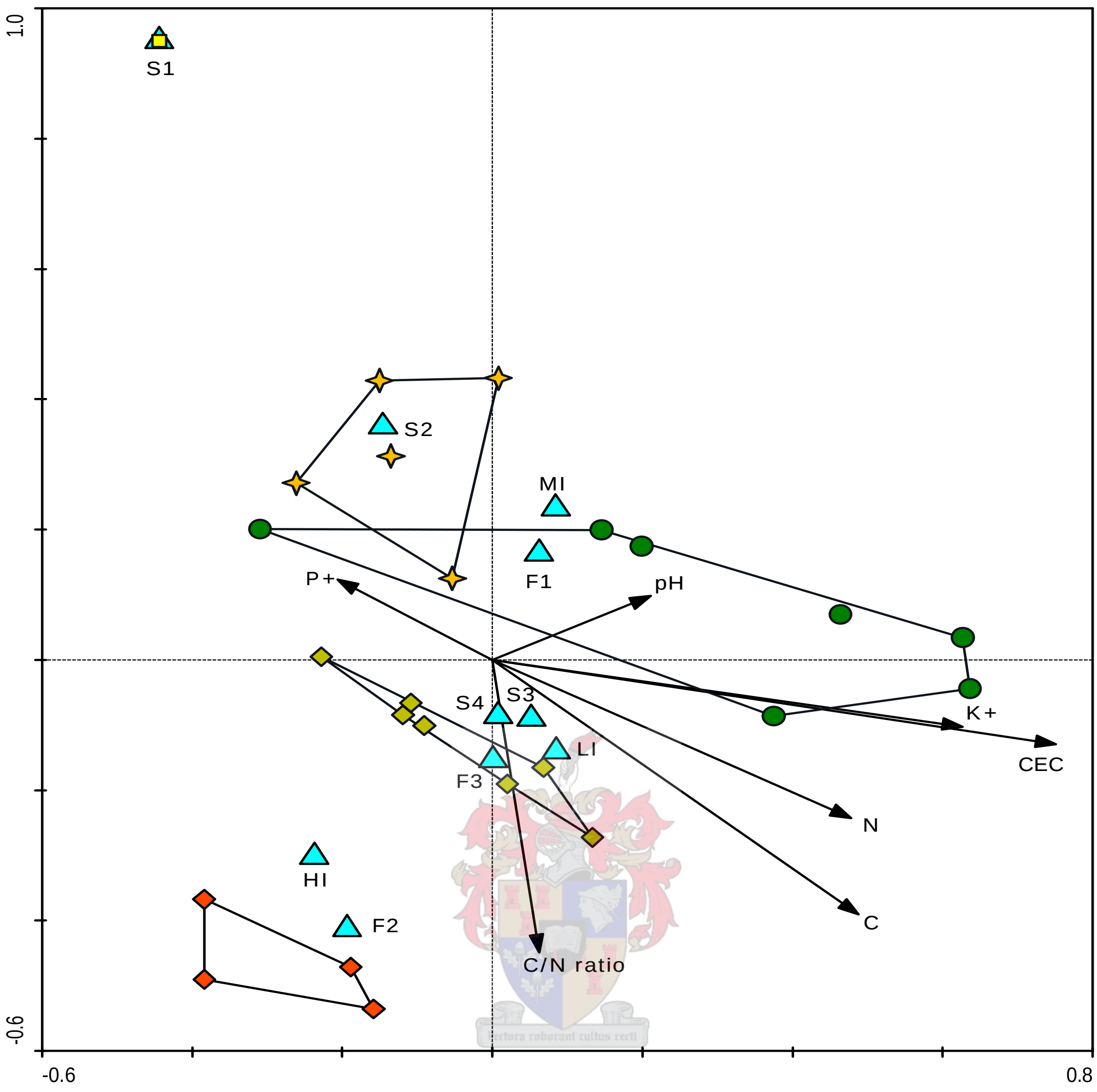

Figure 3.7b: CCA ordination diagram of the first two axes of 24 relevés (1000 m^2) with environmental variables. Nominal environmental variables (blue triangles) are: seral stage (Sere 1 = 5-year-old field; Sere 2 = 15-year-old fields; Sere 3 = 30-year-old fields and Sere 4 = unploughed renosterveld), grazing intensity (LI = low intensity; MI = moderate intensity and HI = high intensity) and fire-age (post-fire age: F1 = 1982; F2 = 1988; F3 = 1999). Numerical variables are: C/N ratio, C = carbon, N = nitrogen, K+ = Potassium, P+ = phosphorus and CEC = total sum of exchangeable cations, with pH measured in an interval scale. Species richness of relevés was entered as a passive numerical co-variable. Sample objects are classed loosely according to assumed habitat type, with polygons that recover the habitat (in the form of an envelope enclosing all samples of related habitat). The yellow square for Sere 1, orange stars for old fields of the plains, brown diamonds for 30-year-old fields at Voëlvlei and Krantzkop (with a single control) and green circles for the elevated ridges, and red diamonds for elevated 30-year-old fields at Krantzkop (with one control)

3.4. Discussion

3.4.1. Vegetation Community Patterns

Acocks (1988) showed a picture of renosterveld at the AGC (Welbedacht Farm) and listed species occurring in both renosterveld and fynbos, apparently descriptive for “western” coastal renosterveld then. A tentative phytosociological survey of fynbos and renosterveld vegetation at Elandsberg was done by Diemer (2000). The renosterveld “community” has species found in my survey of renosterveld, but I failed to establish the relevé size at which the survey was done. An attempt at classifying renosterveld on the Tygerberg Hills, excluding the annual and geophytic components, was made by Paterson (1982). The informal classification was not comprehensive and many taxa remained unidentified. A phytosociological study of renosterveld on Signal Hill by Joubert and Moll (1992) is comprehensive, and two separate tables are shown for perennial versus ephemeral taxa. Group I, an overlap of two communities, seems to correspond with the *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland of this study, albeit on steep slopes of Signal Hill with different component species. The most comprehensive study of renosterveld vegetation with classification, description and mapping of communities to date was conducted by Boucher (1987), who also included relevés sampled at Krantzkop (Welbedacht Farm) and Elandsberg. The communities described by Boucher (l.c.) at Krantzkop and Elandsberg include the *Ischyrolepo-Leucospermum calligeri* (Boucher 1987, Figure 104), the “*Oleo-Eucleetum acutifoliae* bush-clump”, and the “*Ischyrolepo-Leucadendron brunioides*” (Boucher 1987, Figure 105), both subordinate to the *Ehrharto - Elytropappetalia rhinocerotidis* and the *Elytropappo - Ischyrolepion capensi*. Here both Alluvium Shale Fynbos has been classified together with Swartland Shale Renosterveld, which are two distinct vegetation types. Boucher (l.c.) described many renosterveld and derived communities on both flat and sloped ground at the Bottelary Hills, Devon Valley, Groeneberg, Helderfontein Farm, Kanonkop, Paardeberg and Saron. Taylor (1996) described the *Ischyrolepis capensis - Elytropappu*s *rhinocerotis*, occurring in the Cederberg Pakhuis shale band, as distinct from the surrounding mountain fynbos with 16 exclusive taxa. There is a high cover and diversity of the graminoid element on these fine textured soils and the community is dominated by *Elytropappus rhinocerotis* with occasional emergent orthophyllous proteoids. The difference between Taylor’s community and the *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland is that the former occurs at higher elevations often on slopes probably within a higher rainfall regime, and the suite of species is entirely different. Linder (1976) correlated percentage clay and silt in soil with pH and found renosterveld communities had a preference for higher values than fynbos on the Piketberg. Linder's Renosterveld community had two strata only with an 80%-90% shrub cover (and occasional open patches with grasses *Ehrharta* and *Merxmuellera* co-dominant). This community occurs on shale without fynbos elements (up to 600 m) and shares constant species (like *Elytropappus rhinocerotis*, *Eriocephalus africanus*, *Euryops speciosissimus* and *Mohria caffrorum*) with the *Relhania squarrosa* "Dry Fynbos" community on lower slopes (between 300-600 m). Thus the Renosterveld community would be unlike that which I have described here only in terms of being on a slope at a higher altitude, as there is a high richness of annuals and geophytes. An inventory of the Darling Hills was done by Heydenrych and Littlewort (1995) who listed 420 species (of which nearly one third were monocotyledonous), but did not attempt a community description. Rebelo et al. (1991), using a structural approach (see Linder and Campbell 1979, Campbell et al. 1981, Campbell 1985), described a renosterveld shrubland in the Riversdale Plain as a Series within the Karroid and Renoster Shrubland Group. This renosterveld shrubland was differentiated on the basis of low total cover, a high asteraceous cover, presence of succulents, and absence of fynbos flagship taxa (proteoids, ericoids and restiods). The Bokkeveld Shale formation was shared by the renosterveld shrubland in the west and Kaffrian Succulent Thicket in the east (almost discretely divided by the Kafferkuils River), the latter on deeper soils and steeper topography. Cowling (1984) surveyed South Coast Renosterveld in the Humansdorp region describing four communities of renosterveld there. Similarly Cowling et al. (1988) did a phytosociological survey of the Agulhas Plain using Campbell's approach and also described a Renoster Shrubland Group which shared the dominant *Elytropappus rhinocerotis* with the Mesotrophic Asteraceous Fynbos Sub-series.

Thus the communities described here are unique at the association level in the Fynbos Biome. The *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland has in part been described before but not as this association. The *Ursinio anthemoidis–Cynodontetum dactyli* Grassland description is unique, probably as old fields have not ever been described locally. The diagnostic species for both communities will provide a key to the identification of communities in the field. The communities described will add to an ecological understanding of renosterveld and form part of a larger framework of renosterveld vegetation classification and description.

3.4.2. Gradient Analyses

The communities described were investigated further in relation to explanatory (environmental) variables (seral stage, grazing intensity and post-fire age). The ordination and grouping of vegetation samples was similar to that of the numerical vegetation classification. Thus an indirect gradient analysis (PCA) showed the variants of Community 1 to be discrete entities and dissimilar to Community 2, whilst the two Sub-communities of Community 2 were similar to each other. With a constrained ordination (CCA) using the explanatory variables it was clear that the seral stage of the samples was the most discriminating factor and that the chronosequence or secondary succession was effectively recovered along the first axis. With the inclusion of species richness as a co-variable, it was shown that 30-year-old fields were similar to unploughed renosterveld. This implies that species richness and their cover-abundance of 30-year old fields had sufficient time to resemble unploughed renosterveld.

The CCA ordination thus shows a pattern of difference in species composition with time or the advancement of succession. The temporal change in species composition with succession shows a turnover of species, where ruderal species are replaced by more typical renosterveld species. Thus renosterveld appears to be resilient to a destructive ploughing event, especially if the ploughing frequency is low or occurred once only, and if given ample rest.

The constrained ordination (CCA) of 24 samples (at the 1000 m^2 scale) with the explanatory variables (soil properties, seral stage, grazing intensity, post-fire age and species richness) was not clear. Perhaps an unequal replication of samples for all levels of disturbances was a limitation in producing a pattern of discrete groups of similar samples. However both the 30-year-old fields and unploughed renosterveld showed a wide variation in soil characteristics probably attributed to micro-habitat differences, and were similar in that regard. Thus some 30-year old fields were either not often ploughed (as was the case at Elandsberg) and their soils properties were not irreversibly altered like the often ploughed younger old fields. The group of 15-year-old fields were a discrete entity in terms of similar soil characteristics, notably with high phosphorus content relative to the other samples. Thus the artefact of the addition of lime to the agricultural fields was recovered in the ordination, as this had not effectively been diluted from the site. The phosphorus content was independent of the carbon and nitrogen content in this study, which is unusual (Dr. A. Rozanov, personal communication), indicating that besides the organic phosphorus content of the soil the addition of mineral phosphorous (and persistence in the soil) has made these variables independently related. What the ordination did show anecdotally was the difference in micro-habitat soil characteristics-especially along Axis 2 with the C/N ratio-which I loosely categorized (on the basis of personal observations) into: old fields of the “plains”, elevated ridges, 30-year-old fields (from Voëlvlei, with one control, and Krantzkop) and elevated 30-year-old fields from Krantzkop (with one control). Thus even after transformation, soil properties are probably determined by the micro-habitat and local soil forms which determine the “type” of vegetation more so than a previous ploughing event.

3.5. References

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Chapter 4

Vegetation Dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa

Figure 4.1: Grazing plains zebras (*Equus burchelli* “quagga’s”) on an old field at Elandsberg Private Nature Reserve

4.1. Introduction

Vegetation patterns and dynamics in renosterveld and associated different-aged old fields are the objects of study here. This explorative study describes succession on: (a) set-aside old fields, and (b) set-aside old fields with different grazing intensities (Figure 4.1). Little has been documented regarding vegetation dynamics of renosterveld in relation to disturbances such as ploughing and grazing. An understanding of the trajectory of secondary succession on old fields proximate to indigenous propagule sources at the Agter-Groeneberg Conservancy (hereafter denoted AGC) will be gained. Life-form richness and cover-abundance in unploughed renosterveld vegetation and different-aged old fields was quantified and compared, with different grazing intensities. This study of life-form patterns will be used to infer general processes relating to renosterveld dynamics.

Disturbance, defined by White and Pickett (1985), is "a discrete event in time and space that alters the structure of populations, communities and ecosystems". Biotic density, biomass and spatial distribution are altered by a change in resource and substrate availability and distribution, or by an alteration of the physical environment. Natural and more recent anthropogenic disturbances are known to influence patterns in vegetation (Walker and Willig 1999). Plant functional group classification based on morphological and ecological traits (Grime 1985, 2001) is used to study vegetation responses to both natural and anthropogenic disturbances. A classification of species into life-forms was deemed necessary, in order to assess the effects of ploughing and grazing disturbances on vegetation dynamics.

Disturbance by herbivory may select for both physical and chemical defence strategies (Ruiz et al. 2002) in plant species. Spinescence is prevalent in renosterveld (Campbell 1986) in shrubs and dwarf shrubs such as: *Aspalathus spinosa*, *Asparagus capensis*, *Berkheya rigida*, *Cliffortia juniperina*, *Gymnosporia buxifolia*, *Lycium afrum* and *Muraltia heisteria*; hemicryptophytes like *Arctopus echinatus*, *Berkheya armata* and therophytes like *Gorteria personata.* A pertinent issue is to determine which life-forms herbivory would: promote, favour, or facilitate; and which life-forms it would disturb, stress or diminish. A synopsis of the life-form groups occurring at different seral stages would, in part, reveal this. It would be logical to assume that endo-zoochorous species will be favoured as well as spinescent species (the latter often palatable such as *Aspalathus spinosa* or *Asparagus retrofractus*). By keeping plant communities in a state of intermediate levels of disturbance (*sensu* Connell 1978), herbivores may maintain high levels of species richness and diversity (Bakker and Olff 2003) either by creating open spaces in a shrubland matrix or dispersing seed whilst browsing and grazing, and especially by a combination of these processes. Dispersal of plant species by herbivores is an important function in vegetation composition influencing vegetation patterning (Vera 2000). Pioneering plants (annuals, some forbs and geophytes also short-lived perennials) adapted to frequent or intense disturbance, whether by herbivory or fire, are equally suited to ruderal conditions caused by anthropogenic disturbances (Petsikos et al. 2004, Van Rooyen 2002).

Ploughing is a destructive, rapid and intense unnatural disturbance event resulting in the complete removal of above- and below-ground biomass. It effectively resets the system to nil, dramatically altering successional pathways in comparison to those either caused by grazing or fire disturbance events. With cessation of ploughing one therefore expects plant species arriving on to old fields and which increase in abundance, are species adapted for long-distance dispersal or have propagules that survive ploughing. Certain plant traits are well suited to the novel disturbance of low frequency ploughing. These include dormant seeds or vegetative plant parts (stolons), bulbs, corms, rhizomes and tubers. Deep rooted plants able to reproduce clonally or vegetatively: for example *Rumex cordatus* and *R. crispus* (Zaller 2004) can escape ploughing. Geophytes that grow deeper each season to avoid predation by gazelles (Ward and Saltz 1994), mole rats (*Georychus capensis*) or porcupines (*Hystrix africaeaustralis*, foraging for *Babiana odorata* and *Cyanella hyacinthoides*, B.A. Walton, personal observation), or diggings by aardvarks (*Orycteropus afer*) would be equally suited to escape the plough. Selected species are adapted to survive predator diggings (Lovegrove and Jarvis 1986) by either shedding bulbils (and/or cormlets) or by growing deeper each year like *Babiana stricta* (see Michell 1922). Similarly, size matters and small bulbs of *Oxalis purpurea* (sorrel/suuring) or *Romulea rosea* (froetang) are well adapted to evade large ploughs, enabling persistence on some old fields unlike large geophytes from the Amaryllidaceae like *Crossyne guttata*.

What determines species and life-form composition of renosterveld vegetation and associated-old fields? Disturbances by fire, herbivory and foraging (see Gutterman 2001, Bragg et al. 2005) processes influence the vegetation patterning. The pathway of succession on old fields is related to the site disturbance history; contemporary disturbances and proximity to propagule sources (see Pickett et al. 1987). The specific habitat where succession occurs is of prime importance as successional pathways are affected by topography, soil quality, hydrology, wind, erosion and previous applications of chemicals (and contemporary run-off from adjacent agriculture). Succession on old fields depends on species mobility (from a proximate propagule source), seed dispersal agents (wind, water, birds, ants, porcupines, small and large mammals), competitive interactions, herbivory and propagule persistence. Old fields of renosterveld are generally dominated by indigenous and alien annuals and a perennial stoloniferous C_4 grass *Cynodon dactylon*, with a characteristic guerrilla-type space acquisition strategy, dispersed by tillage (Guglielmini and Satorre 2004) as well as herbivores (Shiponeni 2003). Some bunchgrasses do occur on old fields, in pockets (probably in favoured micro-sites due to soil type, B.A. Walton, personal observation), as well as a few shrub species dispersed from nearby stands of natural vegetation. A question often posed is how long, if at all, do old fields take to completely recover or resemble natural stands of renosterveld? Do these old fields ever attain a “natural” state? Since little empirical evidence exists for secondary succession on to old fields following ploughing of renosterveld, this study is an attempt to recognize patterns that will aid in determining the mechanisms and processes of renosterveld dynamics. Understanding these patterns and processes on old fields and in unploughed renosterveld with the interaction of grazing is equally applicable to landscape rehabilitation in an agricultural matrix; or vegetation restoration near extant renosterveld.

The objective of this chapter is to answer the following questions:

1: Does total species and life-form group richness differ between natural vegetation and old fields?

2: Is life-form richness influenced by ploughing and grazing or the interaction between these disturbances?

3: Is life-form cover-abundance influenced by ploughing and grazing or the interaction between these disturbances?

4: Does alien plant species richness differ amongst seres, and with different levels of grazing intensity?

4.2. Materials and Methods

This study was conducted in the Western Cape of South Africa, in three contiguous sites of the AGC in the Wellington District (refer to Chapter Two for a concise account of the study area and environmental characteristics). The AGC is composed of some remaining fragments of Swartland Shale Renosterveld (the vegetation type of focus), and Swartland Alluvium Fynbos (Mucina and

Rutherford 2004). The three sites have different management histories which relate to the presence of different- or single-aged old fields. Patterns of succession on to old fields from adjacent unploughed renosterveld stands were quantified, with cessation of ploughing incorporating three levels of grazing intensities as an interacting effect. Four levels, of three different-aged old fields and of unploughed renosterveld, were classed as seral stages. The different-aged old fields (seres) were used as surrogates, i.e. a chronosequence (see Foster and Tilman 2000), in lieu of temporal studies of permanent plots. Unploughed renosterveld (control) was used as the baseline reference from which to infer community compositional changes caused by previous ploughing disturbances (of set-aside fields) and grazing disturbances (following introduction of herbivores at two sites). In order to determine interacting effects I quantified three levels of grazing intensity (low, moderate and high) at the three different sites in conjunction with previous ploughing disturbances. A sequence of aerial photographs (1938, 1949, 1967, 1973, 1987 and 1997) was used to select suitable sites for relevés in vegetation of the four seral stages within the study area. The aerial photographs give an indication of the decline in extent of untransformed vegetation since 1934 to 1996, especially after the introduction of mechanized farming in the 1950's (M. Gregor, personal communication). A summary of factors contributing to the disturbance history of relevés is given in Appendix 2.

4.2.1. Vegetation Data

The different-aged old fields and renosterveld controls were assigned to a seral stage class: 5-year-old fields (Sere 1), 15-year-old fields (Sere 2), 30-year-old fields (Sere 3) and unploughed renosterveld (Sere 4), as a nominal scale. Initially it was intended that all four seral stages, of three replicates each, be sampled at all three sites totalling thirty-six relevés in a completely crossed design. Not all seral stages could be met at Voëlvlei or Krantzkop, as both these sites were last ploughed in the 1970's prior to the expropriation of agricultural land by: Cape Metropolitan Council (for a water treatment plant and storage dam) and CapeNature at Voëlvlei; and Armscor (for a munitions factory) at Krantzkop (last ploughed in 1975), respectively. Only unploughed renosterveld and 30-year-old field replicates existed at Voëlvlei and Krantzkop; an unbalanced design for the first two seres. Elandsberg has old fields of different set-aside ages last ploughed in the 1960's, 1987, and in 1997, respectively. The actual frequency of ploughing on a given field was not measured; rather the set-aside age was used as a surrogate measure of the succession trajectory.

The vegetation of old fields and unploughed renosterveld was sampled with forty-two 1000 m^2 relevés containing nested quadrats (see Figure 3.2). Relevés were placed at representative sites with similar habitat conditions, either unploughed renosterveld or different-aged old fields with a low (5- and 15-year-old fields) or high shrub cover (30-year-old fields) subjectively. All species present were recorded on field data sheets (Appendix 3.1) and assigned to a life-form group for use in life-form richness tests. A list of the forty-two relevés and corresponding environmental factors and respective levels used for life-form richness tests is given in Table 4.1.

Table 4.1: Details of ploughing and grazing disturbance factors for 42 relevés analyzed for differences in life-form richness amongst states. Relevés from sere 3 and sere 4 were analyzed for interaction effects of ploughing and grazing

Factor	State	Relevés	Voëlvlei	Elandsberg	Krantzkop
Grazing intensity			low: 1	moderate: 2	high: 3
Seral stage	sere 1: 5-year-old field	3	0	3	0
Seral stage	sere 2: 15-year-old field	6	0	6	0
Seral stage	sere 3: 30-year-old field	18	6	4	8
Seral stage	sere 4: unploughed renosterveld	15	6	6	3

Table 4.2: Details of ploughing and grazing disturbance factors for 36 relevés containing 72 quadrats (2 per relevé) analyzed for differences in life-form cover-abundance amongst states. Relevés from sere 3 and sere 4 were analyzed for interaction effects of ploughing and grazing

Factor	State	Relevés	Voëlvlei	Elandsberg	Krantzkop
Grazing intensity			low: 1	moderate: 2	high: 3
Seral stage	sere 1: 5-year-old field	3	0	3	0
Seral stage	sere 2: 15-year-old field	6	0	6	0
Seral stage	sere 3: 30-year-old field	17	5	4	8
Seral stage	sere 4: unploughed renosterveld	10	4	3	3

The 10 m^2 quadrats (72 in total) were used for analyses of life-form cover-abundance amongst seral stages (see Table 4.2) to determine patterns. All species encountered were recorded on field data sheets (Appendix 3.1) with their corresponding refined Braun-Blanquet cover-abundance code

(Barkman et al. 1964) estimated at the 10 m^2 quadrat scale. All species were assigned to a life-form group as above.

Species which are not native to the Cape flora are considered as "alien" here. Alien species richness is a subset of total species richness for relevés and they occur in more than one life-form, thus analyzing differences in cover-abundance amongst seres was incalculable. Typical of other mediterranean-type ecosystems is the abundance of annual grasses of Mediterranean origin, introduced during successive travels by early colonists transporting grains and food (Burchell 1967). Alien phanerophytes sporadically encountered were the invasive *Acacia mearnsii* and *A. saligna* travelling along watercourses and sandy areas respectively; or *Eucalyptus cladocalyx* radiating from woodlots (prominent after fire).

4.2.2. Environmental Data

Grazing intensity increased along a gradient at the three sites (see Chapter Two: Study area) and were assigned to three states of; low intensity (LI), moderate intensity (MI) and high intensity (HI), respectively, as a nominal scale. Voëlvlei (861.86 ha in extent) has a low grazing intensity, Elandsberg (3800 ha in extent) has a moderate grazing intensity and Krantzkop (total area of 2500 ha utilized by large herbivores) has a high grazing intensity. A total stocking density per site for large herbivores was calculated (Table 4.3). To obtain this figure the number of individuals per species was multiplied by their metabolic equivalent (a fraction of a standard Large Animal Unit (LAU) with a mass of 450 kg, Bothma 2002). Dividing the sum of the LAU's per site by the area in hectares (Σ (n *LAU)/ha) gives the value of 0.05 LAU/ha (or 19.81 ha/LAU) for Elandsberg and 0.11 LAU/ha (or 9.19 ha/LAU) for Krantzkop, respectively. Thus the stocking rate at Krantzkop is precisely 2.2 times that of Elandsberg. Calculation of a sustainable stocking rate was not attempted, only a direct measurement of existing stock. The grazing intensity gradient used here assumes that the levels are indeed low, moderate and high. However the high grazing intensity may in fact be more similar to the moderate level and may not have actually attained a high level of grazing intensity. Also the effect of grazing was passively (or indirectly) observed in that no measurements of herbage consumption were obtained. I use the term "grazing" to refer to both grazing and browsing by large herbivores, and have ignored the effects of browsing by small mammals, termites and tortoises.

Table 4.3: Large herbivore census (for 2003) at Elandsberg (3800 ha) and Krantzkop (2500 ha), with Large Animal Unit (LAU) fraction equivalents (sensu Bothma 2002). n = number of individuals

Species	Elandsberg 2003	Krantzkop 2003	LAU equivalent	Elandsberg (n*LAU)	Krantzkop (n*LAU)
Black Wildebeest	40	22	0.46	18.40	10.12
Blue Wildebeest	0	28	0.50	0	14.00
Bontebok	100	47	0.22	22.00	10.34
Eland	90	87	1.02	91.80	88.74
Gemsbok	11	67	0.56	6.16	37.52
Hartebeest	12	50	0.37	4.44	18.50
Kudu	0	5	0.42	0	2.10
Mountain Zebra	0	20	0.62	0	12.40
Ostrich	45	0	0.25	11.25	0
Plains Zebra	30	5	0.66	19.80	3.30
Springbok	120	480	0.15	18.00	72.00
Grey Rhebok	0	30	0.10	0	3.00
Total n	448	841			
Total LAU’s				191.85	272.02
LAU/ha				0.05	0.11
ha/LAU				19.81	9.19

4.2.3. Life-form Classification

The life-form classification of Raunkiaer (1934) grouped plants by regenerative capacity according to meristem position, based on over-wintering adaptations of plants (Clements 1928). This approach was the most rapid here as life-histories of many species were not adequately understood or referenced, nor were specific traits in relation to grazing (palatability or toxicity) and ploughing (regeneration capacity) identified from the onset of this study. There are numerous systems of life-forms with varying levels of detail that were not used here (see Barkman 1988). Species were categorized by their observable life-form features and assigned to a life-form group regardless of their phylogeny and life-history, on the basis of their growth habit and meristem position, following Raunkiaer and Mueller-Dombois and Ellenberg (1974). This definition implies form is an expression of adaptations. Raunkiaer’s classes are not entirely transposable for use in Southern African sclerophyllous vegetation thus some modifications were deemed necessary. The grouping of species across phylogenetic relationships allowed for comparisons of renosterveld and old field community structure on the basis of life-form group richness and their cover-abundance.

Eight life-form classes (or groups) were allocated: therophytes, cryptophytes, hemicryptophytes, nano-chamaephytes, chamaephytes, phanerophytes, lianellas and parasites. Characteristics used in allocating each species to a class are given below, with differences between my working definitions and that of Raunkiaer's explained.

Therophytes (annuals) are "plants whose shoot and root system dies after seed production and which complete their life cycle within one year". Ephemerals, annuals and biennials were included as therophytes, as were alien taxa usually classed as forbs (i.e. *Trifolium repens*).

"Perennial (including biennial) herbaceous plants experiencing periodic shoot reduction" are divided into two categories namely: hemicryptophytes and cryptophytes. Hemicryptophytes have "periodic shoot reduction to a remnant shoot system that lies relatively close to the ground surface". Hemicryptophytes here are all graminoids and include rosette-like asteroids (for example *Berkheya armata*). Cryptophytes have a "periodic reduction of the complete shoot system to storage organs embedded in the soil" during unfavourable growth conditions. Cryptophytes included all types of geophytes with below ground storage organs. The genera *Drosera* and *Triglochin* were excluded from this class as marginal in a synopsis of geophytes of the Capensis region by Procheş and Cowling (2004), but included here. Geophytic grasses were assigned as hemicryptophytes.

Chamaephytes as defined by Raunkiaer, are "plants whose mature branch or shoot system remains perennially within 50 cm above ground surface, or plants that grow taller than 50 cm, but whose shoots die back periodically to that height limit". The size class structure of Raunkiaer's chamaephyte was modified to reflect size classes of renosterveld shrubs. Chamaephytes were defined as growing upward from 35 cm to 2.5 metres, and include woody dwarf shrubs and shrubs, for example *Asparagus capensis*, *Athanasia trifurcata* and *Elytropappus rhinocerotis*. Chamaephyte juveniles were assigned to the same category. The nano-chamaephyte class included dwarf shrubs which were woody and consistently small, i.e. below 35 cm like *Helichrysum asperum* and succulents like *Lampranthus aduncus* and *L. leptaleon*.

Phanerophytes or trees, include orthophyllous species that are largely clumps of tall woody plants confined to termitaria (heuweltjies) and natural drainage lines in renosterveld. These include *Olea europaea* subsp. *africana* and other bird-dispersed fleshy fruited species (for example *Maytenus oleoides*, *Rhus lucida*) that favour friable soils. Alien phanerophytes are predominant in some areas as strays from woodlots or riparian invasions: typically *Acacia mearnsii*, *A. cyclops*, *A. saligna* and *Eucalyptus cladocalyx*.

Lianellas encountered which were geophytic (*Cyphia volubilis*) were classed according to growth form, i.e. as lianella.

Parasites contained few species, with hemi-parasites like *Thesium funale*.

4.2.4. Statistical Analyses of Life-forms

Life-form Richness at the 1000 m^2 Scale

Life-form richness of forty-two relevés at the 1000 m^2 scale, in both unploughed renosterveld vegetation and different-aged old fields was compared, using univariate statistical tests of significance (StatSoft 2004) when statistical assumptions were not violated (Gotelli and Ellison 2004). These forty-two relevés contained no less than 411 species. The data were tested for normality using Lilliefors test and systematically checked for homogeneity of variance within groups using Levene's test and the Cochran-Bartlett test. Non-normal distributions were due to: low or uneven occurrences in the group (hemicryptophytes), low species numbers (lianella, phanerophyte and parasite groups) or absence across factor levels. Phanerophyte and lianella life-forms did not occur at the first two seres whilst the parasite life-form was absent at the first sere. Life-form groups non-normally distributed or heteroschedastic were analyzed using non-parametric statistical tests; either Kruskal-Wallis ANOVA by ranks or a Mann-Whitney U test, for multiple or two independent group comparisons, respectively. Most of the heterogeneity of variance within groups was due to an unequal replication of samples amongst levels, and in some cases low variable counts, possibly inflating or deflating some results.

The interactions between ploughing and grazing were analysed using multivariate statistical tests of significance (ANOVA) for relevés with comparable seral stages, namely 30-year-old fields and unploughed renosterveld, (n = 33). All three sites were analyzed using the grazing intensity factor but not all seral stages were available, as Elandsberg is the only site with all four seral stages. Where the data were non-normally distributed (Lilliefors test) or heteroschedasticity of the samples occurred (Levene's test, Cochran-Bartlett test), a bootstrapping (resampling, Simon and Bruce 1991, Nel and Kidd StatSoft 2004 macro) test was performed to reveal the true variance between treatments. The bootstrap test relies on sample variations within levels and shows whether the confidence intervals found in the Bonferroni test (least square means) are actually alike or not.

Life-form Cover-abundance at the 10 m^2 Scale

The quadrats at the 10 m^2 scale (n = 72) were used in analyses for quantifying differences in cover-abundance within life-form groups amongst seral stages. The interactions between grazing and ploughing were analysed using multivariate statistical tests of significance (ANOVA) only for those relevés (n = 33) with comparable seral stages as explained for the richness tests above. The refined Braun-Blanquet (Barkman et al. 1964) cover-abundance data were transformed to an ordinal scale (van der Maarel 1979) prior to export from TURBOVEG (Hennekens and Schaminée 2001). Cover-abundance values of each species in life-form groups was summed per quadrat, and used in statistical analyses in StatSoft (2004). The data were tested for distributions of normality using Lilliefors test, and heteroschedasticity (the uneven distribution of data) in relevés was measured with Levene's test and the Cochran-Bartlett test.

Where the data were non-normally distributed (Lilliefors test) or heteroschedasticity of the samples occurred (Levene's test, Cochran-Bartlett test), a bootstrapping test was performed (to compensate for non-normal distributions or heteroschedasticity) to reveal the true variance between treatments. Non-parametric statistics were employed for the main effects when no significant interacting effects occurred; either Kruskal-Wallis ANOVA by ranks (for multiple independent groups) or a Mann-Whitney U test (for two groups). Again most of the heterogeneity of variance was due to an unequal amount of samples amongst treatments, and in some cases low counts per variable.

4.2.5. Ordination at the 10 m^2 Scale

The 72 quadrats at the 10 m^2 scale which were used for quantifying differences in cover-abundance were also used to perform ordination analyses. The aim here was to investigate response curves of selected species in seral development. The species cover-abundance values were transformed from the refined Braun-Blanquet scale (Barkman et al. 1964) into an ordinal scale (van der Maarel 1979) prior to export from TURBOVEG (Hennekens and Schaminée 2001). No further data transformation was done in CANOCO prior to ordination. The vegetation samples were analyzed using Detrended Correspondence Analysis (DCA). The program package CANOCO (ter Braak and Šmilauer 2002, Lepš and Šmilauer 2003) was used to perform the DCA. In CanoDraw the DCA axis 1 was used to plot a select group of species in a Generalized Additive Model (GAM) to show their response along the compositional gradient of secondary succession.

4.3. Results

I found that ploughing generally had a negative effect on life-form richness and life-form cover-abundance. When considering the combined effects of ploughing and grazing, I found that only hemicryptophyte life-form richness showed a positive interaction in relation to the presence of grazing. Similarly, combining the effects of ploughing and grazing for life-form cover-abundance, a positive interaction with grazing for total cover-abundance occurred. Therophyte and cryptophyte cover-abundance also showed an interaction effect (in opposing directions).

4.3.1. Life-form Richness at the 1000 m^2 Scale

An overview of the life-form spectral composition is given here. The total species richness of 42 relevés (1000 m^2 scale) is 411 taxa. The cryptophyte life-form contributes 34% of the total species count (Figure 4.2) and is not surprising given that renosterveld is characterized by a large geophytic component.

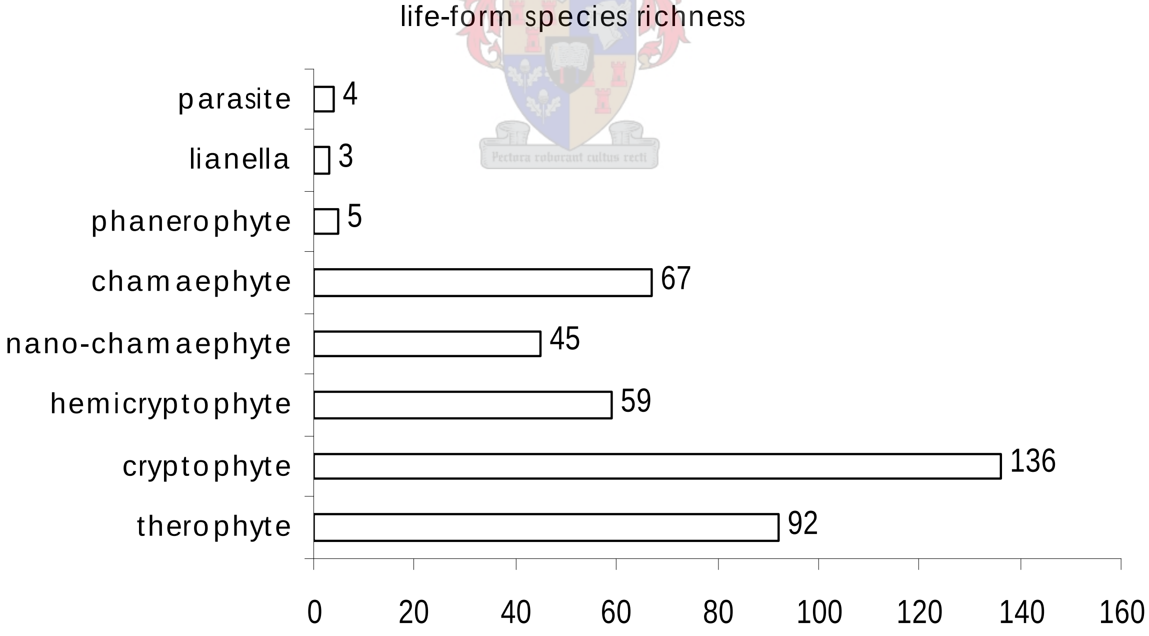

Figure 4.2: Life-form species richness of 42 relevés (1000 m^2) used in statistical analyses

A list of the average total species and average life-form group richness per sere is shown in Table 4.4. A common trend was revealed: total species richness, cryptophyte, hemicryptophyte, nano-chamaephyte and chamaephyte life-form richness was highest in unploughed renosterveld vegetation (sere 4), and life-form richness increased with secondary succession. Conversely therophyte life-form richness was highest on sere 1 (5-year-old fields), the most recently disturbed site. However a detailed investigation of the life-form data was required to corroborate this potential recovery of vegetation following the cessation of ploughing.

Table 4.4: Summary of average life-form and total species richness of 1000 m^2 relevés per sere, with standard deviation (s.d.). For this chronosequence: sere 1 = 5-year-old fields, sere 2 = 15-year-old fields, sere 3 = 30-year-old fields and sere 4 = unploughed renosterveld

Life-forms	Sere 1 (n = 3)		Sere 2 (n = 6)		Sere 3 (n = 18)		Sere 4 (n = 15)	
	average	s.d.	average	s.d.	average	s.d.	average	s.d.
therophyte	19	2.89	14	5.01	15	5.55	17	7.90
cryptophyte	10	7.55	19	6.57	15	7.69	24	10.99
hemicryptophyte	5	0.58	9	2.42	10	3.01	12	6.64
nano-chamaephyte	1	0.58	2	1.33	6	3.57	7	3.71
chamaephyte	0	0.58	4	2.66	10	4.55	13	5.27
phanerophyte	0	0.00	0	0.00	0	0.57	0	0.80
lianella	0	0.00	0	0.00	0	0.50	1	0.65
parasite	0	0.00	0	0.52	1	0.55	1	0.92
richness	36	9.61	49	7.25	56	14.43	76	25.65

Life-form Richness with Ploughing

Life-form species richness (Table 4.4) was different amongst seres, and total species richness differed significantly amongst seres. The life-form data were not all evenly distributed in terms of basic tests of normality (both Kolmogorov-Smirnoff and Lilliefors tests for normality). Also factor levels for some life-form groups were heteroschedastic (both Levene’s test and Cochran-Bartlett test), therefore warranting the use of non-parametric statistical tests since violating assumptions of ANOVA (Gotelli and Ellison 2004).

Heteroschedasticity was depicted on graphs as wide confidence intervals, possibly not revealing accurate seral stage differences in some cases (probably the cryptophytes), due to unequal replication of all seres. Significance values obtained from non-parametric tests were usually less than those obtained from ANOVA. Total species richness and hemicryptophyte, nano-chamaephyte, chamaephyte and lianella life-forms were tested non-parametrically with a Kruskal-Wallis test.

Total species richness was significantly different amongst seres (Figure 4.3; Kruskal-Wallis H $_{(3,\ 42)}$ = 14.847, $p < 0.01$) with sere 4 (unploughed renosterveld) having the greatest species richness. Unploughed renosterveld and 30-year-old fields were similar to each other, but different from 5- and 15-year-old fields.

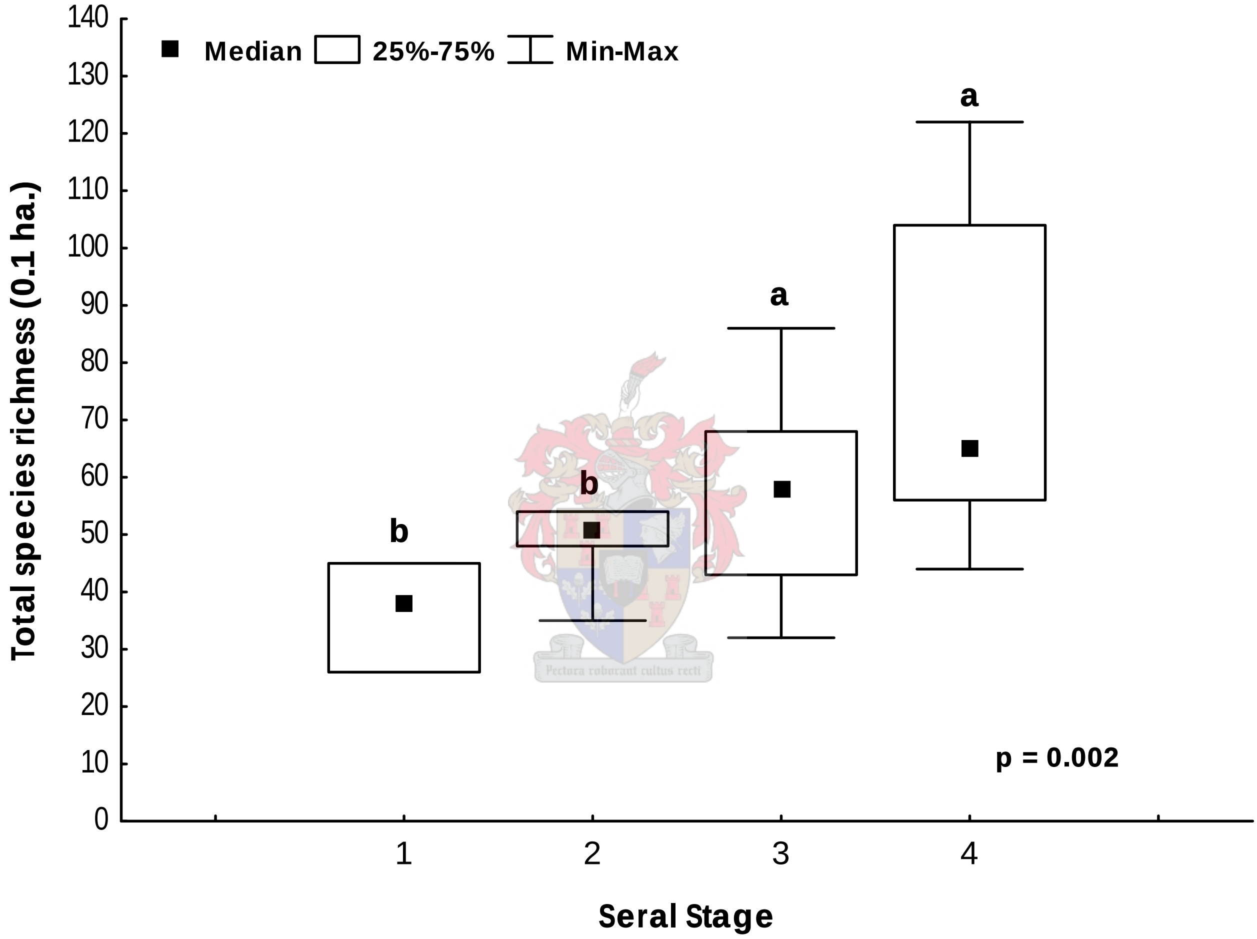

Figure 4.3: Total species richness of 1000 m^2 relevés (n = 42) for different seres; 1 = 5-, 2 = 15-, 3 = 30-year-old fields and 4 = unploughed renosterveld

Parasite (Figure 4.4, absent at sere 1), phanerophyte (Figure 4.4, absent at the first two seres), therophyte (Figure 4.4) and hemicryptophyte (Figure 4.5) life-forms did not differ significantly in species richness amongst seres. Cryptophytes had the highest species richness in unploughed renosterveld (Figure 4.4; ANOVA, F $_{(3,\ 38)}$ = 4.2346, $p < 0.05$), in light of the fact that many of these species have short dispersal trajectories. The 30-year-old fields were significantly different from unploughed renosterveld, but were similar to the 5- and 15-year-old fields. Unexpectedly the 5- and

15-year-old fields were also similar to unploughed renosterveld as the pattern of cryptophyte richness increased during the first two seres and then declined at sere 3 (Figure 4.4) suggesting a higher richness at sere 2 (which is unlikely, personal observation). This could be an artefact of unequal sample replication of younger fields (seres 1 and 2) relative to 30-year-old fields and unploughed renosterveld, where wide confidence intervals overlapped with the levels of older seres and may not reflect the true chronosequence. Similar studies are required to verify the pattern.

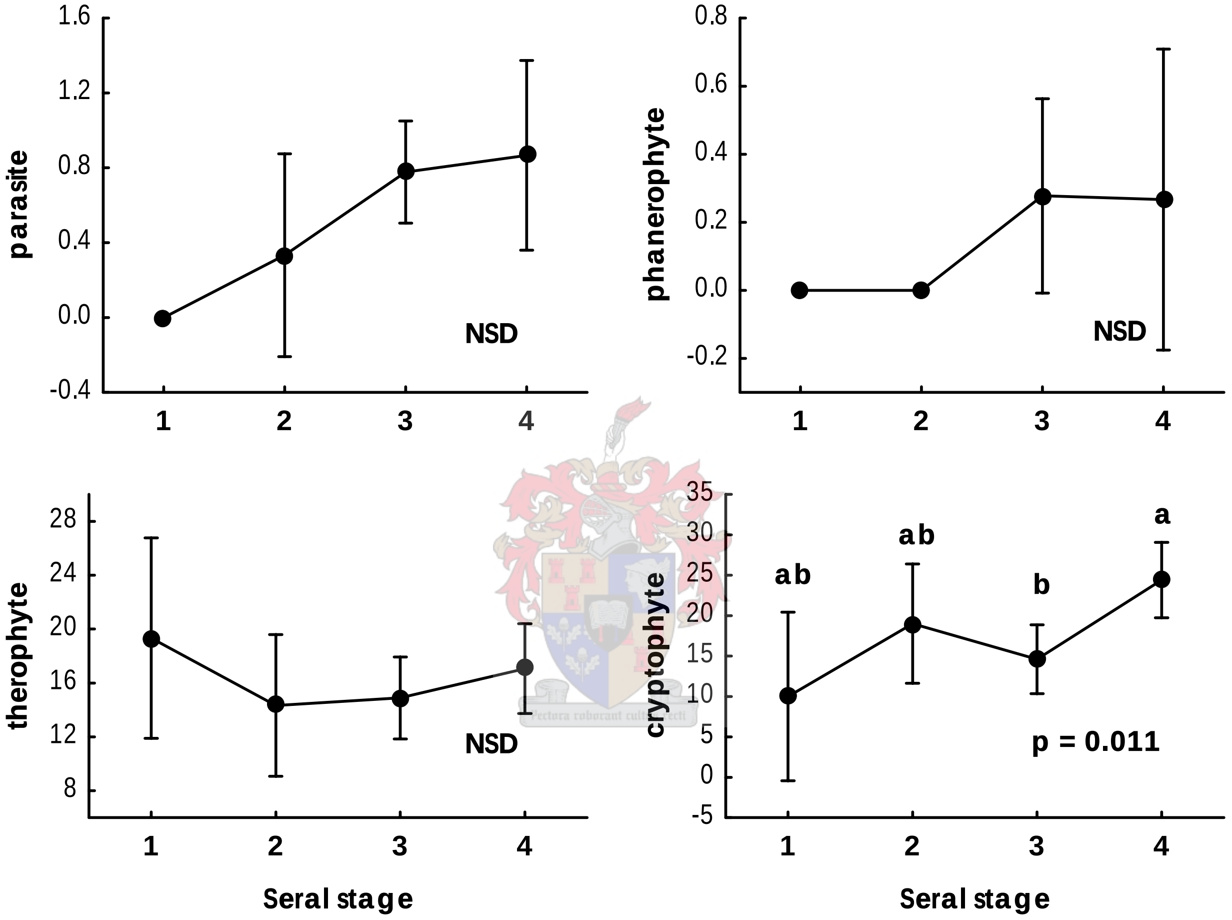

Figure 4.4: A one-way ANOVA test of parasite (weighted means), phanerophyte (weighted means), therophyte, and cryptophyte average species richness per sere (y-axes). 1 = 5-, 2 = 15-, 3 = 30-year-old fields and 4 = unploughed renosterveld. Vertical bars denote 0.95 confidence intervals; characters depict Bonferroni degree of similarity. NSD = no significant differences

Lianellas differed in species richness between the two seres in which it occurred (absent at the first two seres), (Figure 4.5; Kruskal-Wallis $H_{(3, 42)} = 15.649$, $p < 0.01$; also Mann-Whitney U test $p = 0.016$). For nano-chamaephytes a significant difference in species richness occurred amongst seres (Figure 4.5; Kruskal-Wallis $H_{(3, 42)} = 14.348$, $p < 0.01$), specifically unploughed renosterveld was different from the 5- and 15-year-old fields.

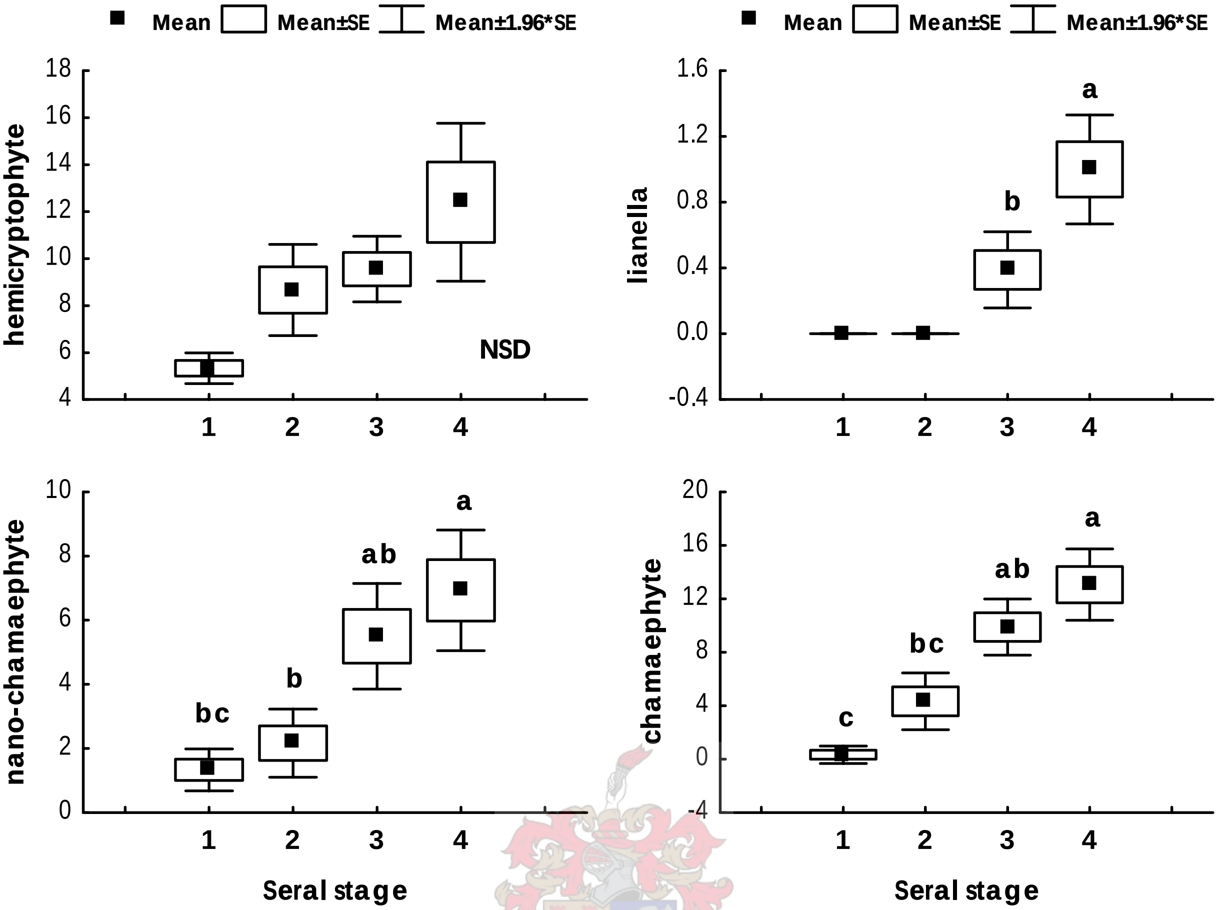

Figure 4.5: Hemicryptophyte, lianella, nano-chamaephyte and chamaephyte species richness per sere (y-axes). 1 = 5-, 2 = 15-, 3 = 30-year-old fields and 4 = unploughed renosterveld. Vertical bars denote means and standard errors; characters depict multiple comparisons p-values degree of similarity. NSD = no significant differences

Chamaephyte species richness had a similar pattern to that of nano-chamaephytes (Figure 4.5; Kruskal-Wallis H $_{(3,\ 42)}$ =18.584, $p < 0.001$), where 30-year-old fields and unploughed renosterveld were similar to each other and different from 5-year-old fields. The 30-year-old fields were also similar to 15-year-old fields, whereas 15-year-old fields were similar to 5-year-old fields.

Life-form Richness with Ploughing and Grazing

Since different-aged old fields were not replicated at all sites, use in multivariate analyses with both ploughing and grazing factors was possible only for sere 3 (30-year-old fields) and sere 4 (unploughed renosterveld), (n = 33). Vegetation samples were replicated amongst three grazing intensities: low, moderate and high. The data were tested for normality (Kolmogorov-Smirnoff and

Lilliefors test for normality) and homogeneity of variances within groups (Levene's and Cochran-Bartlett tests), and found to be non-normally distributed and heteroschedastic for most life-forms, respectively. In other words the result from a two-way ANOVA test was not always reliable, as assumptions were violated (on account of the residuals being non-normally distributed). Some main effects tests were presented here when interacting effects were not significant, and where normally distributed the use of ANOVA was warranted otherwise they were tested non-parametrically. No interaction between ploughing and grazing occurred for: total species richness; therophyte, cryptophyte, nano-chamaephyte, chamaephyte, phanerophyte, lianella and parasite life-forms. A significant interaction occurred between ploughing and grazing for hemicryptophytes only.

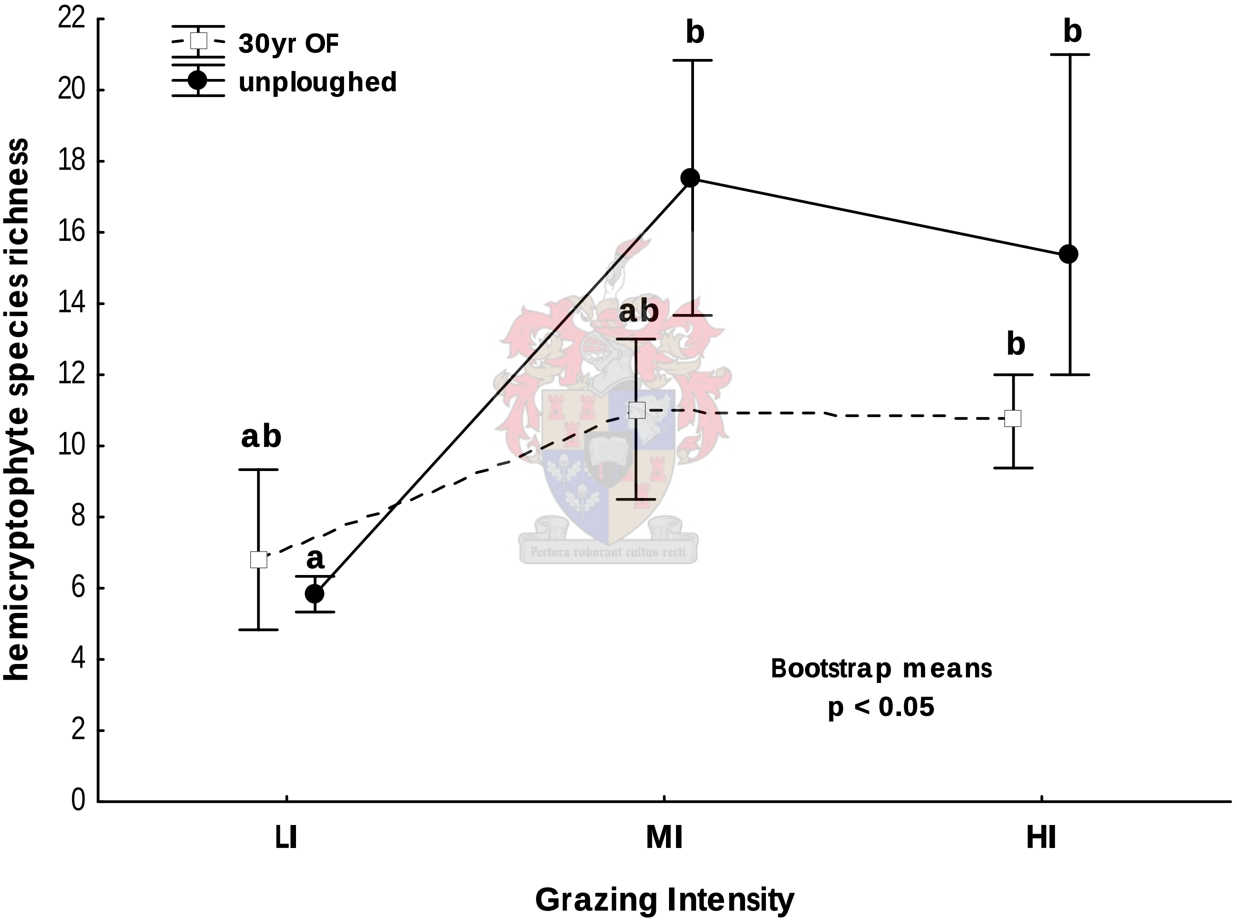

Figure 4.6: The interaction of seral stage and grazing intensity on hemicryptophyte species richness. Vertical bars denote 0.95 bootstrap confidence intervals. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing

For hemicryptophytes a significant interaction effect between ploughing and grazing occurred. As the data were non-normally distributed a bootstrapping technique was employed (Figure 4.6, bootstrap means, $p < 0.05$). There was a significant difference in species richness without ploughing between sites with grazers (regardless of intensity) and sites without (lower average hemicryptophyte species richness). After ploughing (30-year-old fields) hemicryptophyte species richness was similar at all sites (no significant difference, bootstrapped Bonferroni post-hoc test).

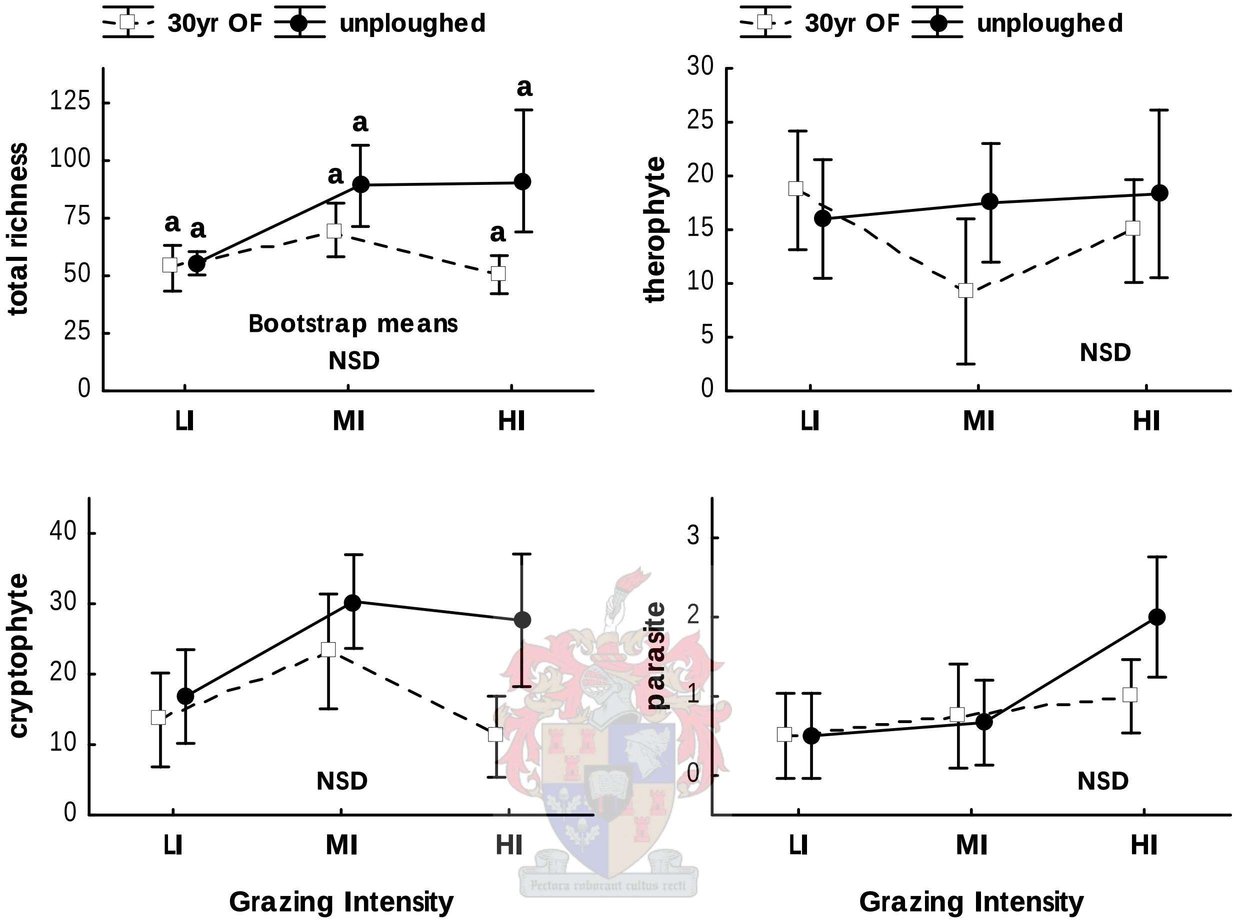

Figure 4.7: The interaction of seral stage and grazing intensity on total, therophyte, cryptophyte and parasite species richness (y-axes). LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. Vertical bars denote 0.95 confidence intervals for life-forms and bootstrap confidence intervals for total richness. NSD = no significant differences

For average total species richness no interaction between ploughing and grazing occurred (Figure 4.7). The data were normally distributed but heteroschedastic, therefore bootstrapped. It appears as if there is a significant difference in total species richness between seres, however the presence of grazers did not positively influence total species richness significantly. For the main effects the data were heteroschedastic requiring the use of non-parametric statistical tests. Total species richness differed significantly for both ploughing and grazing factors independently. Thus ploughing reduced total species richness, (Figure 4.8, Mann-Whitney U test, $p < 0.05$). Species richness was significantly less with a low grazing intensity compared with moderate and high grazing intensities (which were similar), (Figure 4.8, Kruskal-Wallis test H $_{(2, 33)}$ = 8.411598, $p < 0.05$).

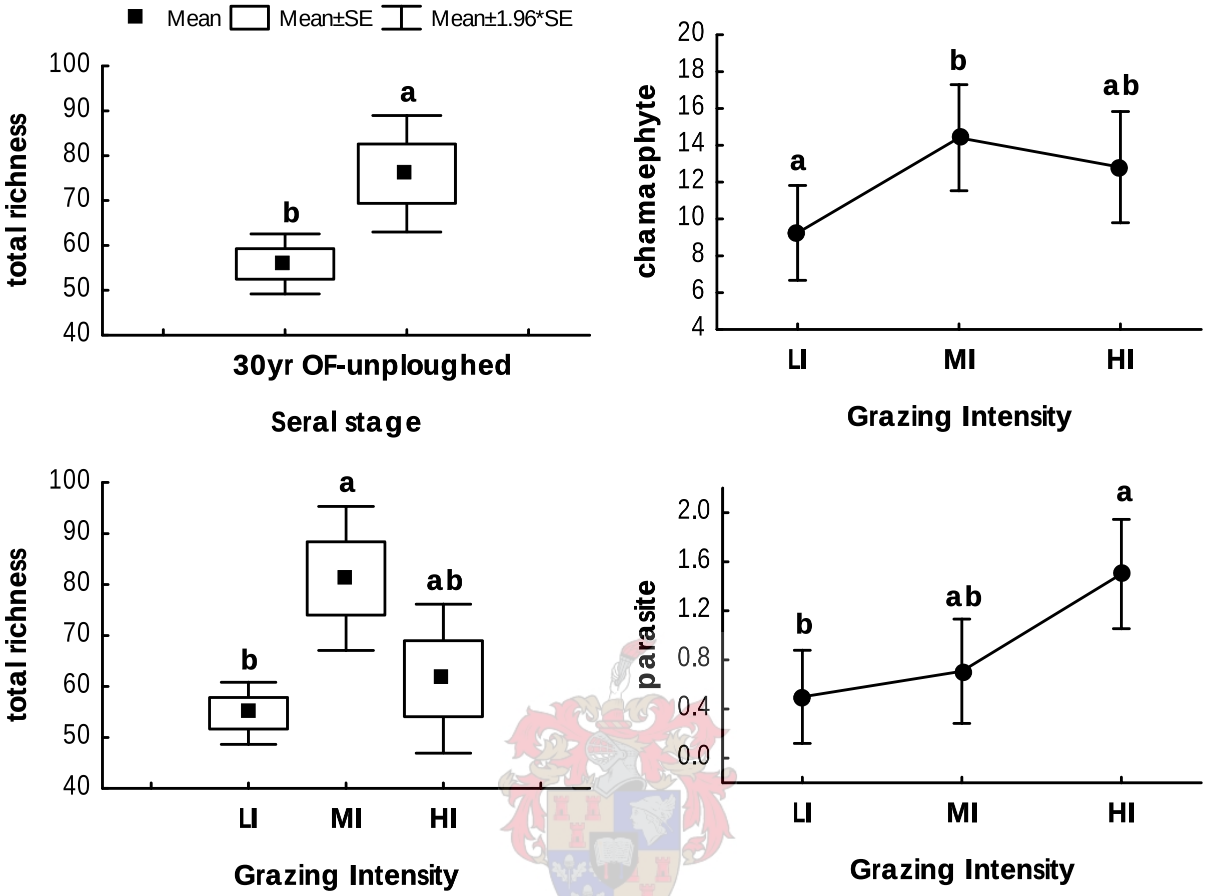

Figure 4.8: Main effects of seral stage differences (Mann-Whitney test) and grazing intensity (Kruskal-Wallis test) on total species richness (y-axes) at left; and single ANOVA main effects of grazing intensity on chamaephyte and parasite life-form species richness (y-axes) at right. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing

No interaction between ploughing and grazing occurred for: therophytes, cryptophytes or parasites (Figure 4.7). No significant main effects were found for therophytes either. For cryptophytes a non-parametric test was used for both main effects due to non-normality. There was a significant difference in species richness between 30-year-old fields and unploughed renosterveld (Figure 4.9; Mann-Whitney U test, $p < 0.001$), showing that ploughing had a negative effect on cryptophyte species richness. There was also a significant difference in species richness amongst different levels of grazing intensity (Figure 4.9; Kruskal-Wallis H $_{(2, 33)}$ = 10.56838, $p < 0.01$). For parasites a significant main effect occurred with different grazing intensities (Figure 4.8; ANOVA, F $_{(2, 27)}$ =

6.51596, $p < 0.005$). Most parasite species occurred with a high grazing intensity, least with a low grazing intensity, and both similar to sites with a moderate grazing intensity.

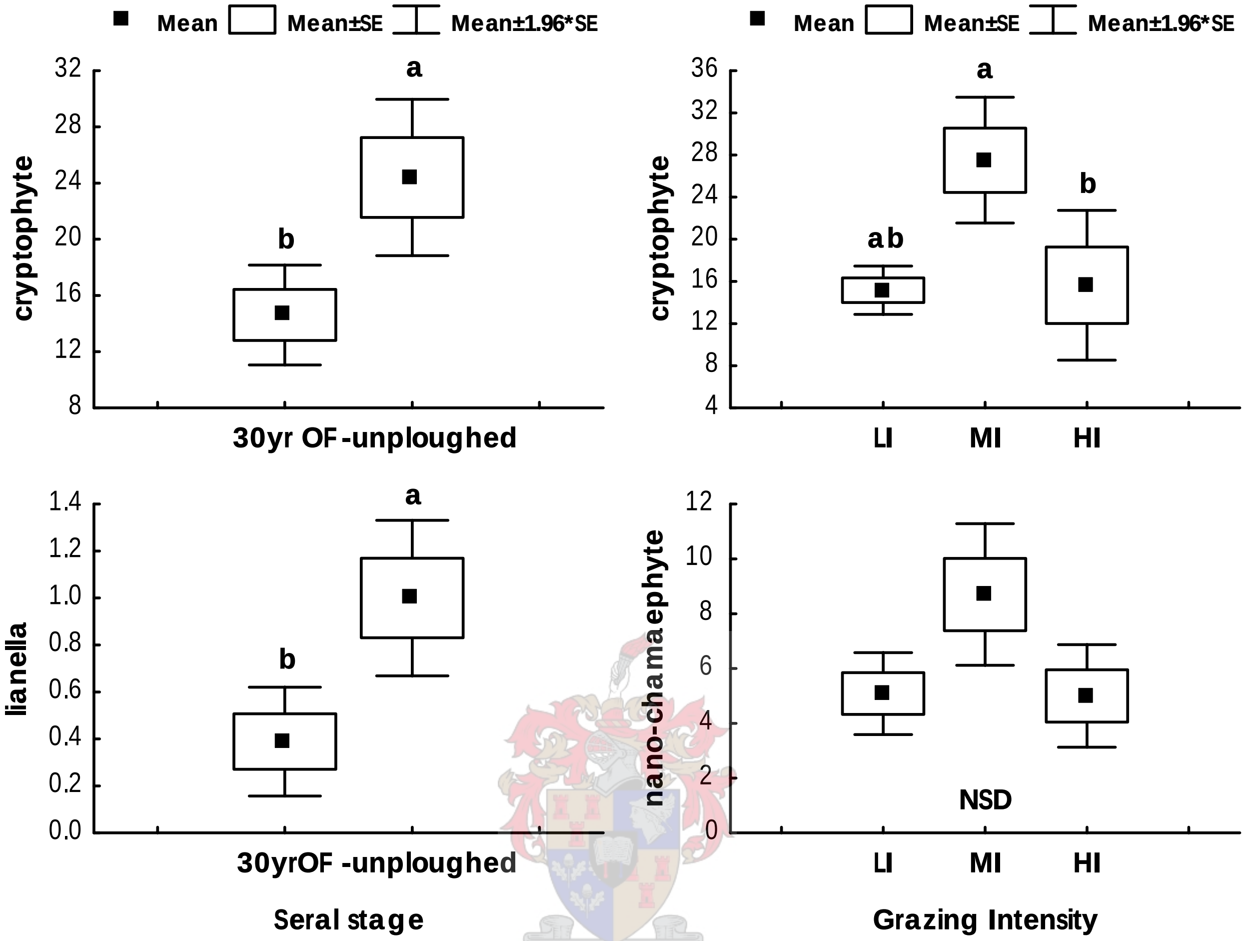

Figure 4.9: Main effects (Mann-Whitney) of seral stage differences for cryptophyte and lianella life-form species richness (y-axes) at left; and main effects (Kruskal-Wallis) of grazing intensity on cryptophyte and nano-chamaephyte life-form richness (y-axes) at right. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. NSD = no significant differences

No interaction between ploughing and grazing occurred for: nano-chamaephytes, chamaephytes, lianellas and phanerophytes (Figure 4.10). For nano-chamaephytes the data were non-normally distributed and a non-parametric test showed that the main effect of grazing intensity was not significant (Figure 4.9, Kruskal-Wallis $H_{(2, 33)} = 5.347416$, $p = 0.069$), perhaps due to a low overall species count. For chamaephytes the data were normally distributed and homoschedastic, where the only significant main effect was with grazing intensity (Figure 4.8; ANOVA, $F_{(2, 27)} = 4.0255$, $p < 0.05$). Chamaephyte species richness was highest with a moderate grazing intensity and significantly different from sites with a low grazing intensity. However sites with a high grazing intensity were not significantly different from sites with a low- or moderate grazing intensity. For lianellas no interacting effect was found to occur probably due to the occasional occurrence and sample size of species. A significant main effect of ploughing occurred for lianellas between seres (Figure 4.9; Mann-Whitney U test, p = 0.016). Logically, this suggests that ploughing alters vegetation structure and reduces lianella life-form richness.

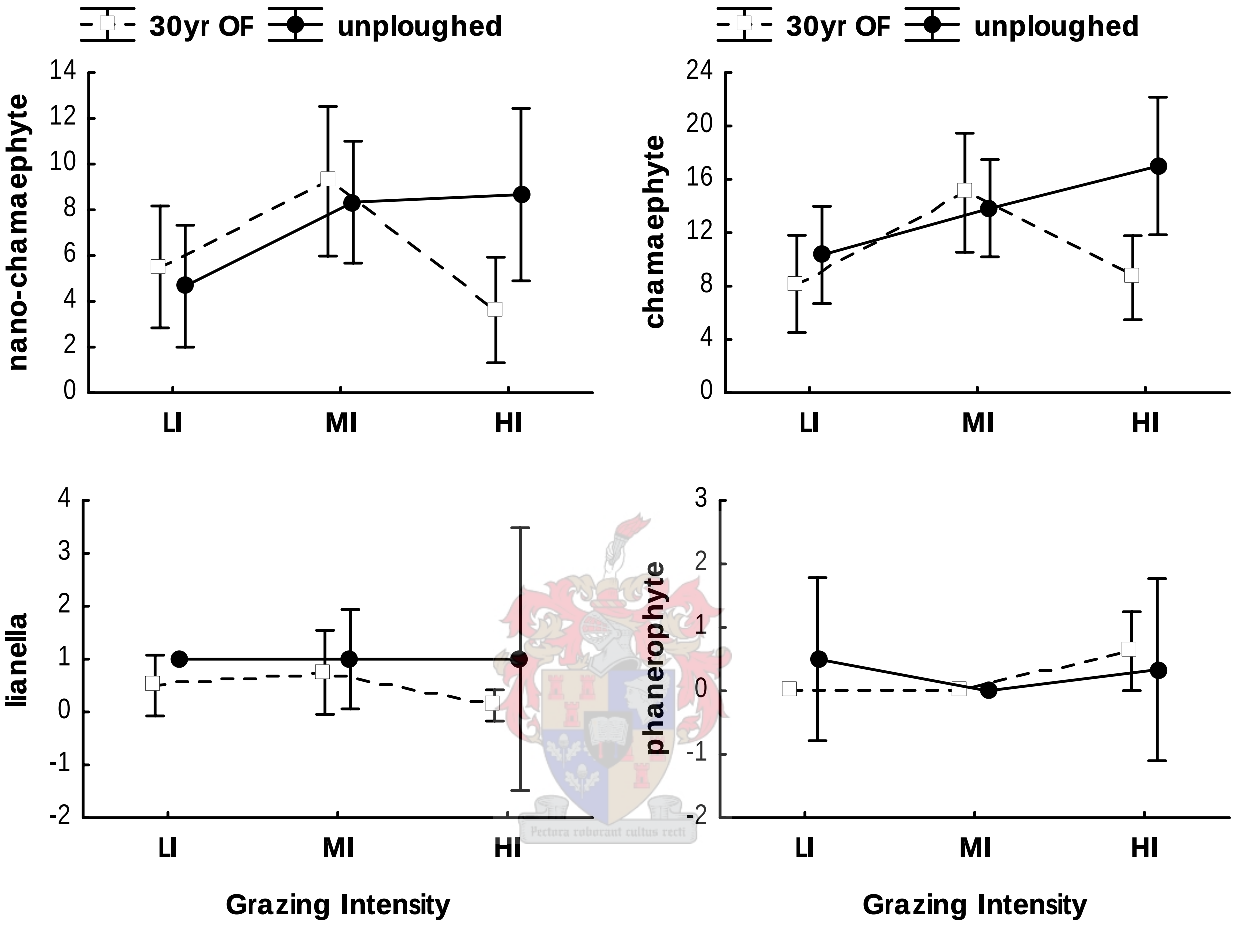

Figure 4.10: The interaction of seral stage and grazing intensity on nano-chamaephyte, chamaephyte, lianella (weighted means) and phanerophyte (weighted means) species richness (y-axes). LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. Vertical bars denote 0.95 confidence intervals

4.3.2. Life-form Cover-abundance at the 10 m^2 Scale

The Influence of Ploughing on Life-form Cover-abundance

Cover-abundance data from the 10 m^2 quadrats (n = 72) were used in these analyses. Phanerophytes did not occur in the 10 m^2 quadrats analyzed here. As the data were non-normally distributed a bootstrap randomization test was used. The life-form groups responded to ploughing differently in terms of their cover-abundance (Table 4.5). In unploughed renosterveld (sere 4) all life-forms were present and showed an even distribution. These quadrats were dominated evenly by: a low stratum of therophyte, cryptophyte and hemicryptophyte life-forms and a high stratum of chamaephytes. A middle stratum of nano-chamaephytes, parasites and occasionally lianellas were also present. The 30-year-old fields (sere 3) had a lower cover-abundance of: nano-chamaephytes, chamaephytes, lianellas and parasites. The 15-year-old fields (sere 2) had the highest cover-abundance of the hemicryptophyte life-form of all seres (dominated by the stoloniferous lawn grass *Cynodon dactylon*), with less chamaephyte cover-abundance than 30-year-old fields. Finally 5-year-old fields (sere 1) lacked many life-forms (and structural elements), mostly dominated by therophytes.

Table 4.5: Summary of average life-form and total cover-abundance of 10 m^2 quadrats per sere, with standard deviation (s.d.)

life-form	5yr OF (n = 6)		15yr OF (n = 12)		30yr OF (n = 34)		unploughed (n = 20)	
	average	s.d.	average	s.d.	average	s.d.	average	s.d.
therophyte	34.67	3.44	31.58	12.98	21.03	12.00	17.30	10.90
cryptophyte	7.83	8.01	18.25	10.15	16.91	9.32	20.00	8.53
hemicryptophyte	13.67	5.99	13.33	2.67	12.97	5.44	16.75	11.19
nano-chamaephyte	0.00	0.00	2.33	2.67	3.24	3.04	5.45	3.39
chamaephyte	0.00	0.00	2.42	3.12	10.38	7.65	19.10	6.59
lianella	0.00	0.00	0.00	0.00	0.12	0.48	0.90	1.37
parasite	0.00	0.00	0.17	0.58	0.32	0.81	1.10	2.13
total cover-abundance	56.17	9.81	68.08	18.87	64.97	15.76	80.60	22.83
richness	14	4.92	20	5.83	20	6.23	26	9.93

Firstly the data from 72 quadrats were analyzed using univariate tests of significance (ANOVA) to quantify whether life-form cover-abundance in relation to ploughing was significantly different amongst seres. The data were non-normally distributed (average total cover-abundance) and heteroschedastic for most life-forms. Thus a non-parametric test (Kruskal-Wallis) was employed where necessary. Total average summed cover-abundance was significantly different amongst seres (Figure 4.11; Kruskal-Wallis $H_{(3,\ 72)} = 11.57146$, $p < 0.01$). Unploughed renosterveld was similar to 15-year-old fields for total average cover-abundance and significantly different from the other seres. Average total cover-abundance of 15-year-old fields was similar to 30- and 5-year-old fields.

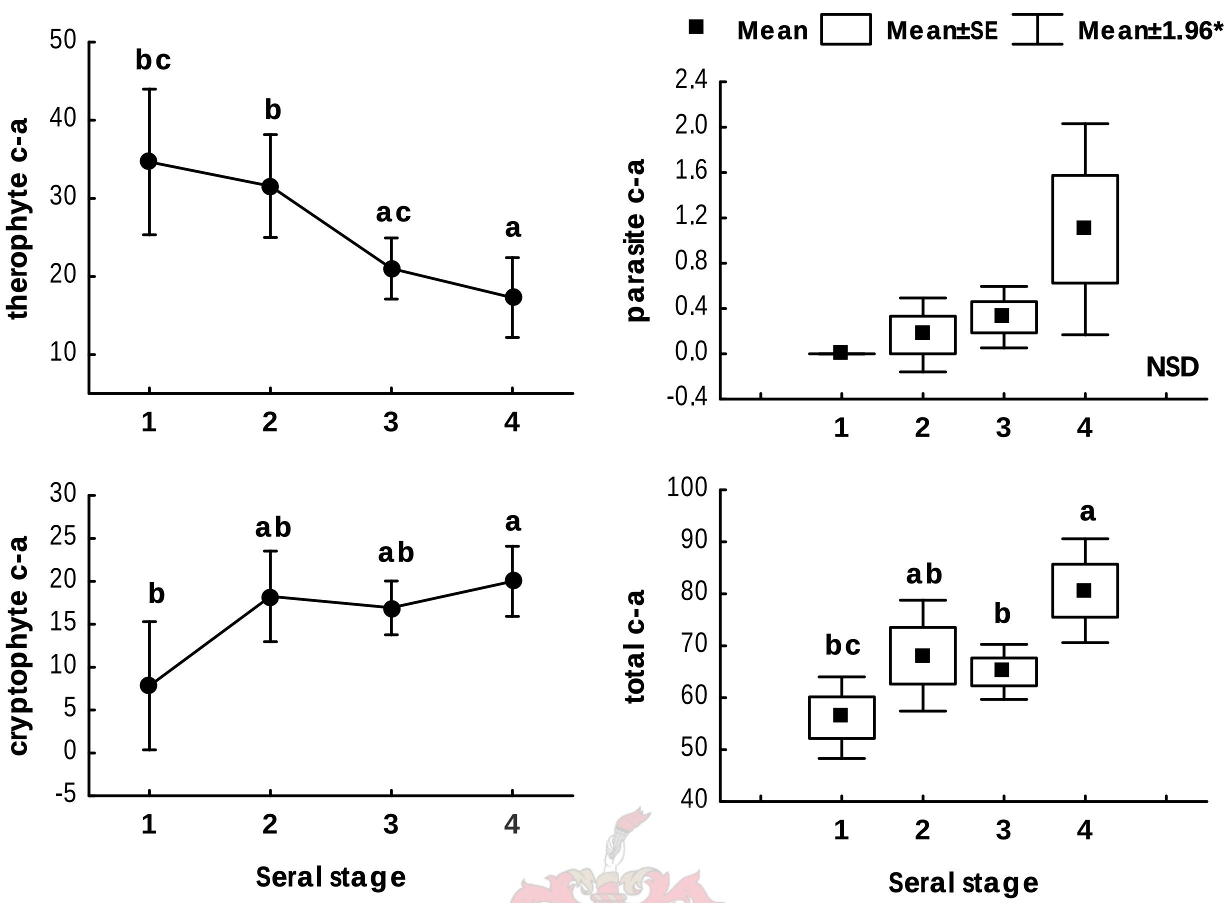

Figure 4.11: Average summed cover-abundance (y-axes) of therophyte, cryptophyte, parasite and total life-forms at the $10\ m^2$ quadrat scale (n = 72) for different seres. Vertical bars denote confidence limits for graphs at left with corresponding characters depicting Bonferroni degree of similarity within life-form groups, whilst boxplots at right denote confidence intervals with multiple comparisons p-values. c-a = cover-abundance, NSD = no significant differences

No significant difference in cover-abundance amongst seres occurred, where present, for: parasites (Figure 4.11, absent from sere 1), hemicryptophytes (Figure 4.12) and lianellas (Figure 4.12, absent at the first two seres). Therophytes were significantly different in cover-abundance amongst seres (Figure 4.11; ANOVA, $F_{(3,\ 68)} = 6.3081$, $p < 0.001$), specifically between 15-year-old fields and unploughed renosterveld. Highest therophyte cover-abundance occurred on 5-year-old fields declining with an advance in secondary succession, with least in unploughed renosterveld. Therophyte cover-abundance on 5- and 15-year-old fields were similar, as were 5- and 30-year-old fields, whilst 30-year-old fields were similar to unploughed renosterveld. For cryptophytes a significant difference in cover-abundance occurred amongst seres (Figure 4.11; ANOVA, $F_{(3,\ 68)} = 2.7775$ $p < 0.05$). Highest cryptophyte cover-abundance occurred in unploughed renosterveld; whilst similar to 30- and 15-year-old fields it was significantly different from 5-year-old fields (with lowest cryptophyte cover-abundance). The average cover-abundance of nano-chamaephytes was significantly different amongst seres (Figure 4.12; Kruskal-Wallis H $_{(3,\ N = 72)}$ =18.79332, $p < 0.001$; absent from sere 1). Average cover-abundance of chamaephytes was significantly different amongst seres, with an increase in cover-abundance with an advance in secondary succession (Figure 4.12; Kruskal-Wallis H $_{(3,\ N = 72)}$ =34.93441, $p = 0.0$; absent at sere 1). Chamaephyte cover-abundance was significantly different between unploughed renosterveld and 30-year-old fields, whilst 30- and 15-year-old fields were similar in average chamaephyte cover-abundance, suggesting a gradual recovery in terms of cover.

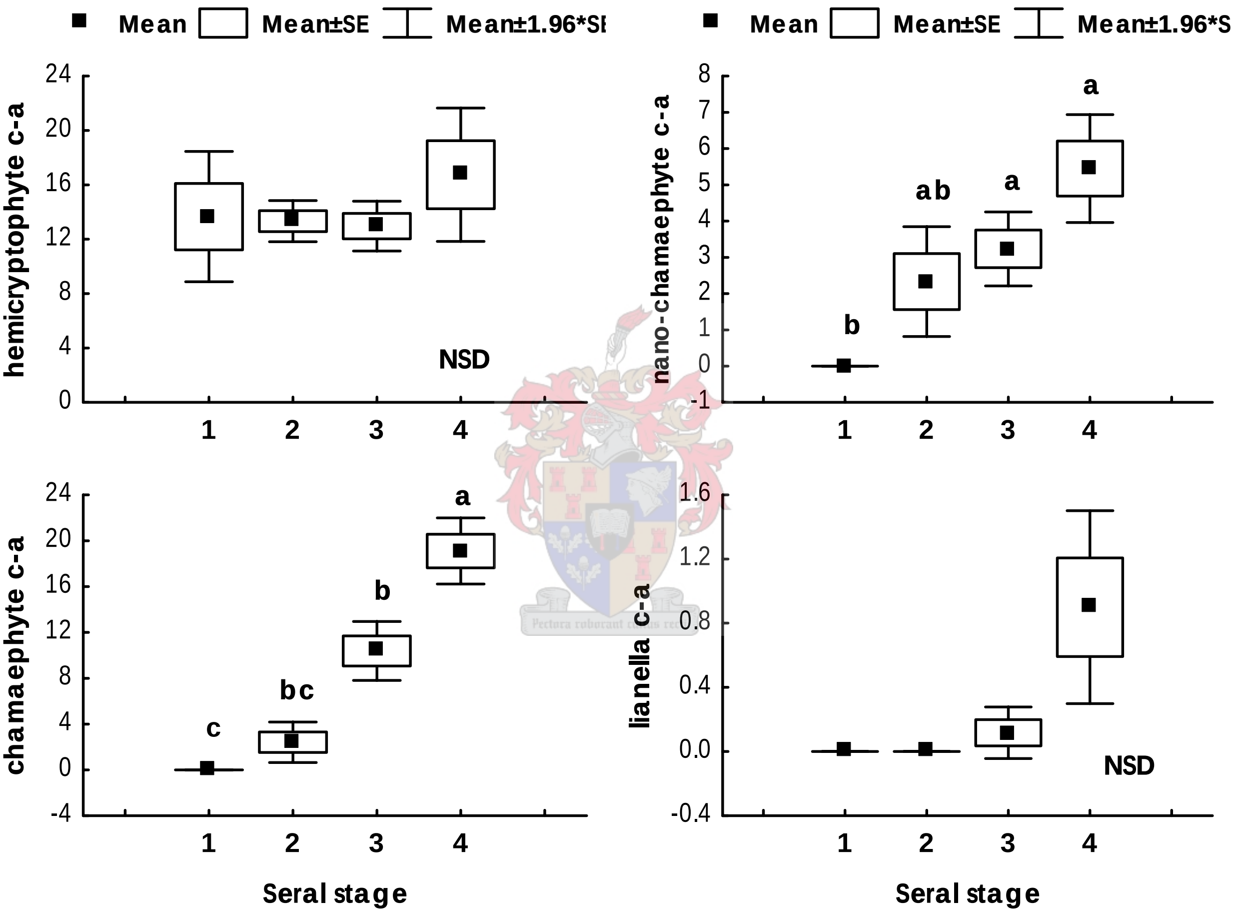

Figure 4.12: Average summed cover-abundance (y-axes) of hemicryptophyte, nano-chamaephyte, chamaephyte and lianella life-forms at the 10 m^2 quadrat scale (n = 72) for different seres. Vertical bars denote confidence limits with multiple comparisons p-values as characters depicting degree of similarity within life form groups. c-a = cover-abundance, NSD = no significant differences

The Influence of Ploughing and Grazing on Life-form Cover-abundance

Life-form cover-abundance in relation to both ploughing and grazing disturbances was analyzed only between the last two seres (30-year-old fields and unploughed stands, n = 54), as previously mentioned due to unequal replication of earlier seres. For interacting effects with grazing after ploughing a bootstrapping test was performed as the data were non-normally distributed for: cryptophytes, hemicryptophytes, parasites and total cover-abundance; as well as heteroschedastic for: therophytes, hemicryptophytes, parasites and total cover-abundance.

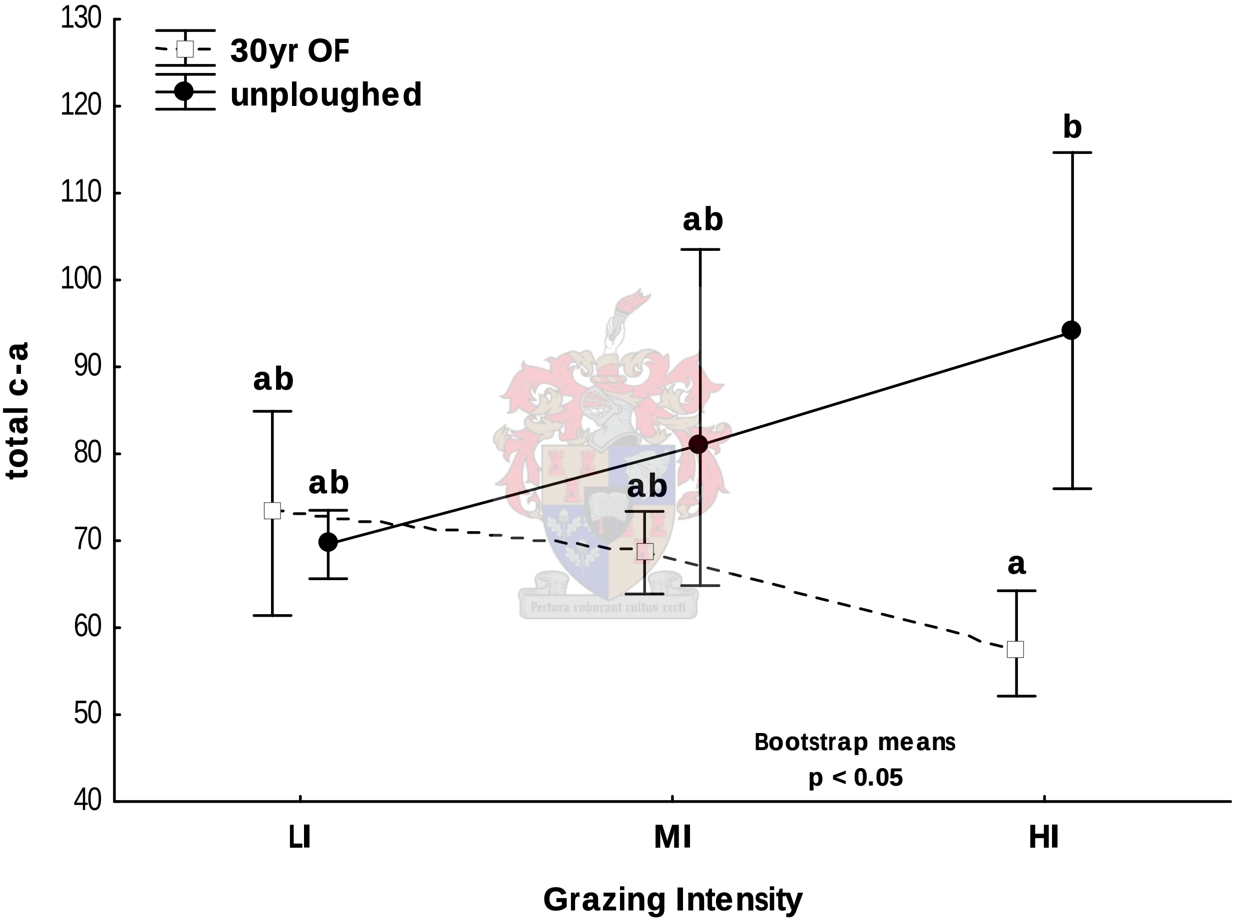

Figure 4.13: Total cover-abundance of all life-forms at the 10 m^2 quadrat scale (n = 54) with the interaction of ploughing and grazing intensity. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. Vertical bars denote bootstrap means, characters depict Bonferroni degree of similarity, c-a = cover-abundance

Figure 4.13 (bootstrap means $_{(2, 48)}$, $p < 0.05$) shows a significant interaction between ploughing and grazing on total cover-abundance of all life-forms. Only with a high grazing intensity is there a difference in cover-abundance between unploughed renosterveld and 30-year-old fields (the latter with lower cover-abundance). Interestingly there was no interaction with ploughing and grazing on therophyte cover-abundance but it was shown to have an interaction following a bootstrapping test. There were no interacting effects for: hemicryptophytes (Figure 4.14), nano-chamaephytes, chamaephytes, lianellas and parasites (Figure 4.14), thus the main effects were analyzed using non-parametric tests as the data were non-normally distributed.

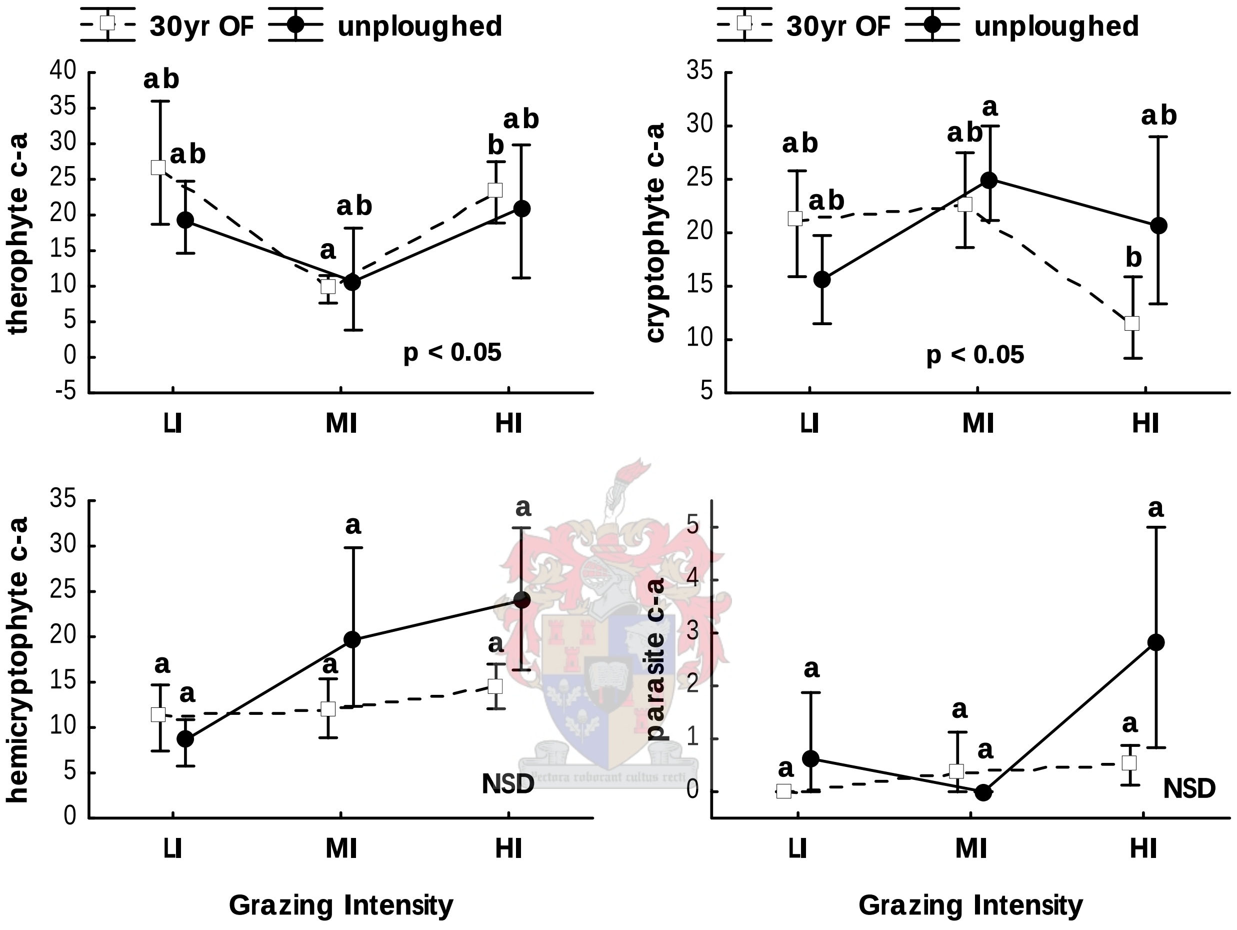

Figure 4.14: Cover-abundance (c-a) (y-axes) of therophyte, cryptophyte, hemicryptophyte and parasite life-forms at the 10 m^2 quadrat scale (n = 54) with the interaction of ploughing and grazing intensity. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. Vertical bars denote 0.95 bootstrap confidence intervals; characters depict Bonferroni degree of similarity. NSD = no significant differences

A significant difference in therophyte cover-abundance was found when considering the interaction of ploughing and grazing (Figure 4.14; bootstrap means $_{(2,\ 48)}$, $p < 0.05$). Specifically an increase in cover-abundance occurred between a moderate or high grazing intensity on 30-year-old fields (with highest cover-abundance at the latter site). This would suggest an increase in this group with high grazing intensities following ploughing, whereas there was no significant difference in cover-abundance amongst unploughed renosterveld, regardless of grazing intensity. For cryptophyte cover-abundance a significant interaction between ploughing and grazing occurred (Figure 4.14; bootstrap means $_{(2,\ 48)}$, $p < 0.05$). Specifically highest cover-abundance was found with a moderate grazing intensity in unploughed renosterveld which was significantly different to 30-year-old fields with a high grazing intensity. Whereas there was no significant difference in cryptophyte cover-abundance regardless of grazing intensity in unploughed renosterveld.

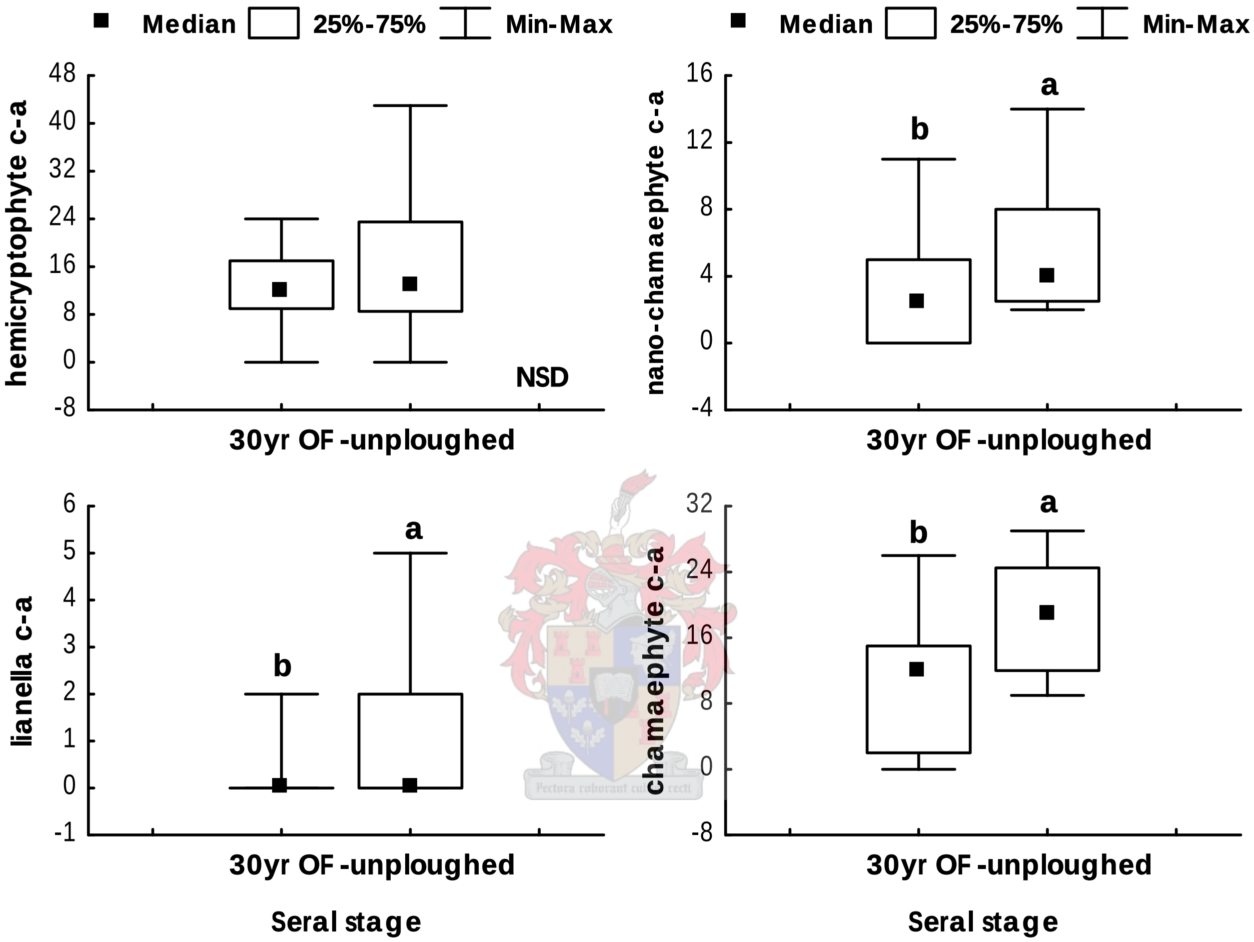

Figure 4.15: Cover-abundance (y-axes) of hemicryptophyte, nano-chamaephyte, lianella and chamaephyte life-forms at the 10 m^2 quadrat scale ($n = 54$) with the main effect of ploughing. OF = old fields, c-a = cover-abundance. Vertical bars denote minima and maxima; characters depict degree of similarity. NSD = no significant differences

The main effect of ploughing, between 30-year-old fields and unploughed renosterveld, showed that hemicryptophyte cover-abundance was not significantly different (Figure 4.15; Mann-Whitney U test $_{(2,\ 54)} = 301$, $p = 0.49$), whilst for the main effect of grazing intensity hemicryptophyte cover-abundance was significantly different amongst sites (Figure 4.16; Kruskal-Wallis H $_{(2,\ 54)} = 8.211838$, $p < 0.05$). Specifically highest hemicryptophyte cover-abundance occurred with a high grazing intensity. The cover-abundance of nano-chamaephytes with the main effect of grazing intensity was not significantly different. With the main effect of ploughing there was a significant difference (Figure 4.15; Mann-Whitney U test $_{(2, 54)}$ = 204, $p < 0.05$), suggesting ploughing has an adverse effect on nano-chamaephytes. With the main effect of ploughing, chamaephyte cover-abundance was highest in unploughed renosterveld (Figure 4.15; Mann-Whitney U test $_{(2, 54)}$ = 147.5, $p < 0.001$) relative to 30-year-old fields. With the main effect of grazing intensity alone cover-abundance was found to be highest with a moderate grazing intensity (Kruskal-Wallis H $_{(2, 54)}$ = 16.3607, $p < 0.005$).

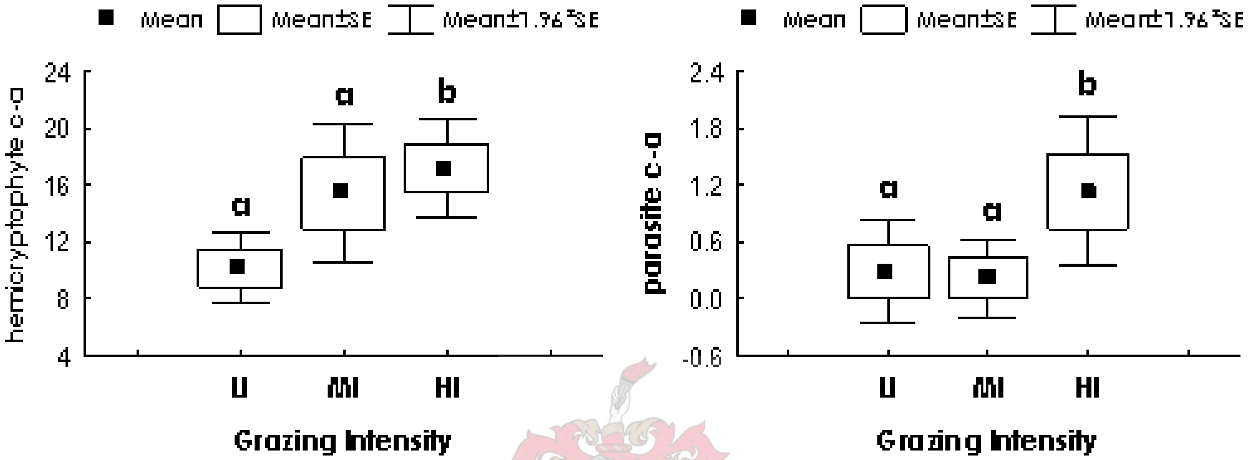

Figure 4.16: Cover-abundance (c-a) (y-axes) of hemicryptophyte and parasite life-forms at the 10 m^2 quadrat scale (n = 54) with the main effect of grazing intensity. LI = low intensity, MI = moderate intensity and HI = high intensity of grazing. Vertical bars denote means and standard error; with multiple comparisons p-values as characters depicting degree of similarity

For lianellas there was a significant difference between 30-year-old fields and unploughed renosterveld (Figure 4.15; Mann-Whitney U test $_{(2, 54)}$ = 224, $p < 0.05$), suggesting ploughing has an adverse effect on cover-abundance. For parasites only the effect of grazing intensity showed a significant difference in cover-abundance amongst sites (Figure 4.16; Kruskal-Wallis $_{(2, 54)}$ = 8.728477, $p < 0.05$) with highest cover-abundance occurring with a high grazing intensity.

4.3.3. Alien Species

There are 44 alien species (Figure 4.17) in the 42 (1000 m^2) relevés. Alien species comprise 10.7% of the total species count (of 411 species), whilst therophytes contribute 75% of all alien species. Alien species richness was significantly different amongst seres (Figure 4.18; ANOVA, F $_{(3, 38)}$ = 3.9553, $p = 0.015$). Most alien species occurred on the most recently disturbed old fields. As the data were non-normally distributed a bootstrapping technique was employed revealing that there was no significant interaction with ploughing and grazing (Figure 4.18).

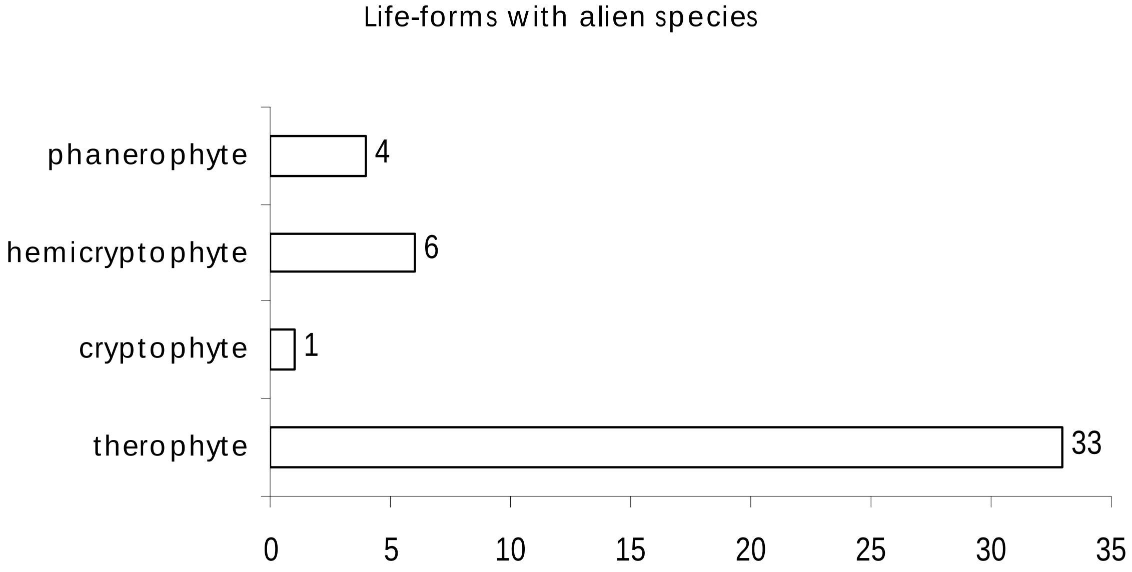

Figure 4.17: A count of alien species for each life-form in which they occur

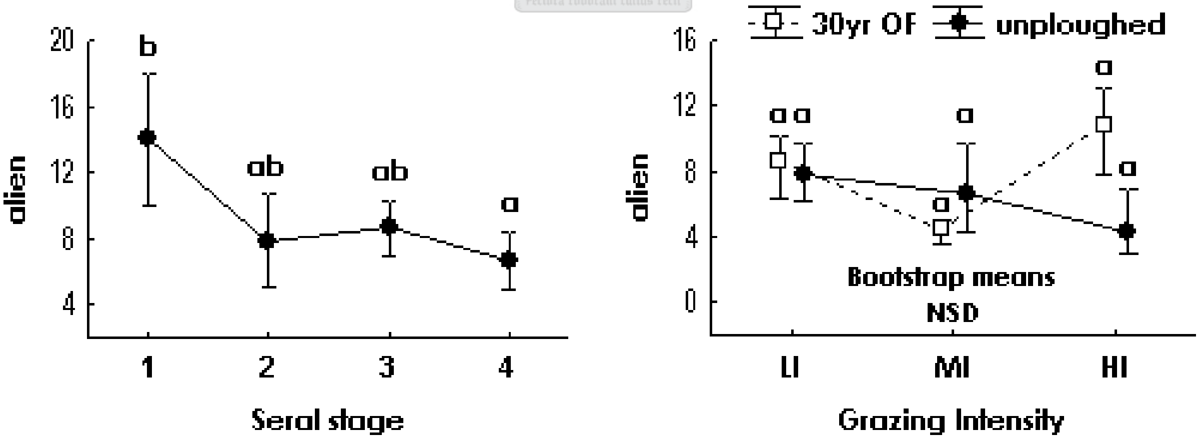

Figure 4.18: Alien species richness (y-axes) of different seres at left (n = 42, 1 = 5-, 2 = 15-, 3 = 30-year-old fields and 4 = unploughed controls) and alien species richness with different grazing intensities at right (n = 33, LI = low intensity, MI = moderate intensity and HI = high intensity of grazing), respectively. NSD = no significant differences

4.3.4. Species Response Curves

Firstly the diagnostic species of communities from the vegetation classification (see Chapter Three) were plotted along the first compositional axis (DCA) using a GAM (Generalized Additive Model) to show the species individual responses, in terms of cover-abundance. Figure 4.19 shows the gradient between the *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland Community and *Ursinio anthemoidis–Cynodontetum dactyli* Grassland Community with some overlap of species response curves. Notably *Pterygodium catholicum* is restricted to unploughed renosterveld as is *Arctotheca calendula* generally restricted to sere 1 (5-year-old fields) of the grassland community. *Cynodon dactylon* and *Ursinia anthemoides* are at a similar position along the compositional gradient, differing only in their amplitude of response (cover-abundance). Figure 4.20 shows a group of important indigenous graminoids to herbivores. The high response of *Cynodon dactylon* relative to other grasses at other seres is evident; compared with *Tribolium hispidum* which is most common in unploughed renosterveld. Figure 4.21, is a select group of shrub species, clearly showing the dominance of *Elytropappus rhinocerotis* relative to the other sub-dominant shrubs. Interestingly the sub-dominant shrubs are nested together in varying responses along the compositional gradient. A select group of alien grass species (Figure 4.22), showing their relative importance or response along the compositional gradient, are mostly concentrated at the early seres. *Aira cupaniana* and *Bromus pectinatus* are shown to penetrate deeper into unploughed renosterveld than other grasses.

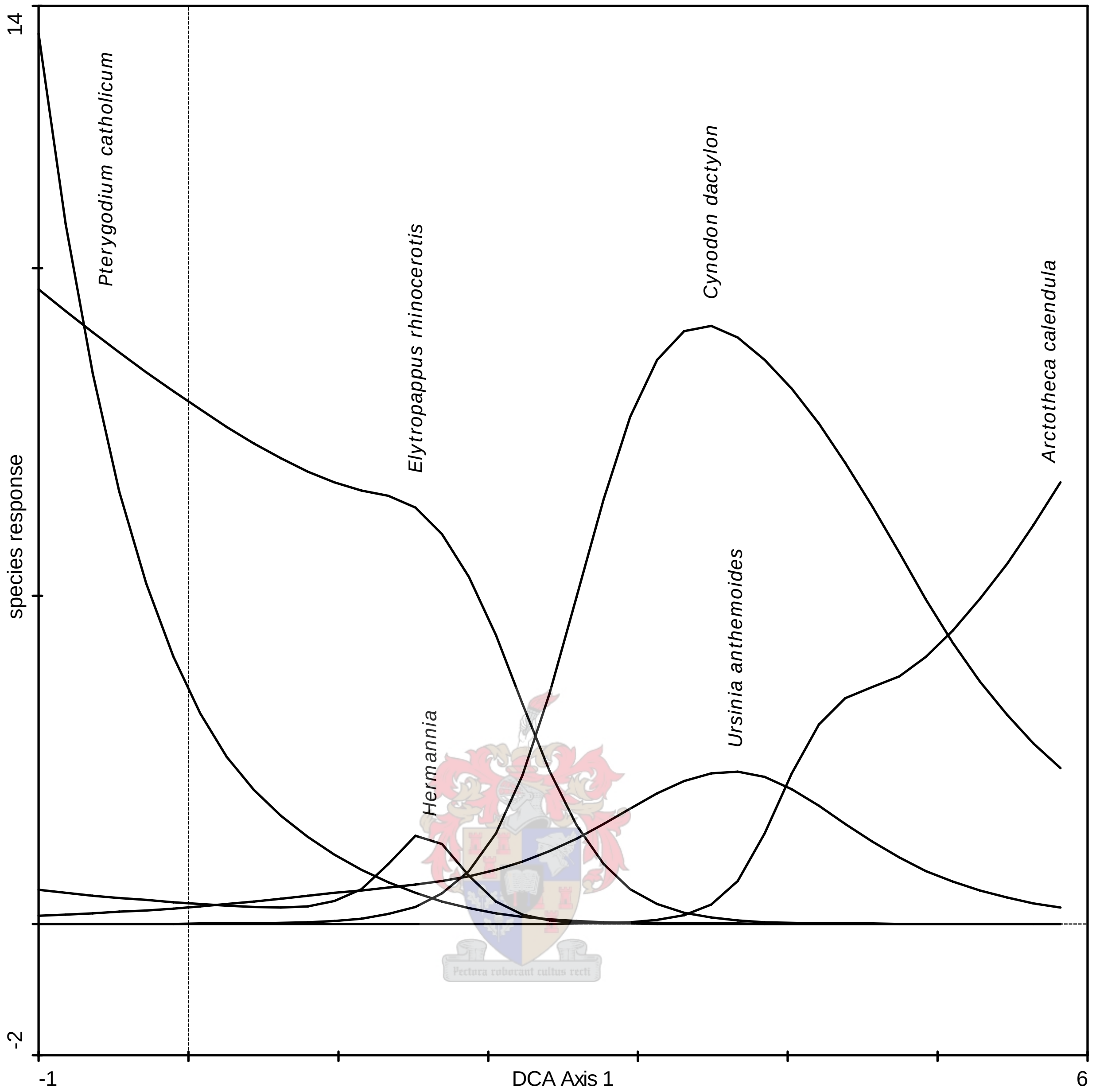

Figure 4.19: Response curves of six species fitted using generalized additive models. Species are diagnostic for different communities: *Pterygodio catholici–Elytropappetum rhinocerotis* Shrubland with *Elytropappus rhinocerotis*, *Pterygodium catholicum* and *Hermannia*; and *Ursinio anthemoidis–Cynodontetum dactyli* Grassland with *Arctotheca calendula*, *Cynodon dactylon* and *Ursinia anthemoides*

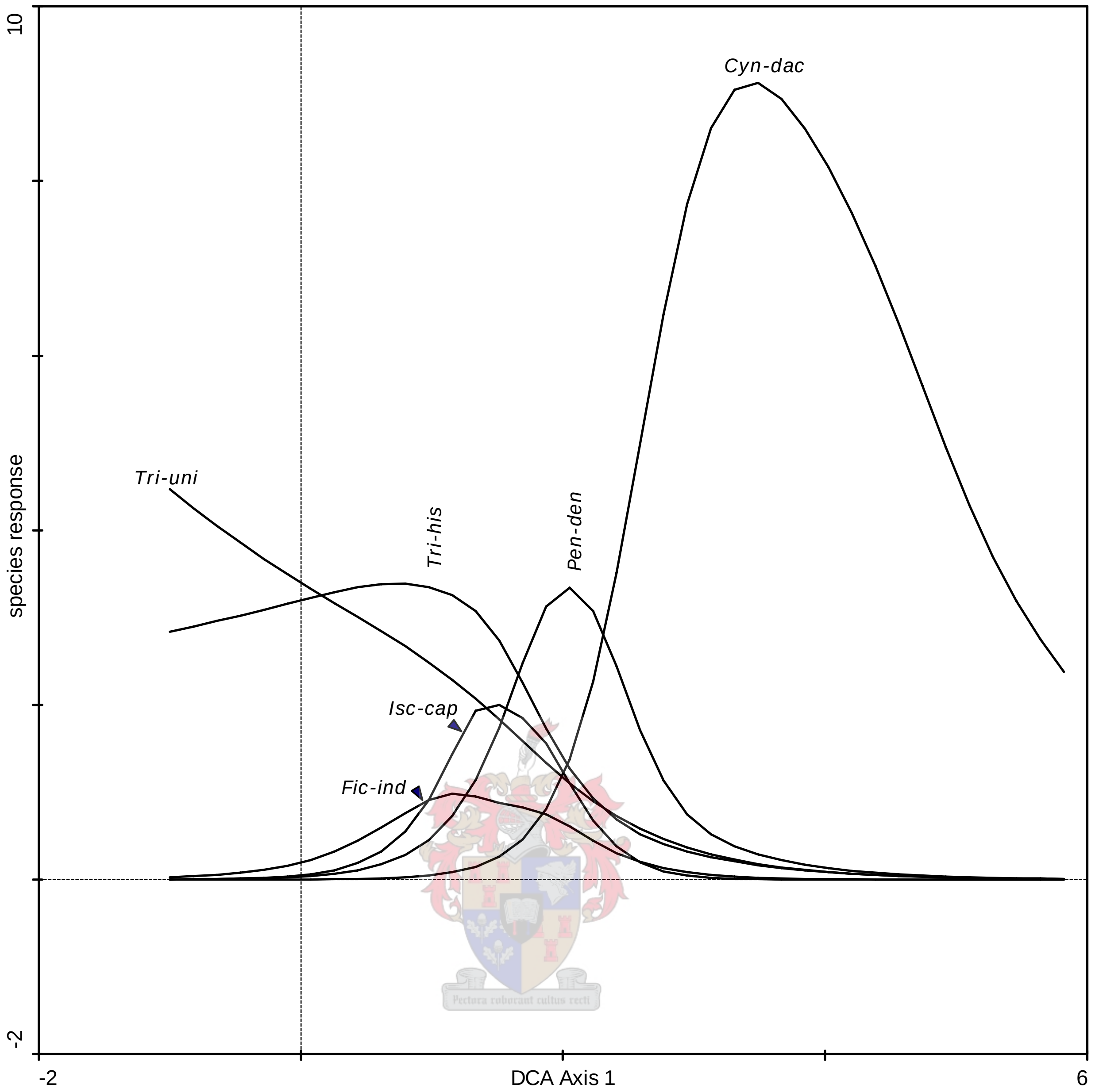

Figure 4.20: Response curves in relation to the first DCA axis of six selected graminoids that frequently occur at the AGC. Species were fitted using generalized additive models. Cyn-dac = *Cynodon dactylon*, Fic-ind = *Ficinia indica*, Isc-cap = *Ischyrolepis capensis*, Pen-den = *Pentachistis airoides*, Tri-his = *Tribolium hispidum* and Tri-uni = *Tribolium uniolae*

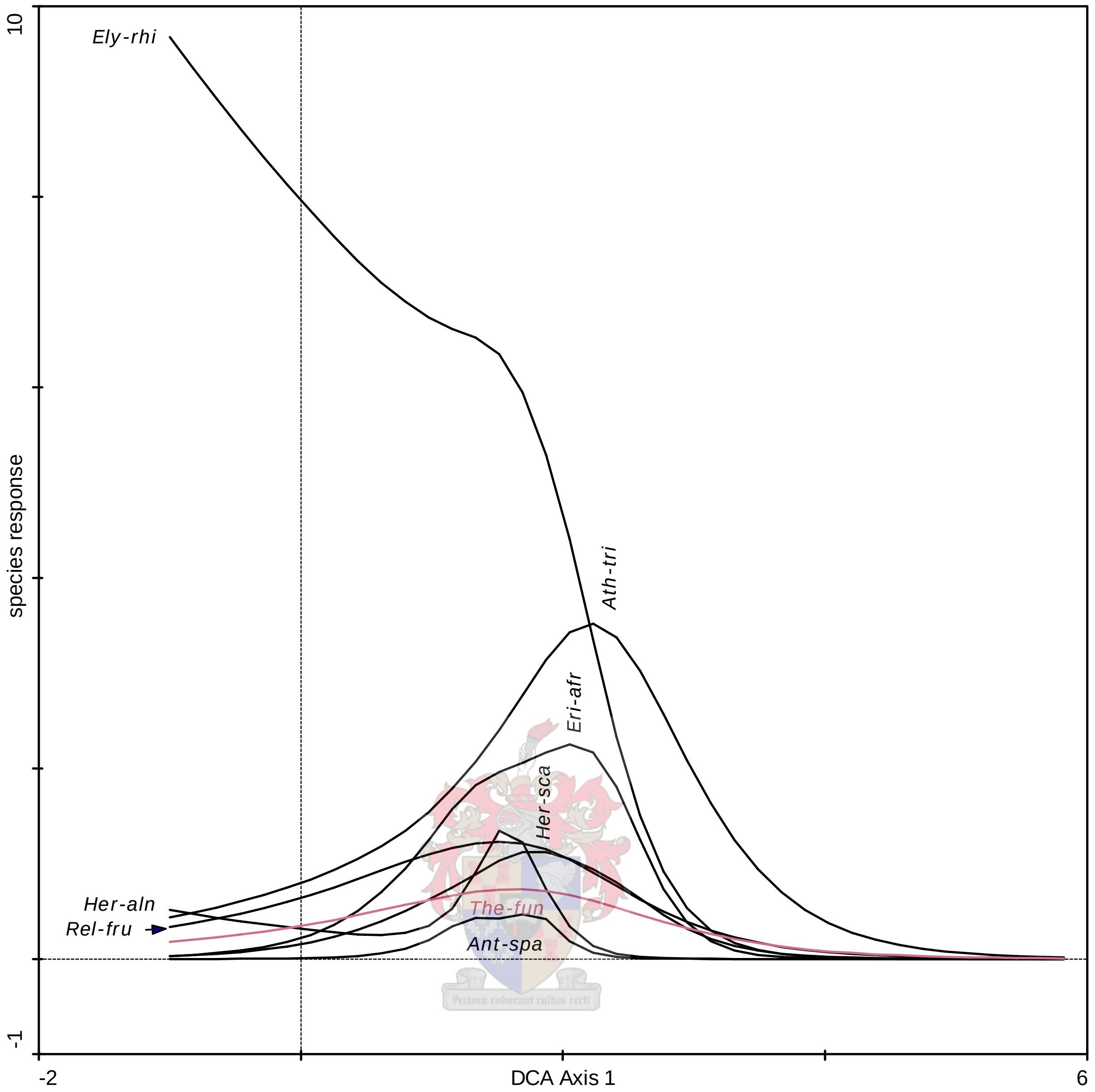

Figure 4.21: Response curves of eight selected perennial shrub species fitted using generalized additive models. Note the strong dominance by *Elytropappus rhinocerotis*, and the nested response by sub-dominant shrubs. *Athanasia trifurcata* appears to be dominant initially following disturbance by ploughing. Ant-spa = *Anthospermum spathulatum*, Ath-tri = *Athanasia trifurcata*, Eri-afr = *Eriocephalus africanus*, Ely-rhi = *Elytropappus rhinocerotis*, Her-aln = *Hermannia alnifolia*, Her-sca = *Hermannia scabra*, Rel-fru = *Relhania fruticosa*, The-fun = *Thesium funale*

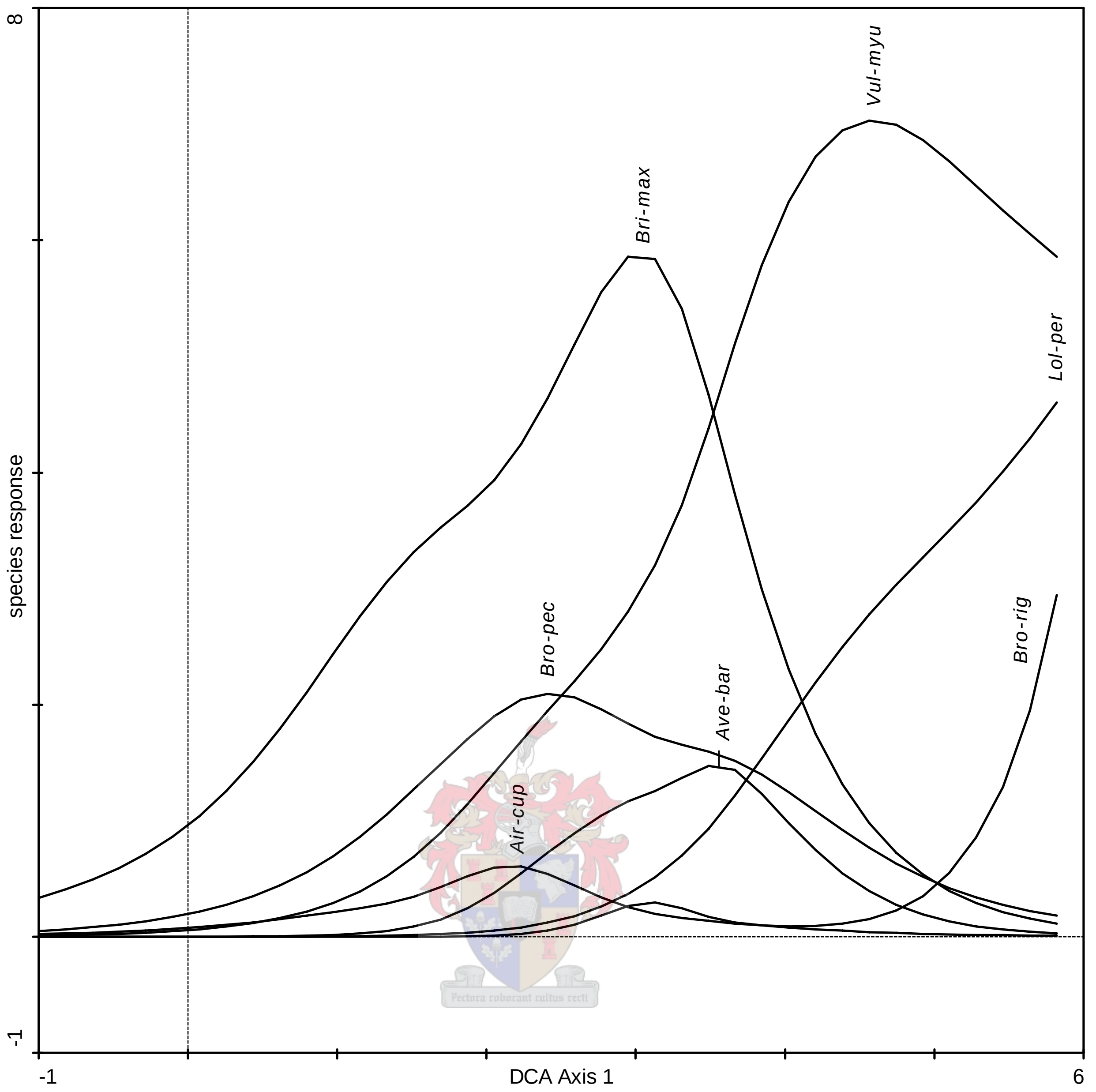

Figure 4.22: Response curves of six selected alien annual grass species fitted using generalized additive models. Air-cup = *Aira cupaniana*, Ave-bar = *Avena barbata*, Bri-max = *Briza maxima*, Bro-pec = *Bromus pectinatus*, Bro-rig = *Bromus rigidus*, Lol-per = *Lolium perenne*, Vul-my = *Vulpia myuros*

4.4. Discussion

This study considers secondary succession on set-aside old fields in a chronosequence of 30 years or more. Renosterveld vegetation is highly fragmented and these findings have relevance for restoration or rehabilitation of old fields and degraded landscapes of Swartland Shale Renosterveld (Mucina and Rutherford 2004). In some respects the destruction of vegetation by ploughing is irreversible, in others not. Certain life-forms are more sensitive to ploughing than others. Life-forms that do not re-colonize old fields would have to be manually seeded or planted on to old fields; in contrast to life-forms freely able to arrive on to old fields by dispersal from proximate propagule sources.

General patterns of life-form change, with respect to richness and cover-abundance on old fields relative to unploughed renosterveld is discussed. The observed chronosequence here is acknowledged as being dependant on close proximity to a propagule source. I thus doubt that a similar pattern would occur on set aside fields deep inside an agricultural matrix (where indigenous bunchgrasses are absent, a major problem for restoration of valley grasslands in California (Keeley 1990). From the perspective of life-form richness and cover-abundance, 30-year-old fields resemble that of unploughed renosterveld. Thus they are pleasing to the eye and fulfilling the functional cover over the landscape, alleviating rapid soil erosion by wind and water and sustaining many biotic interactions. In reality many species are lost by ploughing particularly those species with naturally narrow distribution ranges. Common species like *Pterygodium catholicum* may also lack the ability to disperse on to old fields due to pollinator dependencies (Pauw 2004) on viable (large) fragments for nesting sites to ensure sexual reproduction. Also species with short dispersal trajectories would be affected by fragmentation. Thus a lack of certain species on old fields may have something more to do with pollinator interactions or suitable micro-habitat requirements than dispersal alone.

Dispersal syndromes of species were studied by Kemper (1997) and Shiponeni (2003) where a 1:1 ratio of wind dispersed versus biotically dispersed species was found. Wind dispersed species like *Elytropappus rhinocerotis* (renosterbos) have long dispersal distances compared to short seed rains of some geophytes like *Babiana angustifolia*. Seed rain of bird dispersed species falls close to perches in matorral (Feuntes et al. 1986). Similarly in renosterveld and strandveld, bird-dispersed species form bush-clumps (heuweltjies, associated with *Olea europaea* subsp. *africana*, Boucher 1987). Bird perch dependency limits entry of these species on to old fields, and perches are typically lacking. Thus wind dispersed species would be the primary group of colonizers on to old fields adjacent to a propagule source. Biotically dispersed species like succulents (see Milton and

Dean 2001); chamaephytes such as *Hermannia alnifolia* and *H. scabra*; and the hemi-parasite *Thesium funale* could be the secondary group of arrivals on to old fields transported in herbivore dung. In accompaniment of seed mobility is the extant seed bank. Logically the seed bank of old fields would be depauperate or exhausted compared with unploughed renosterveld, and the former seed bank would consist of many ruderal and/or alien species with few indigenous geophytes (see Shiponeni 2003). Thus the speciose seed bank propagule source of unploughed renosterveld would be a constant source for old fields. In addition many species like some geophytes occur in discrete microhabitats and are naturally locally rare, often persisting in marginal habitats (unsuitable for agriculture until quite recently, wetland verges and hard-pans). These specialized species are not always able to advance on to unsuitable old fields habitats.

Renosterveld is a hardy shrubland vegetation, enduring hot summers and desiccating winds. Unploughed renosterveld is in a cyclical state or suspended succession, rather like a climax state, dominated by shrubs with open spaces and grasses throughout. Seedlings of the dominant stratum can germinate, and reach maturity mostly only in open spaces in the natural matrix (similar to coastal sage scrub DeSimone and Zedler 1999, Keeley 1984). The author has seen seedling germination between adults of shrub species thereby indicating partial reliance on fire-stimulated germination, and Boucher (1981) noted robust renosterbos individuals of at least 50 years on old fields. This does not imply that seedlings and even young juveniles are tolerant of severe dry (drought-like) periods. Seedling recruitment in renosterveld may occur in pulses, coinciding with above-average and consistent winter rains with or without fire. Indigenous seedbanks would be depleted as a result of ploughing, thus old fields would only contain a subset of the original composition. In addition seedbanks of old fields would be exhausted as germination occurs and heat and wind kill most recruits, and this process would repeat itself until all seeds are spent. Seedbank "exhaustion" may explain why some old fields are not recruiting an observable shrub stratum. In this scenario colonization of fields can only occur with the arrival of propagules either blown/washed in or dispersed by organisms.

4.4.1. Life-form Richness Patterns at the 1000 m^2 Scale

Unploughed renosterveld has most species and highest life-form richness compared with recovering old fields, but had a similar species richness to 30-year-old fields. Similarly, the interaction of ploughing and grazing did not influence species richness patterns, although a moderate grazing intensity (relative to a low grazing intensity) favoured highest species richness. Once renosterveld is ploughed it takes as long as 30 years for succession to advance to a structural state resembling that of unploughed renosterveld. The horizontal structure of 30-year-old fields is similar to unploughed renosterveld and species richness is almost as high but never entirely recovered.

Therophytes were equally speciose at all seres suggesting that they were not promoted, or at least affected, by ploughing relative to other life-forms. This is in contrast to that shown by Krug et al. 2004. Many alien and/or ruderal species are therophytes generally adapted to regularly disturbed environments. Certain therophytes may be restricted to, or benefit from, places shaded by a dense cover of chamaephytes (shading and protection affect for *Nemesia barbata*, *Hemimeris racemosa*), as is the case in matorral (Holmgren et al. 2000). The species composition of therophytes differs amongst seres, thus there is a turnover as a result of anthropogenic disturbance and species occurring in unploughed renosterveld. No interaction occurred with ploughing and grazing for therophytes thus one can only assume that another factor or disturbance mechanism influences their patterning. Perhaps the trampling effect and dispersal both ways by grazers between old fields and unploughed renosterveld mitigates the contrast in richness at recently disturbed sites (an exogenous propagule source) with unploughed renosterveld (an endogenous propagule source).

Cryptophytes were the most speciose life-form comprising 34% of the sampled pool here (and 17% of the Cape flora, Goldblatt and Manning 2000), with unploughed renosterveld vegetation containing highest cryptophyte species richness. Seed dispersal distances are often short and individual species have narrow distribution ranges like *Gladiolus watsonius* (Goldblatt and Manning 1998). Ploughing adversely affected this group however cryptophyte richness was similar after 30 years of recovery, yet complete richness was never attained. A moderate grazing intensity seemed to favour highest richness, in accordance with the intermediate disturbance hypothesis (*sensu* Connell 1978), suggesting that a high grazing intensity decreased certain cryptophytes. Cryptophytes are favoured by porcupines and mole-rats as a food-source and aid in their dispersal (Lovegrove and Jarvis 1986). Above ground cryptophyte plant parts are occasionally browsed (leaves, flowers or fruit of *Romulea flava*, B. A. Walton, personal observation) and are also harvested by termites (*Babiana odorata* and *Moraea galaxia*, B. A. Walton, personal observation). It appears that cryptophytes are unhindered by *Cynodon dactylon* of old fields, as they are capable of sending apical shoots directly through the “lawn”.

Pioneering cryptophytes are numerically abundant on old fields, for example: *Baeometra uniflora* (winged seed), *Moraea lewisiae* (usually winged seed) or species adapted to frequent disturbance like *Oxalis obtusa*, *Oxalis pes-caprae* (Petsikos et al. 2004), *Oxalis purpurea*; and/or dispersed biotically like *Geissorhiza aspera* (granular seed) and *Romulea flava* (granular seed). Cryptophytes like *Babiana angustifolia*, *Moraea villosa* and *Triglochin bulbosa* persisting on or near old fields as part of original micro-habitats contribute to local propagule sources. Some 30-year-old fields had heuweltjies with associated geophytes like *Moraea flaccida* that once colonized increase and persist undeterred by browsing pressure since they are toxic. Cryptophytes favouring sandier conditions, typically *Gladiolus alatus* occurred on 15-year-old fields, often forming regular patches or in a clumped distribution pattern. Dispersal no doubt occurred in many geophytic species as their seed generally remains viable for about three years (or less, Manning et al. 2002) only.

Hemicryptophytes were not adversely affected by ploughing, and if given an appropriate amount of resting time, can potentially re-colonize old fields. This is in contrast to preliminary findings shown by Krug et al. (2004), as hemicryptophyte richness did not increase with an advance of succession (merely a slight turnover of species occurred). Long dispersal distance of bunchgrass seed by wind (Hensen and Müller 1997) ensures colonization on to old fields, as well equally aided by ecto- and endo-zoochorous dispersal vectors. From this study it appears that grazers perform an important and necessary dispersal function of hemicryptophytes in unploughed vegetation, relative to sites with a low grazing intensity. In ploughed vegetation this effect was not apparent. Herbivore grazing stimulates vegetative growth preventing a moribund state, resembling disturbance by fire. Mammalian herbivores browse sedges such as *Ficinia indica* commonly, and occasionally graze new growth of restioids (*Elegia filacea*; B. A. Walton, personal observation). Bunchgrasses are favoured when in shoot by large mammalian herbivores: for example *Digitaria eriantha*, *Ehrharta calycina*, *Ehrharta capensis*, *Eragrostis capensis*, *Heteropogon contortus*, *Pentachistis densifolia*, *Themeda triandra*, *Tribolium hispidum*, and *Tribolium uniolae*. The abundant presence of *Themeda triandra* in Elandsberg and Krantzkop is promising suggesting that current managed stocking rates have not yet caused a severe decline of this preferred bunchgrass (whilst *Digitaria eriantha* is rare)- although this could indicate disturbance (Linder 1989). *Cynodon dactylon* is continuously grazed by large mammalian herbivores on old fields, therefore reducing the effect of competition by this stoloniferous grass on emerging annual and perennial (shrub) seedlings. A feedback loop possibly arises whereby herbivores browse annual and perennial species, thus retarding the rate of succession of shrubs on to old fields (arrested secondary succession or even retrogressive succession, see Walker et al. 2000).

Nano-chamaephyte recovery was promising after 30 years. It appears ploughing affects this group severely. This group is composed of disturbance tolerant species, for example *Helichrysum asperum* (palatable) and disturbance intolerant decumbent or erect succulents (dispersed by water, some favouring moist sites, others dispersed by herbivores). Chamaephytes were negatively affected by ploughing, but recovery was also promising after 30 years, and grazing seemed to influence richness. Overgrazing signs are visible at Krantzkop where numerous shrubs: *Elytropappus rhinocerotis, Eriocephalus africanus* subsp. *paniculatus, Lobostemon argenteus and Relhania fruticosa*, have been uprooted either due to trampling, strong browsing pressure (also rooting by Eland) or feral pig activity. Palatable shrub and dwarf shrub recovery on to old fields is delayed by grazing especially for: *Anthospermum galioides*, *Anthospermum spathulatum*, *Hermannia alnifolia*, *Hermannia scabra* and *Thesium funale*, which are kept trimmed to about 15 cm. This “bonsai-effect” is especially evident on 15-year-old fields, but also occurs on both 30-year-old fields and in unploughed renosterveld. Less palatable shrub species: typically *Athanasia trifurcata* and *Elytropappus rhinocerotis* are only occasionally browsed enabling their dominance in the vegetation. However the former is browsed by termites whilst the latter is occasionally browsed by mammals (B.A. Walton, personal observation) as are the new shoot tips of the potentially toxic *Salvia chamelaeagnea*. *Athanasia trifurcata* is potentially toxic (Kellerman et al. 1988), hence a valid reason for its dominance (or preference for lime-deficient soils). The deep-rooting ability of renosterbos (Scott and van Breda 1937) might be the primary reason of its ease of advance on to old fields relative to more shallow-rooted shrubs, as well as penetration being facilitated by a ploughed surface.

Presence of (a) parasite(s) at the site with a high grazing intensity could reflect that herbivores favour them and are responsible for dispersal of palatable hemi-parasites like *Thesium funale* (also related to an increase in host plants). Most lianella species occurred in unploughed renosterveld, attributed to chamaephyte presence as their necessary structural support (requiring vegetation maturity). Phanerophytes were negligible here in terms of richness and not often sampled.

4.4.2. Horizontal Structure and Patterns at the 10 m^2 Scale

Total cover-abundance was significantly different amongst seres, increasing with an advance in succession. After 30 years of rest from ploughing the total cover-abundance decreased with an increase in grazing intensity. Herbivores had an effect on total cover-abundance of renosterveld (by browsing and trampling) which was more pronounced only after ploughing. This warrants close inspection and monitoring of the condition of vegetation and stocking densities on recovering landscapes.

Therophyte cover-abundance was highest on recently disturbed ground (i.e. 5-year-old fields), whilst cryptophyte and chamaephyte cover-abundance would logically be highest in natural or well recovered vegetation. Grazing (especially of a high intensity) influenced therophyte cover-abundance on 30-year-old fields but not in unploughed renosterveld. Cryptophyte cover-abundance was significantly different amongst seres, specifically low on 5-year-old fields and increasing with an advance in succession. Cryptophyte cover-abundance was affected by a high grazing intensity especially following ploughing. Cryptophytes flourish in abundance on *Cynodon dactylon* old fields as a "shield" and the lack of shrubs allows for colonizing geophyte species to benefit and spread in large numbers (especially wind-dispersed species like *Moraea lewisiae*), or those tolerant to heavy disturbance like *Oxalis purpurea*. Conversely other (shade-tolerant) geophytic species may require the facilitative (nurse-plant) effect of a shrub cover for persistence and even arrival - either as a wind-trap or perch.

There was no difference in cover-abundance of hemicryptophytes amongst seres. Directly attributable to an anemochorous dispersal strategy, thus they were blown back on to old fields. This is in contrast to preliminary findings shown by Krug et al. (2004), as hemicryptophyte cover-abundance did not increase with an advance of succession, after initial colonization. Grasses like: *Bromus rigidus*, *B. pectinatus*, *Cynodon dactylon*, *Eragrostis curvula*, *Pentachistis densifolia*, *Tribolium hispidum* are dispersed in herbivore dung (Shiponeni 2003). *Cynodon dactylon* is disturbance tolerant, an early pioneer in succession and occasionally occurring in unploughed renosterveld. Interestingly this study shows that hemicryptophyte cover-abundance is similar at all seres, i.e. with or without a shrub stratum. However younger old fields are dominated by *Cynodon dactylon* and 30-year old fields or unploughed renosterveld have a more diverse cover-abundance. There was no interaction with ploughing and grazing for hemicryptophyte cover-abundance. Highest hemicryptophyte cover-abundance occurred with a high grazing intensity (contrary to patterns of other life-forms) no doubt due to this life-forms adaptation to browsing.

Nano-chamaephyte cover-abundance was significantly affected by ploughing. As observed some succulents are sensitive to disturbance by ploughing, and many occurring here require sufficient moisture to persist like *Lampranthus aduncus*, consequently occurring in specific micro-habitats near drainage lines on open old fields. Hardy dwarf shrubs would be expected to occur throughout the chronosequence and even decline in abundance in unploughed vegetation due to shading. This was not the case, for example *Helichrysum asperum* is palatable (van Breda and Barnard 1991)-so it probably is dispersed into the shrubland matrix. Nano-chamaephytes were most abundant in unploughed vegetation implying sensitivity to disturbance (especially succulents-with short dispersal distances).

Chamaephyte cover-abundance was affected by ploughing, and recovered fully after 30 years. This is unlike findings presented by Krug et al. (2004) which showed no difference in cover-abundance amongst seres. Chamaephyte cover-abundance increased with an advance in succession, following the trend for species richness. This group is the most prominent stratum in the vegetation and affected by ploughing but able to effectively recover unlike some more sensitive dwarf shrubs or cryptophytes. Chamaephyte cover-abundance was highest in unploughed stands compared with 30-year-old fields, and highest at the site with a moderate grazing intensity. Given time chamaephytes increase in cover on a field and reduce cryptophyte and hemicryptophyte cover-abundance, and possibly facilitate the arrival of more specialist-dispersed species (even increase richness) as observed around many shrubs in the fields. Renosterbos has a facilitative effect on more sensitive or shade-tolerant species, either dispersed by birds/animals or wind (even water along channels and drainage lines). Chamaephyte re-entry on to old fields is limited by moisture requirements during germination. Abundant moisture also traps seed after wind has blown seed of dominant species into depressions, following drying they are stored *in situ* and with sufficient moisture availability they germinate. The presence of chamaephytes along drainage lines on old fields may be related to the slight depressions in an otherwise homogeneously ploughed landscape trapping wind blown seed. Further waves of succession of chamaephytes or later arrivals might occur in cohorts coinciding with above average annual rainfall in the appropriate season, allowing for their tap roots to penetrate deep prior to summer drought.

There was no significant difference in cover-abundance for lianellas and parasites amongst seres. Not surprising as these groups are low in richness, and lianellas require a structure to grow on (perhaps bird-dispersed?) whilst the parasites are low in abundance (as cover not occupancy) on old fields and are palatable and browsed continuously by the herbivores (*Thesium funale*). Some lianella species like *Microloma sagittatum* (van Breda and Barnard 1991) are palatable and may avoid direct browsing pressure by their entwined habit amongst spiny or soft shrubs. Lianella cover-abundance was highest in unploughed renosterveld whilst parasite cover-abundance was highest with a high grazing intensity (no doubt related to endo-zoochorous dispersal).

McDowell (1988) compared the cover of plant families and species in relation to grazing versus non-grazing at Jan Briers Louw (hereafter referred to as JBL, formerly Eensaamheid Private Nature Reserve). JBL consists of both Swartland Alluvium Fynbos and Swartland Shale Renosterveld vegetation types. Heavy grazing increased the asteraceous and iridaceous components, whilst causing a decline in the poaceous and rutaceous components (even decimating the proteoid species), but no significant difference occurred in total plant cover and diversity. McDowell (1988) stated that well-managed pasturage was a “minor threat to the extinction of floristic elements” and certain species would benefit from grazing-however a turnover of species occurred. These grazing effects were not studied in renosterveld only, and the mention of proteoid elements depicts that. Stander (1988) compared the cover of functional groups between grazed and ungrazed renosterveld at JBL, and showed that with grazing there was a higher cover of reseeder shrubs as well as more species of shrubs and geophytes than without grazing. This scenario is more likely to occur with overgrazing promoting woody colonization-perhaps a useful strategy towards restoring the woody stratum to grassy old fields by reducing the competitiveness of grasses? A study in mesic coastal Californian prairies focused on the impact of cattle grazing on native annual forbs and found that species richness and cover (also exotic annual grass and forb cover) were higher on grazed sites (Hayes and Holl 2003). Indigenous grass species richness and cover showed no difference between paired grazed and ungrazed sites, unlike indigenous perennial forb richness and cover, which was higher at ungrazed sites. This suggests an adaptive and flexible management approach is necessary to ensure all species are equally conserved - especially palatable species.

The response curves of selected groups indicated changes in abundances with the sequence of succession. For the phytocoena there was a clear distinction in abundance between the renosterveld shrubland and the grassy old fields. The response curves of selected hemicryptophytes showed the overwhelming abundance of *Cynodon dactylon* at early seres compared with the more speciose later seres. Revealing the composition of species occurring at a given sere in secondary succession, as well as the obvious dominant and early colonizers allows for indicators of accurate restorative and rehabilitative work. Species not found to occur after ploughing would have to be manually added.

4.4.3. Renosterveld Dynamics and Resilience

Generally the mode of succession here would be facilitation (*sensu* Connell and Slatyer 1977) by dominant and sub-dominant shrubs, later changing into a mode of tolerance. The use of floristic data is more deterministic than using groups of dominant types (Lepš 1987) when describing succession. The described phytocoena (see Chapter Three) were ordinated using CCA which showed a unidirectional sequence along axis 1, i.e. the succession was effectively recovered, and 30-year-old fields resembled unploughed renosterveld.

Different directions and outcomes of secondary succession are related to disturbance type and history, as well as the life history traits of the final crop prior to abandonment (see Myster and Pickett 1994). Succession on old fields here has been uninterrupted by ploughing for 30 years or more. These 30-year-old fields have differing disturbance histories: some were ploughed often and extensively utilized for agriculture; whilst others were briefly ploughed then abandoned when deemed unsuitable due to rockiness and/or high water-level of substrate. Most 30-year-old fields here are either surrounded by, or are proximate to unploughed renosterveld. In addition, species may have been dispersed more frequently here since the introduction of large mammalian herbivores (1974 for Elandsberg and 1982 for Krantzkop). Herbivores (both large and small) create micro-sites suitable for the establishment of propagules (Bakker and Olff 2003, Gutterman 2001). Fires no doubt influence the heterogeneity of the vegetation causing small and large scale patterning effects.

Perhaps lacking in models of succession is the assumption of a retention of propagules following ploughing especially in cryptophytes adapted to annual subterranean movement (*Cyanella hyacinthoides*) and the downward percolation of small versus large seed into the seed bank (Luzuriaga et al. 2005). Thus a propagule source would remain after ploughing of a mixture of species. Ploughing definitely irreversibly altered the seed bank richness. Thus the synanthropic community is a state (Westoby et al. 1989) unlike that of unploughed renosterveld, as a consequence of seed bank depletion, a mere “subset” of its former composition. Species which remained are those that endured ploughing. Arrivals on old fields are dispersed by various vectors (abiotic and biotic). However at small spatial scales habitat characteristics determine the community composition, like: drainage (either wetland, seasonally inundated, open plain or rocky area); chemistry (nutrient status) and the fire regime. Marginal habitats never ploughed may contain naturally rare and localized species which contribute to the adjacent old field succession if the habitat is suitable.

Some areas of both natural vegetation and old fields are either strongly dominated by renosterbos or klaaslouwbos (*Athanasia trifurcata*). This patchy domination may be the result of the timing of fire in relation to flowering. Their flowering times are six months apart in general (renosterbos in May/June and klaaslouwbos in December/January) and seed production followed by fire at a certain time may determine which of these two potentially dominant species will produce the most recruits. The growth phases occur at the same time from late summer to autumn. An alternative hypothesis (from the knowledge of farmers) is that klaaslouwbos prefers lime deficient soils, thus this pattern may indicate a response to the nutrient status of the soils. So as seed is annually produced fire timing may produce different dominant patches over the landscape in combination with soil preferences. In this “nutrient-non-limited” environment seed production is copious in many dominant species which therefore rely on fresh seed for recruits. Klaaslouwbos also tends to retain its seed in capitula (“serotinous-mimicry”) for a short while perhaps until rain knocks them off - as is the case with succulent plants.

Variation in grassiness in renosterveld is comparable to fynbos in succession. Fynbos is characteristically dominated by many shrub species, giving it a colourful and varied textural appearance, which easily affords an idea of richness (or diversity) to the observer. A monotypically dominated shrubland like renosterveld with a uniform textural appearance does not appear as speciose to the untrained observer-which it is. Hence it is often not perceived as a vegetation type with a unique identity, similar in richness to fynbos but different in its coarse textural appearance. To wade “betwixt” the shrubbery is to acquaint oneself with its inherent richness. Disturbance by fire destroys above-ground vegetation structure and shrub-dominated “climax” state causing a relapse or rejuvenation into an initially graminoid-dominated state. The graminoid-dominated state is similar to the immediate post-fire succession in fynbos where therophytes, cryptophytes and hemicryptophytes take advantage of extra light and flower profusely. Cryptophyte richness is not diminished as post-fire succession advances (B. A. Walton, personal observation) similar to lowland fynbos (Hoffman et al. 1987), only flowering of certain species may decline like *Satyrium erectum*, (or increase for shade-tolerant species, like *Pterygodium catholicum* or *Sparaxis villosa*).

Evidence obtained here suggests that renosterveld vegetation is resilient (see Lavorel 1999) and able to “bounce back” into a structurally diverse state. This occurs after sufficient “resting” time by being set aside following an initial or recurring destruction by ploughing. It is a very different outcome from that following fire (or brush-cutting) as typically resprouting perennial geophytes, graminoids and shrubs have been destroyed, which usually form the vegetative bulk of post-fire regeneration. The initial colonizers following ploughing are often ruderal species if adjacent to agricultural fields, and wind dispersed species, indigenous or alien, able to grow on barren land.

Large fields take longer to be colonized and covered by plant species than small fields. Old fields adjacent to indigenous vegetation could become colonized in time as opposed to old fields distant or isolated from propagule sources. Some 30-year-old fields in this study were completely surrounded by unploughed vegetation, ensuring colonization which culminated in a state of dense shrubland vegetation. A different scenario would exist if old fields are isolated or inherently different habitats (adjacent to wetlands) as was found in other grassy 30-year-old fields-which have did not advance into a structurally diverse state. Renosterveld is resilient up to certain thresholds limited by propagule source material (and distance from source) and also grazing following ploughing.

There is a lack of shrub cover on some old fields at Elandsberg below Slangkop ridge, previously ploughed and assumed to be renosterveld in the past. Careful inspection of the surrounding vegetation and their ecology, aerial photographs and species present, has led me to infer that perhaps Alluvium Shale Fynbos was more prevalent at the site. Also vegetation of Slangkop ridge (another habitat) adds to local propagule sources. On the whole that site is seasonally inundated and contains many geophytic species which thrive in these conditions. Those fields which were part of alluvial rivulets and river terraces were unsuitable for agriculture and thus less of a liability as an addition to the reserve and thus set-aside. Surrounding these rivulets and wetlands are tall grasses and the shrub stratum tends to step back to some agreeable zone of moisture. Thus a closed canopy of shrubs in a wetland site is not likely to occur and is a possible explanation of the “slow” recovery on some old fields. In addition old fields occupied by territorial Bontebok or Eland are continuously grazed short and thus remain as old fields. This is evident at De Hoop Nature Reserve along a fence-line contrast of a short “lawn” versus the roadside verge with taller “lawn” grasses.

Life-forms under threat from ploughing, like nano-chamaephytes (succulents especially) and some cryptophytes, require manual reintroduction to areas for rehabilitation. Certain species thrive in disturbed conditions whilst others do not. Perennial grasses return to old fields generally, but might require a specific habitat subsequently transformed by ploughing. Rare or common species can equally be negatively affected by ploughing. Large or “bulky” geophytes like *Brunsvigia elandsmontana* and *Crossyne guttata* are rarely encountered on old fields. They have an effective wind dispersal mechanism able to be transported over long distances to rest in depressions or barriers (shrubs/fences). However they may require amenable habitat and moisture conditions in which to germinate and persist. Some species, by default, are marginal or have low population densities thus chance (a lottery effect, see Dewi and Chesson 2003) would play a major role in the composition of old fields whereby local species would be represented before distant (and suitable) species.

In terms of continuous grazing pressure one would assume only weedy geophytes, toxic or spinescent woody species are able to persist in mature vegetation and on old fields, as is the case in degraded renosterveld on slopes in the South Coast Renosterveld (B.A. Walton, personal observation). However simplicity is hardly a solution for a speciose and complex ecosystem. The spinescent *Aspalathus spinosa* is palatable and browsed intermittently and palatable shrubs such as *Hermannia scabra* and *Thesium funale* frequently occur on old fields (dispersed endo-zoochorously or by birds in the latter example).

4.4.4. Alien Species

Most alien species occurred on recently ploughed fields, following a pattern of a decrease in richness with an increase in resting period (see Meiners et al. 2002) - or a closing of "invasion windows" (see Myster and Pickett 1994) with a decrease in the rate of succession. However grazing intensity did not influence patterns of alien species richness. Vlok (1988) studied the alpha diversity of 1 m^2 relevés in lowland fynbos and renosterveld showing that with an increase in alien annual cover there was a corresponding decrease in indigenous annual and geophytic species richness. Similarly the indigenous annual cover and geophyte density declined. This may have an effect on old fields where alien annual cover is high, allowing only for tall geophytes to persist in 80% infested sites. Vlok (1988) mentioned that few annuals such as *Arctotheca calendula* and *Dimorphotheca pluvialis* persist under dense infestation, as observed here on 5-year-old fields, and rare and localized species may decline. Most alien species are therophytes here (75%) specifically annual forbs and grasses, and these colonizing species tolerate or prefer recently disturbed sites. Similarly in Australian rangelands the annual forb and grasses contribute between 67% and 77% of the alien flora (Grice 2004). This is a challenge for natural ecosystem management as alien species are continuously and inadvertently sown onto pastures (or purposely like *Lolium perenne*) or remnants of previous plantings or dispersed in livestock feed. Alien species are thus invading and re-invading old fields and unploughed renosterveld by endo-zoochorous dispersal (see Shiponeni 2003, Balsamo et al. 2004), or ecto-zoochorously.

The *Ursinio anthemoidis–Cynodontetum dactyli* Grassland Community is characterized by a high dominance of alien annual and ruderal species (see Chapter Three) which thrive on these recently disturbed sites. Their "naturalization" in the ecosystem should be tested for the possibility of displacing cryptophytes and indigenous annuals. I think competition would arise between alien forbs with a rosette growth form (like *Hypochaeris radicata*), and indigenous annuals and some geophytes; whereas erect annual grasses do not tend to smother other plants. I would not suggest spraying of poison to reduce their cover-abundance but rather allow for the shrub layer to reduce or displace them. In addition restriction of herbivore movement in certain camps may alleviate the spread of many of these alien taxa. However in some instances herbivory, especially shortly after flowering, may reduce seed production of *Echium plantagineum* (Patterson's curse) (Smyth et al. 1997). Alien annual grasses however may change the natural fire regime by increasing the fire frequency. Their dry biomass at the end of summer is particularly susceptible to being burnt in some instances. If burning occurs frequently this would remove the shrub component, as is the case with fire-breaks which resemble "grasslands" amongst fynbos.

A high grazing intensity following ploughing appeared to influence and increase alien species richness, relative to unploughed renosterveld at the same grazing intensity. In reality those old fields at the site with high grazing intensities are close to a source of alien phanerophytes (choking the nearby river) whilst the other sites are closer to agricultural fields (which are by practice constantly cleared of alien phanerophytes both manually and with poisons) or are completely surrounded by unploughed renosterveld.

Disturbances, including ploughing and grazing, have been shown to promote invasions of alien plant species in fynbos, succulent Karoo (Milton 2004) and Valley grasslands/chaparral (Keeley 1990, 1993, D'Antonio and Vitousek 1992). In other vegetation types herbivory has promoted alien herbaceous plants (see Hobbs and Huenneke 1992), as has prairie dog foraging (Larson 2003). Alien plants could also influence the direction (vector) of succession by altering the equilibrium state by type-conversion. This in turn could influence vegetation (forage) quality and animal behaviour whereby palatable mediterranean alien species such as: *Avena barbata*, *Briza maxima*, *Briza minor*, *Bromus pectinatus*, *Medicago sativa* and *Lolium perenne*, are grazed then dispersed on to old fields and in natural vegetation. Type conversion of perennial grasslands in western United States has occurred by alien annual forbs or grasses which now resemble old fields (see LeJeune and Seastedt 2001, Brown and Rice 2000). Also invasive bunchgrasses have led to a decrease in diversity of prairie or shrublands (see Heidinga and Wilson 2002, Lambrinos 2000).

Vegetation could be restored for, and facilitated by, indigenous small and large herbivore breeding programmes. In addition ecosystem restoration would improve biodiversity conservation and benefit land users by reducing erosion, increase soil moisture infiltration and retention, and increase floral and faunal ecotourism. Rural landscapes and old fields could be rehabilitated by an improved stock farming model further providing fodder and shelter for sheep, as is the desire of some land users. These varied management aims require diverse states of vegetation composition or minimum habitat quality conditions to achieve the desired goals. Biodiversity conservation requires that an ecosystem resembles and includes the high richness and diversity of indigenous plant taxa occurring at untransformed sites, thus retaining sufficient complexity and functionality, and ensuring the maintenance of evolutionary processes

In summary I conclude that, from evidence discovered in this study, ploughing destroys natural vegetation. Succession on old fields is retarded by grazing (even after old fields have been initially set-aside without grazers). The highly palatable or preferred species to selective grazers are initially consumed and virtually displaced. Species which remain are either largely unpalatable (or toxic) otherwise spinescent. Subsequently these species are also grazed for roughage (for example renosterbos). Thus the lawn grass sustains the large herbivore component, and even Eland graze it (B.A. Walton, personal observation). Old field are species depauperate nevertheless they fulfil an important function and platform for herbivore conservation. Some old fields do contain important or even rare species, as relicts from the untransformed vegetation and usually are particular to specific sites or micro-habitats. Structurally all old fields are similar but their component species differ and thus must be considered as an important part of area-wide or landscape conservation planning. I would add that to enable effective landscape restoration in an agricultural sea with scattered bejewelled islands ("life-boats") these old fields form the major contribution toward greenbelts connecting valuable fragments. Singularly small renosterveld fragments cannot sustain herbivores without compromising plant resilience, whereas old fields can.

4.5. References

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Chapter 5

Synthesis

Figure 5.1: *Aspalathus aculeata* Thunb. a lowland "special" (endemic and threatened) flowering at Krantzkop in October, with *Athanasia trifurcata* (L.) L. in bud in the foreground

5.1. Synthesis

Renosterveld, unlike fynbos often forms a monotypic stand of *Elytropappus rhinocerotis* (renosterbos) and sometimes it's open with a variety of shrub species (see Figure 5.1). It is this seemingly homogeneous matrix that conceals its true nature when observed during the summer months (although graminoids are flowering). However during the winter months the ground layer is rich in species and almost totally covered - this is where life-form richness or structural diversity occurs - whereas fynbos visually has a diverse structural composition in the top layer.

Since no model exists for succession of species on post-ploughed fields that were previously renosterveld, I have composed a conceptual model (Figure 5.2). Life-form composition in renosterveld was studied in four different states (seres) as described in Chapter Four, namely: 5-year-old fields; 15-year-old fields; 30-year-old fields and unploughed renosterveld (controls). Evidence of four states was obtained, however they were not available at all sites. Thus the first two seres lack empirical evidence of their structural composition at both a low and high grazing intensity. A range of factors ultimately determine the outcome of succession towards one or another stable or unstable state (see George et al. 1992). Notably exogenous factors can have more influence over determining state characteristics than endogenous factors like grazing (see Jackson and Bartolome (2002). However old fields are an unnatural phenomenon thus population dynamics come to the fore on recovering landscapes as found by Midoko-Iponga (2004) where *Cynodon dactylon* competition negatively affected both *Athanasia trifurcata* and *Relhania fruticosa* juvenile plants. When renosterveld vegetation is ploughed there is a crash in total species and life-form richness, which advances through different seral states to almost resemble that of unploughed vegetation. Conversely following ploughing there is an initial increase in alien species, and with seral development a reduction in alien species occurs. On 30-year-old fields the presence of grazers reduces the total amount of vegetation cover-abundance from 70% to 60% (without grazers).

In comparison to previous conceptual models of renosterveld vegetation dynamics my model does not attempt to explain vegetation patterns in relation to disturbance by fire (which is not the object of this study). Cowling et al. (1986) tentatively suggest that the season of burning coupled with grazing determines whether the renosterveld vegetation state is very grassy or not (Figure 5.3). This model suggests that non-grassy renosterveld when burnt in autumn (and grazed) turns into grassy renosterveld which in turn reverts to non-grassy renosterveld when burnt in spring (and grazed).

This model is uni-directional without suggesting the outcome of non-grassy renosterveld when burnt in spring or grassy renosterveld when burnt in autumn.

The conceptual model proposed by Rebelo (1995) includes burning again, and compares vegetation dynamics of grassland (grassveld) and thicket with renosterveld (Figure 5.4). These are vastly different habitats and one can assume that vegetation response to fire would differ amongst thicket vegetation and renosterveld or grasslands. This model suggests that if renosterveld is grazed then annuals and grasses flourish (by marginally reducing total cover-abundance as shown in my model). If this annual- and grass-dominated renosterveld is burnt the model suggests that this state will succeed into shrubby renosterveld. Empirical evidence is required to validate or refute these models.

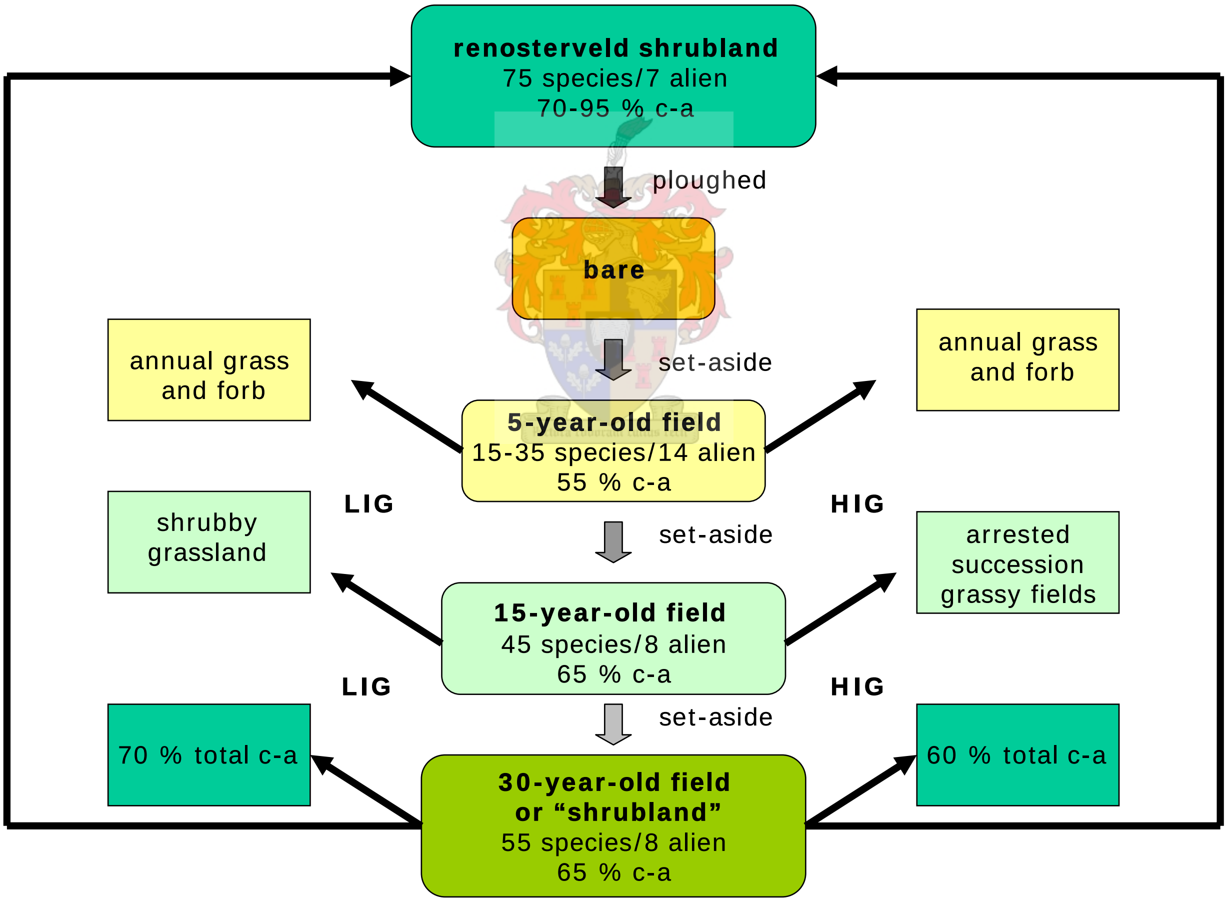

Figure 5.2: A conceptual dynamic model for renosterveld after initial ploughing then disturbance by grazing. LIG = Low Intensity Grazing and HIG = High Intensity Grazing, c-a = cover-abundance

Of further interest would be to ascertain the effects of over-burning of old fields (and renosterveld) and the influence it has on structural diversity.

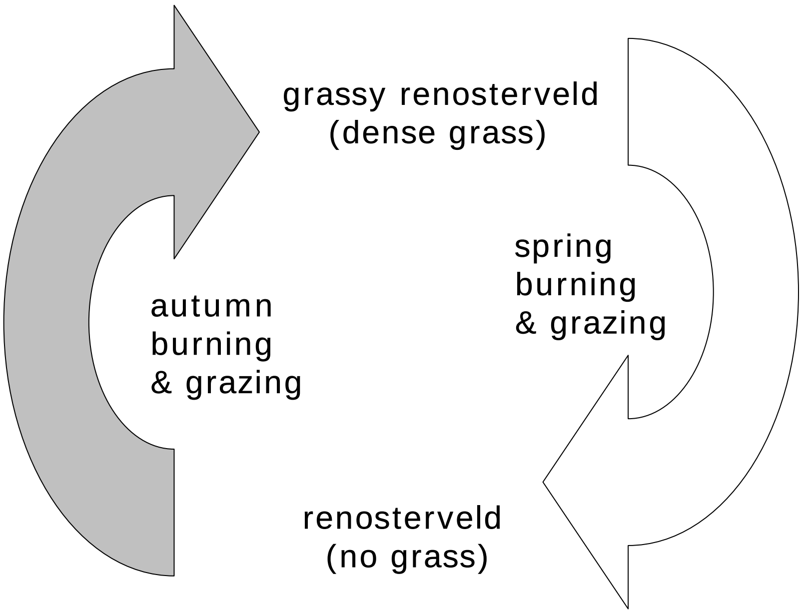

Figure 5.3: A conceptual dynamic model for renosterveld in relation to fire and grazing disturbances (Cowling et al. 1986)

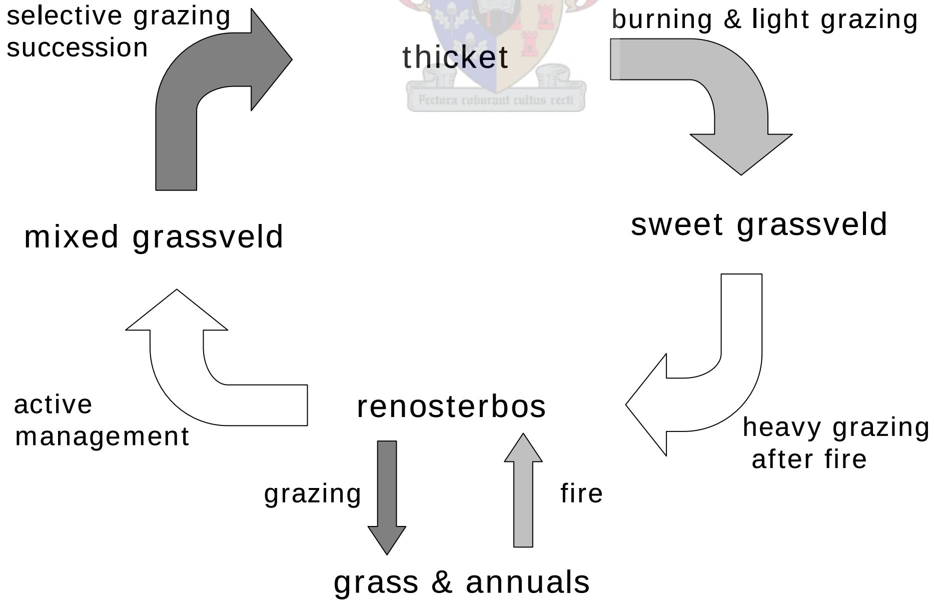

Figure 5.4: A conceptual dynamic model for renosterveld in relation to fire and grazing disturbances (Rebelo 1995)

5.2. Management Recommendations

A valuable knowledge of renosterveld vegetation structure and composition in the natural state is essential to management purposes. Identifying secondary states resulting from anthropogenic transformations and natural disturbances is the crux of the matter in ecosystem restoration or rehabilitation. Indicators of ecosystem health as a benchmark in formulating restorative activities are useful in applying the most effective approach. The local site conditions would be the major determinants of a potential advancement of succession towards any preferred or expected climax state - usually dominated by one or many shrub species.

Firstly it should be clearly defined as to what the preferred outcomes of restoration are, as this will determine which steps to pursue in reaching those goals. Rehabilitation implies a rectification of a degraded and eroded ecosystem or habitat towards an improved functioning ecosystem, usually where the threshold of remediation has surpassed restorative efforts. To subjectively distinguish between strictly natural ecosystem conservation stewardship and sustainable agricultural motives is warranted. The former would require that all biotic components are sustained with evolutionary patterns and processes maintained for evolutionary advancement. The latter would require efficient soil protection, water consumption, biomass production, carbon (or nitrogen or potassium) sequestration and sustainable yields. Thus biodiversity conservation allows for interacting processes to occur with measures to implement remedial tasks such as alien eradication. Farmers would benefit from natural vegetation on many levels. Natural vegetation has and is used as supplementary feed by sheep, goats and cattle, although necessitating constant assessment of stand quality. Trade-offs of maintaining natural stands to farmers are: erosion control, water cycling (and efficient removal of excessive salts), propagule sources, eco-tourism and are further complemented with initiation of formal conservation strategies.

Caution should be applied when introducing herbivores onto old fields as this is where a delayed succession may occur. It is rather noteworthy that the intensity of grazing does not specifically influence the increase in alien species richness; rather the presence of the indigenous herb layer determines the extent of invasion. Exotic alien annual pasture grasses and herbs on old fields are an artefact of agriculture and would seem they have been integrated into the indigenous vegetation since their arrival. Here large mammalian herbivores play two opposing roles by grazing alien annuals (thus decreasing competition with indigenous annuals and herbs) and further dispersing them in their dung. It is suspected that too frequent fires on old fields would actually facilitate the persistence and spread of exotic alien annual species, conversely decreasing the shrub component and increasing the fire frequency as is the case in Californian annual grasslands (Keeley 1990). Perhaps a fine balance of fire frequency and grazing would promote the arrival and persistence of the shrub component. A suggested appropriate ploughing regime to enable recovery of a complete renosterveld stand - if and when desired - would be a rotation of more than thirty years. This time period is obviously not convenient for land users wishing to plant annual crops, but has the advantage of reducing erosion and conserving plant species.

As my results suggest the life-forms most resilient to ploughing are: therophytes and hemicryptophytes. These are useful for a complete (or perhaps patchy) cover of fields and landscapes suitable for grazers alone. The chamaephyte life-form group returns to full cover and richness after some 30 years providing additional benefits for soil conservation and desalinization, also facilitating other life-forms to exist (lianellas and some delicate cryptophytes). Cryptophytes pose a different concern, perhaps not many are palatable but it is the most speciose life-form in renosterveld. Nano-chamaephytes are equally interesting containing many red data listed succulents, and an undescribed dwarf shrub called *Marasmodes* sp. nov. (Figure 5.5). These are often browsed but seem to require long periods of stability to return to old fields. One taxon *Lampranthus scaber* is quite unusual; it either sheds its leaves or even branches - as a cryptophytic trait (Hartmann 2002).

For management purposes a benchmark means to measure veld quality for grazers would be useful. This would imply using cover-abundance measurements of the grazing forage assemblage, either using relevés or line-intercept methods. Herein lays the key: the assemblage would have to be known by experts and the knowledge transferred to land users and managers.

Biogeographical and edaphic patterns of species composition in renosterveld differ from area to area, necessitating particular local management strategies: for example renosterveld stands in Hermon are densely dominated by renosterbos and klaaslouwbos; whilst those in Darling are dominated by *Otholobium hirtum* (rheebokbos), *Eriocephalus africanus* (kapokbos) and tall *Aspalathus* species. However, despite these site-specific local differences, the object of this project was to identify vegetation patterns of renosterveld at the Agter-Groeneberg Conservancy. Management of renosterveld needs to incorporate all disturbance factors including grazing effects, burning cycles, brush-cutting and ploughing history (with associated recovery period).

Figure 5.5: *Marasmodes* sp. nov (*pinnatifolia*) (lowland special-endemic and threatened) flowering at Elandsberg in May

This research into secondary succession on to old fields will aid in management of both pristine and set-aside land, and indicate patterns of recovery useful for restorative or rehabilitative vegetation projects.

Suggestions for the AGC:

Determine the actual veld conditions, namely; of grass species and palatable shrub composition and densities. Determine indicator-type grasses in terms of grazing quality or degraded veld to enable a rapid assessment of veld deterioration or improvement. Establish permanent plots for vegetation sampling and monitoring of dominant and rare species. Maintain large grazer/browser exclusion plots for long-term data capture on the effects of herbivory in renosterveld. Shrub damage (often uprooted) in mature veld adjacent to old fields is evident at Krantzkop and to some extent at Elandsberg - perhaps as a result of too much trampling by large herbivores and feral pig rooting. The opposite is true for Voëlvlei which lacks herbivores and the shrub stratum is very dense in places (especially the prickly unbrowsed *Aspalathus* species remaining dense, long after fire). Some mammalian herbivores like Eland could be introduced to Voëlvlei.

Combine efforts to tackle the feral pig problem of their excessive rooting of both common and rare geophytes (*Wachendorfia paniculata* was decimated in a small patch of renosterveld at Elandsberg Farms (Pty.) Ltd.; B. A. Walton personal observation). This problem occurs in many parts of the world and expert knowledge of feral pig eradication exists via the Global Invasive Species Programme. Krantzkop regularly maintains and repairs fencing damaged by feral pigs moving from site to site.

At Krantzkop strict management is required of all the areas outside the boundaries of the munitions factory and storage dump. Development of these areas should remain at an absolute minmum. Sensitive geophyte bed areas e.g. the firebreak flats recently had strips bulldozed (N to S) resulting in wider roads to upgrade the drainage to the sludge dams. This area is already transformed as it forms a protective firebreak (> 200 m wide) and thus doesn’t require excessive scouring of the surface to prevent possible spread of fire.

At Voëlvlei a land conservation management agreement with the boat club and other surrounding properties should be facilitated. Similarly the AGC must insist on an unplanted verge on the farmers’ side of the fence to reduce problematic plant invasions, like *Avena barbata* (wild oats) and

Echium plantagenium (Patterson's curse). Maligned animals like rooikat must not be allowed to be hunted in the reserve vicinity.

Alien plant threats are mostly in the therophyte/hemicryptophyte life-forms, namely annual grasses, forbs and some *Acacia* species or *Hakea* species (the latter having being consistently removed). Similarly stands and/or woodlots of *Eucalptus cladocalyx* have been removed recently at Elandsberg thus reducing their spread and visual effect. Alien plants and stands of *Eucalyptus* on Voëlvlei ridge should be removed and replaced with olives and other naturally occurring bush-clump species and trees (as a wind barrier).

Figure 5.6: From top left to right: *Drosera cistifolia* L., *Gladiolus watsonius* Thunb., *Gladiolus alatus* L., *Moraea tulbaghensis* L.Bolus; from bottom left to right: *Euryops thunbergii* B.Nord, *Monsonia speciosa* L., *Moraea villosa* (Ker Gawl.) Ker Gawl. subsp. *villosa*, *Lampranthus elegans* (Jacq.) Schwantes

Suggestions to conservation and farm managers

Good ecological databanks require meaningful data (see Linder 2005) with consistent or long term investment in data collection. Similarly it is important that the agricultural sector compiles farm records of stocking densities per camp including mortalities and births to allow for reliable census counts and growth rate calculations. Also a log book should be thoroughly compiled regarding time of ploughing, crops planted, in which camp, and how often planted or rested. This will enable a valuable account of the sites history which ultimately determines the strategy of restoration should it ever occur. A visitor logbook is of utmost importance to all. Research conducted on farms or in reserves should be official whereby both parties benefit and contracts negotiated ensuring the transfer of information, reports or theses. This is integral to future research incorporating an overview of previous research and an adequate site history.

A proposed management scenario for conservation of renosterveld is a full surveying of the vegetation, correctly identifying species (see Figure 5.6) and classification of samples to describe communities to understand the pattern variability. Managers require accurate plant and animal databases, underlain with mapped vegetation units in conjunction with scientific studies prior to pursuing management strategies and an attempt at applying gross benchmark rules.

Reserve managers need to maintain databases adequately whether printed or electronic material. It is the responsibility of the reserve to ensure that records are stored, updated and collated with related resources both old and new in spite of restructuring efforts and staff turnover. A key function is to also research all the relevant literature and store it on site and make sure that Afrikaans/English documents are translated and stored and not discarded. A booklet including all site information should be compiled in the interests of self reflection, community education and as a potential tourist guideline.

5.3. Future Research Topics

Opportunities for future research of renosterveld vegetation dynamics in relation to disturbance are identified.

1. Determine seedling establishment following fire by species as well as by Plant Functional Type.
2. Quantify the effects of trampling and herbivory (buck, porcupine, aardvark and rodent) on seedling establishment and survival. Do factors such as nutrient deposition (heuweltjies, wallows or diggings) and gap creation (micro-scale disturbances) promote certain guilds?

3. Quantify the response of organisms to fire, where spiders, grasshoppers would positively respond to post-burnt areas, as do large and small mammalian herbivores.
4. Initiate phenological/physiological studies of key species to assess their nutrient-root-shoot interactions.
5. Monitor the impacts of grazing on renosterveld vegetation. A comparison could be made between domestic versus indigenous fauna transformed versus untransformed vegetation.
6. Investigate nutrient cycling of the pedoderm-related organisms. Develop an understanding of the importance of the moss and lichen flora in nutrient cycling.
7. What is the effect of shading by shrubs on geophytes, herbs and dwarf shrubs and the role shrubs play as support for lianellas and delicate geophyte inflorescences?

5.4. References

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Appendices

Appendix 1: A chronological account of the history of Elandsberg Farms (Pty.) Ltd. From Becker (1996)

Before 1705	Freehold land
1705	Bartholomeusklip granted to Franz Joosten van der Lubstadt (Dutch settler)
	Named in commemoration of the St. Bartholomeus' Day massacre of Hugenots in France 1572
1853	Transferred to Daniel Johannes Booysens
1876	Transferred to Barend Gerhardus du Plessis
1890	Transferred to Pieter Eduard Hauman Hamman
1895	Transferred to Sir JH de Villiers (bought Bosplaats)
1924	Transferred to Charles Percy de Villiers
1936	Transferred to Reginald Heinrich Parker (Bartholomeuwsklip, Bosplaats & Elandskloof)
1963	Dale Parker expands agriculture, fencing of veld into livestock camps, planting of exotic trees for shade (*Eucalyptus cladocalyx*, *Pinus* sp.)
1966	Elandsberg Farms (Pty) Ltd. established
1967	Eskom announces construction of powerline across farm
1971	Purchase of portion of Langhoogte agricultural land
1973	*Protea mucronifolia* rediscovered, geometric tortoise found
	Elandsberg Private Nature Reserve (2600 ha.) declared
1974	First springbuck introduced
1974 - 1981	Eland, blue wildebeest, black wildebeest, Hartmann's zebra, red hartebeest, and gemsbok introduced
1977	Armscor attempted expropriation of entire property
1978	Natural veld to south of property purchased
1979	More agricultural land bought
1981	500 ha of natural veld to south forcibly expropriated by Armscor
	Bontebok herd released
1982	Fire sweeps through entire reserve
1983	Reserve enlarged to 3003 ha
1988	Elandsberg PNR declared a Natural Heritage Site, fire sweeps through (entire) reserve, reserve enlarged to 3400 ha
1989	Consolidation of Langhoogte farm, further arable land
1992	Reserve enlarged to 3603 ha
1993	"Quagga's" released into EPNR
1996	Reserve 3603 ha, 2256 ha. wheat, oats and feed crops, 5000 merino sheep, 70 cattle, 20 milking cows
1999	Fire in Reserve
2002	Reserve enlarged to 3800 ha, milking cows sold, blue wildebeest sold
2004	2004/11/16 EPNR formally a member of the Agter-Groeneberg Conservancy

Appendix 2: Relevé disturbance history obtained from aerial photographs in ArcMap 8; E = Elandsberg, K= Krantzkop, V= Voëlvlei sites

Relevé	Sere	Aerial photo 1938	Aerial photo 1949	Aerial photo 1967	Aerial photo 1973	Aerial photo 1987	Aerial photo 1997	Last disturbance (type)	date	History
E1	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt & grazed
E2	2	untouched	untouched	untouched	ploughed	ploughed	ignored	ploughed	1982	Burnt & grazed
E3	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1999	Burnt & grazed
E4	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt & grazed
E5	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt & Grazed
E6	3	untouched	untouched	ploughed	ploughed	ignored	ignored	Burnt	1982	Burnt & Grazed
E7	3	untouched	untouched	ploughed	ploughed	ignored	ignored	Burnt	1982	Burnt & Grazed
E8	3	untouched	untouched	ploughed	ploughed	ignored	ignored	Burnt	1982	Burnt & Grazed
E9	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt & Grazed
E10	3	untouched	untouched	ploughed	ploughed	ignored	ignored	Burnt	1982	Burnt & Grazed
E11	2	untouched	untouched	untouched	ploughed	ploughed	ignored	Ploughed	1987	Ploughed & Grazed
E12	2	untouched	untouched	ploughed	ploughed	ploughed	ignored	Ploughed	1987	Ploughed & Grazed
E13	2	untouched	untouched	ploughed	ploughed	ploughed	ignored	Ploughed	1987	Ploughed & Grazed
E14	1	ploughed	ploughed	ploughed	ploughed	ploughed	ploughed	Ploughed	1997	Ploughed
E15	2	untouched	untouched	ploughed	ploughed	Ploughed?	ignored	Ploughed	1987	Ploughed & Grazed
E16	1	ploughed	ignored	ploughed	ignored	Ploughed?	ignored	Ploughed	1997	Ploughed
E17	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt & Grazed
E18	1	untouched	ploughed	no waypoint	no waypoint	no waypoint	no waypoint	Ploughed	1997	Ploughed
E19	2	untouched	untouched	ploughed	ploughed	ploughed	ignored	Ploughed	1987	Ploughed & Grazed
E20	2	untouched	untouched	untouched	ploughed	ploughed	ignored	Ploughed	1987	Ploughed & Grazed
E21	4	untouched	untouched	untouched	Untouched	untouched	untouched	Burnt	1982	Burnt & Grazed
K1	3	off image	untouched	ploughed	Off image	ploughed	ignored	Ploughed	1970	Ploughed
K2	4	off image	untouched	untouched	Off image	untouched	untouched	Burnt	1982	Burnt & Grazed
K3	3	off image	ploughed	ploughed	Off image	ploughed	ignored	Burnt	1988	Burnt & Grazed
K4	3	off image	ploughed	ploughed	Off image	ploughed	ignored	Burnt	1988	Burnt & Grazed
K5	3	off image	on edge	Off image	Off image	ploughed	ignored	Burnt	1988	Burnt & Grazed
K6	3	off image	untouched	Untouched?	Off image	ploughed	ignored	Burnt	1988	Burnt & Grazed
K7	4	off image	untouched	Burnt?	Off image	ignored	ignored	Burnt	1988	Burnt & Grazed
K8	3	off image	untouched	ploughed	Off image	ploughed	ignored	Burnt	1982	Ploughed
K9	3	off image	ploughed	ploughed	Off image	ploughed	Off image	Burnt	1982	Ploughed
K10	3	off image	untouched	ploughed	Off image	ploughed	ignored	Burnt	1982	Ploughed
K11	4	off image	untouched	untouched	Off image	untouched	untouched	Burnt	1982	Burnt & Grazed

Relevé	Sere	Aerial photo 1938	Aerial photo 1949	Aerial photo 1967	Aerial photo 1973	Aerial photo 1987	Aerial photo 1997	Last disturbance (type)	date	History
V1	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt		Burnt
V2	4	ploughed?	untouched	untouched	untouched	untouched	untouched	Burnt		Burnt
V3	3	untouched	untouched	untouched	Dam roadworks	ignored	ignored	Burnt		Burnt
V4	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt
V5	3	ploughed	ignored	Dam works	Dam works	ignored	ignored	Burnt	1999	Dam works
V6	4	untouched	untouched?	untouched	untouched	untouched	untouched	Burnt	1999	Burnt
V7	3	ploughed	ignored	untouched	Dam roadworks	ignored	ignored	Burnt	1999	Burnt
V8	3	ploughed	ignored?	untouched	Untouched	untouched	untouched	Burnt	1988	Burnt
V9	3	ploughed?	ignored	Dam works	Dam works	ignored	ignored	Burnt	1999	Burnt
V10	4	untouched	untouched	untouched	untouched	untouched	untouched	Burnt	1982	Burnt
V11	4	untouched	off image	untouched	untouched	untouched	untouched	Burnt	1999	Burnt
V12	3	ploughed	off image	ignored	ignored	ignored	ignored	Burnt	1982	Burnt

Appendix 3.1: An example of a floristic data sheet used for all quadrat scales in the 1000 m^2 relevés. Note cover-abundance data recorded only at the 1 m^2 and 10 m^2 scales

Date: 2002/07/05 Floristic Data Sheet Relevé: E9a

Name: Benjamin A Walton Plot size: 1 m^2

Species	ht (cm)	Lf	BB	Species/notes	ht (cm)	Lf	BB
Elytropappus rhinocerotis	65	5	3	trunk 15cm wide			
Tribolium hispidum	25	3	2a	8 cm grazed height			
Mohria caffrorum	13	3	1				
Androcymbium capense	5	2	1				
Oxalis pes-caprae	8	2	1				
Indigofera nitida	15	4	1	synonym of I. psoraleoides			
Cyanella lutea	6	2	1	Leaves look like moederkappie!			
Ornithogalum thyrsoides	3	2	2m				
Oxalis glabra	6	2	plus				
Moraea lewisiae	25	2	plus				
Felicia bergerana	1	1	1	hairy seedlings, dew at 1pm			
Briza maxima	8	1	2m	alien			
Oxalis purpurea	1	2	1				
Torilis arvensis	2	1	r	seedling			

Braun-Blanquet cover-abundance scale (BB):

r = 1 individual, + = <1% very low cover
1 = numerous, <1% cover or
= less abundant, >1% to 5% cover
2m = very numerous, <5% cover
2a = >5% to 12% cover
2b = >12% to 25% cover
3 = >25% to 50% cover
4 = > 50% to 75% cover
5 = >75% to 100%cover

Raunkiaer life-form code (Lf):

1 = therophyte
2 = cryptophyte
3 = hemicryptophyte
4 = nano-chamaephyte
5 = chamaephyte
6 = phanerophyte
7 = lianella
8 = parasite
moss and lichen not sampled

Notes: Lots of fruiting mosses (35% cover) and abundance of ferns, also lots of lichen towards ridge top. Heard Fish Eagle call twice today, Ostrich nearby.

Appendix 3.2: Relevé (1000 m^2) with nested quadrat codes and life-form codes

relevé code	V 1	Voëlvlei relevé 1
	E 1	Elandsberg relevé 1
	K 1	Krantzkop relevé 1
quadrat codes	a to l	1 m^2
	A & B	2 by 5 = 10 m^2
	AA & BB	10 by 10 = 100 m^2
	AAA & BBB	20 by 25 = 500 m^2
	C	20 by 50 = 1000 m^2
Raunkiaer life-form (modified-this study)	1	therophyte (annuals)
	2	cryptophyte (geophytes)
	3	hemicryptophyte (graminoids and rosette perennials)
	4	nano-chamaephyte (dwarf shrubs and succulents)
	5	chamaephyte (shrubs)
	6	phanerophyte (trees)
	7	lianellas (climbers)
	8	parasite (including hemi-parasites)

Appendix 3.3: Habitat data recorded at the 1000 m^2 relevé scale

drainage	0	never inundated
	1	seasonally inundated
	2	permanently waterlogged
	3	standing water
relevé total cover	%	shrub cover
	%	herb cover
	%	graminoid layer
rock cover (presence/%)	1	0.002 to 0.04 m
	2	0.05 to 0.2 m
	3	0.25 to 0.5 m
	4	0.5 m.
soil texture code	1	sand
	2	loam
	3	clay
geology code	1	sandstone
	2	granite
	3	shale
fire-age code	0	burned 30-39 years ago
	1	burned 20-29 years ago
	2	burned 10-19 years ago
	3	burned 5-9 years ago
	4	burned < 5 years ago
seral code	1	5-year-old field
	2	15-year-old field
	3	30-year-old field
	4	unploughed renosterveld

Appendix 3.4: North-Eastern corner relevé coordinates in decimal degrees (Datum WP, configuration WGS84); E = Elandsberg, K = Krantzkop and V = Voëlvlei, (* relevé E021 is a duplicate of relevé E001)

Relevé	decimal degrees South	decimal degrees East	Date
E002	-33.44415282	19.03009585	2001/09/27
E003	-33.44238809	19.02867445	2001/09/28
E004	-33.42779671	19.02677	2001/10/12
E005	-33.43385305	19.03821222	2001/10/30
E006	-33.43671807	19.0466719	2002/07/01
E007	-33.43888002	19.0469133	2002/07/02
E008	-33.42328557	19.04584059	2002/07/04
E009	-33.4238972	19.04544362	2002/07/06
E010	-33.42318893	19.04835641	2002/07/08
E011	-33.44947474	19.03360418	2002/07/17
E012	-33.41565753	19.02931809	2002/07/18
E013	-33.42742698	19.02633556	2002/08/10
E014	-33.41431081	19.0143942	2002/08/24
E015	-33.41754028	19.01790806	2002/08/24
E016	-33.41005691	19.00995246	2002/08/25
E017	-33.43769272	19.05012667	2002/09/08
E019	-33.42623441	19.02259111	2002/09/15
E020	-33.44396004	19.03010666	2003/09/15
E021/E001*	-33.44382056	19.03061628	2003/09/16
K001	-33.50806475	19.04800253	2002/08/17
K002	-33.50598889	19.03196275	2002/08/18
K003	-33.50259145	19.07254457	2002/09/28
K004	-33.50165276	19.07139667	2002/10/12
K005	-33.50509135	19.07838115	2002/10/13
K006	-33.50916831	19.05462197	2002/10/13
K007	-33.51020364	19.05386559	2002/10/16
K008	-33.5081489	19.04425808	2002/10/19
K009	-33.51697337	19.03027833	2002/10/19
K010	-33.50933444	19.0421497	2002/10/20
K011	-33.50685247	19.04810429	2003/10/04
V001	-33.40191331	19.02712941	2001/09/16
V002	-33.39746637	19.02855115	2001/09/17
V003	-33.39650053	19.02457586	2001/11/01
V004	-33.40362498	19.02706504	2002/07/20
V005	-33.37947445	19.02813247	2002/08/03
V006	-33.38300415	19.03128692	2002/08/04
V007	-33.39213816	19.02795553	2002/09/09
V008	-33.39764206	19.03500438	2002/09/10
V009	-33.37784736	19.02851343	2002/09/11
V010	-33.39457361	19.02137876	2002/09/12
V011	-33.3703049	19.02143776	2002/09/29
V012	-33.37095944	19.01484489	2002/09/30

Appendix 3.5: Braun-Blanquet cover-abundance refined scale (Barkman et al. 1964) recorded at the 10 m^2 quadrat scale

refined Braun-Blanquet cover-abundance scale	r	single individual
	+	<1% cover/ low cover
	1 (less abundant)	>1% to 5% cover
	2 m	very numerous, <5% cover
	2 a	>5% to 12.5% cover
	2 b	>12.5% to 25% cover
	3	>25% to 50% cover
	4	>50% to 75% cover
	5	>75% to 100% cover

Appendix 3.6: List of infrequently occurring species (once or twice) omitted from the structured relevé table (Tab. 3.6) with; name, relevé code and cover-abundance value (in brackets)

Diascia parviflora Benth (2, 2), *Polygonum aviculare* L. (3, 1), *Oxalis flava* L. (4, 2), *Romulea cruciata* (Jacq.) Baker (6, 1), *Plantago coronopus* L. (6, 3), *Galenia ecklonis* Walp. (7, 1; 63, 2), *Romulea rosea* (L.) Eckl. (8, 1), *Disperis villosa* (L.f.) Sw. (9, 1), *Ornithogalum suaveolens* Jacq. (10, 2), *Manulea pusilla* E.Mey. ex Benth. (13, 5), *Babiana ambigua* (Roem. & Schult.) G.J.Lewis (13, 5), *Micranthus alopecuroides* (L.) Rothm. (14, 8), *Drosera trinervia* (15, 2), *Stoebe plumosa* (L.) Thunb. (15, 1), *Tribolium echinatum* (Thunb.) Renvoize (20, 7; 64, 8), *Gorteria personata* L. (20, 5; 64, 3), *Convolvulus capensis* Burm.f. (20, 5), *Ehrharta capensis* Thunb. (20, 1; 54, 7), *Polycarpon tetraphyllum* L.f. (21, 2), *Lobostemon fruticosus* (L.) H.Buek (23, 6; 66, 2), *Anagallis arvensis* L. (23, 1; 43, 1) *Senecio paniculatus* P.J.Bergius (23, 1), *Crassula umbellata* Thunb. (24, 2), *Rumex cordatus* Poir. (25, 5), *Melinis repens* (Willd.) Zizka (25, 3), *Phalaris minor* Retz. (27, 3; 50, 2), *Vicia sativa* L. (29, 3), *Hyparrhenia hirta* (L.) Stapf (31, 5), *Trachyandra muricata* (L.f.) Kunth (31, 3), *Vellereophyton dealbatum* (Thunb.) Hilliard & B.L.Burtt (31, 1), *Emex australis* Steinh. (32, 1), *Muraltia heisteria* (L.) DC. (32, 3; 71, 3), *Felicia tenella* (L.) Nees (35, 6; 41, 6), *Gastridium phleoides* (Nees & Meyen) C.E.Hubb. (37, 2; 47, 2), *Satyrium erectum* Sw. (49, 2; 50, 2), *Otholobium uncinatum* (Eckl. & Zeyh.) C.H.Stirt. (49, 1; 51, 3), *Muraltia ericaefolia* DC. (51, 1; 52, 6), *Sutera uncinata* (Desr.) Hilliard (53, 3; 57, 1), *Baeometra uniflora* (Jacq.) G.J.Lewis (53, 2; 56, 1), *Helichrysum teretifolium* (L.) D.Don (53, 2; 54, 2), *Pelargonium pinnatum* (L.) L'Hér. (53, 2, 54, 2), *Senecio pubigerus* L. (64, 3; 68, 3), *Lampranthus* sp. (65, 2; 66, 2), *Selago fruticosa* L. (67, 3; 68, 5), *Heliophila pusilla* L.f. var. *macrosperma* Marais (69, 4; 70, 3), *Pelargonium lobatum* (Burm.f.) L'Hér. (69, 3; 70, 2), *Lachenalia orchioides* (L.) Aiton (69, 2; 70, 1), *Trachyandra* sp. (69, 1; 70, 2), *Lampranthus aduncus* (Haw.) N.E.Br. (70, 1; 71, 3), *Felicia bergerana* (Spreng.) O.Hoffm. (71, 3; 72, 2), *Agathosma serpyllacea* Licht. ex Roem. & Schult. (71, 2; 72, 1), *Aizoon paniculatum* L. (59, 1; 66, 1), *Dorotheanthus bellidiformis* (Burm.f.) N.E.Br. (36, 1), *Muraltia trinervia* (L.f.) DC. (38, 1), *Moraea fugacissima* (L.f.) Goldblatt (39, 1), *Brachypodium distachyon* (L.) P.Beauv. (40, 2), *Galenia africana* L. (41, 5), *Drosanthemum salicola* L.Bolus (41, 5), *Aspalathus aculeata* Thunb. (42, 6), *Microcodon glomeratum* A.DC. (43, 1), *Cotula bipinnata* Thunb. (47, 5), *Poa annua* L. (47, 3), *Nemesia barbata* (Thunb.) Benth. (47, 1), *Sonchus oleraceus* L. (49, 2), *Phylica ericoides* L. (52, 1), *Euclea acutifolia* E.Mey. ex A.DC. (53, 7), *Torilis arvensis* (Huds.) Link (53, 3), *Rhus rosmarinifolia* Vahl (54, 3), *Merxmuellera stricta* (Schrad.) Conert (54, 3), *Phylica plumosa* L. var. *horizontalis* (Vent.) Sond. (57, 1), *Festuca scabra* Vahl (58, 3), *Aspalathus ericifolia* L. (59, 1), *Spiloxene flaccida* (Nel) Garside (59, 2), *Cotula coronopifolia* L. (59, 2), *Hermannia cuneifolia* Jacq. (60, 3), *Erepsia patula* (Haw.) Schwantes (60, 3), *Helichrysum patulum* (L.) D.Don (60, 3), *Drosera alba* E.Phillips (61, 3), *Erica inaequalis* (Klotzch) E.G.H.Oliv. (62, 2), *Geissorhiza imbricata* (D.Delaroche) Ker Gawl. (62, 2), *Stoebe fusca* (L.) Thunb. (64, 1), *Oxalis monophylla* L. (66, 3), *Hesperantha radiata* (Jacq.) Ker Gawl. (66, 2), *Montinia caryophyllacea* Thunb. (67, 2), *Aspalathus perforata* (Thunb.) R.Dahlgren (67, 2), Anginon difforme (L.) B.L.Burtt (67, 2), *Sebaea exacoides* (L.) Schinz (68, 1), *Cullumia ciliaris* (L.) R.Br. (69, 3), *Thesium* sp. (69, 3), *Cymbopogon marginatus* (Steud.) Stapf ex Burtt Davy (69, 3), *Tetragonia portulacoides* Fenzl (69, 3), *Moraea umbellata* Thunb. (69, 2), *Senecio arenarius* Thunb. (69, 3), *Bulbine* sp. (69, 1), *Antimima* sp. (70, 3), *Arctotis incisa* Thunb. (70, 5), *Monsonia speciosa* L. (70, 2), *Drosera pauciflora* Banks ex DC. (70, 2), *Gladiolus alatus* L. (70, 1), *Onixotis punctata* (L.) Mabb. (70, 1), *Lachenalia longibracteata* E. Phillips (70, 1), *Polycarena gilioides* Benth. (70, 2), *Crassula dichotoma* L. (70, 2), *Metalasia dregeana* DC. (71, 3), *Gnidia laxa* (L.f.) Gilg (71, 2), *Corymbium africanum* L. (71, 3), *Microcodon* sp. (71, 3), *Trachyandra paniculata* Oberm. (71, 3), *Othonna heterophylla* L.f. (71, 2), *Cyphia bulbosa* (L.) P.J. Bergius (71, 2), *Lachenalia polyphylla* Baker (71, 2), *Oxalis versicolor* L. (71, 2), *Ornithogalum* sp. (71, 2), *Cliffortia ruscifolia* L. (72, 3), *Cliffortia juniperina* L.f. (72, 2), *Zygophyllum sessilifolium* L. (72, 2), *Brunsvigia* sp. (72, 3), *Berkheya herbacea* (L.f.) Druce (72, 3), *Nemesia versicolor* E.Mey. ex Benth. (72, 2), *Diospyros glabra* (L.) De Winter. (72, 1).

Appendix 4.1: Total species and life-form richness of 42 relevés (1000 m^2): 1 = therophyte (92), 2 = cryptophyte (136), 3 = hemicryptophyte (59), 4 = nano-chamaephyte (47), 5 = chamaephyte (67), 6 = phanerophyte (5), 7 = lianella (3) and 8 = parasite (4); E = Elandsberg, V = Voëlvlei and K = Krantzkop

Relevé	Sere	Grazing	Fire-age	Species	1	2	3	4	5	6	7	8
E1	4	2	1	74	15	35	8	6	8	0	1	1
E3	4	2	4	104	29	37	18	7	11	0	1	1
V1	4	1	1	51	15	18	5	1	11	0	1	0
V2	4	1	1	64	24	18	6	7	8	0	1	0
E4	4	2	1	121	21	47	22	15	12	0	2	2
E5	4	2	1	62	13	17	19	5	8	0	0	0
E9	4	2	1	65	10	19	9	5	21	0	1	0
V4	4	1	1	56	8	21	8	4	14	0	1	0
V6	4	1	4	44	4	14	6	5	10	3	1	1
K2	4	3	1	122	26	42	21	13	15	0	2	3
E17	4	2	1	111	17	32	23	14	23	0	2	0
V8	4	1	2	71	19	17	9	10	14	0	1	1
V10	4	1	1	56	16	18	5	5	10	0	1	1
V11	4	1	4	63	28	12	6	6	9	0	1	1
K7	4	3	2	69	21	12	13	6	14	0	1	2
E21	4	2	1	73	13	31	16	5	7	0	0	1
K11	4	3	1	80	7	29	13	8	21	1	0	1
V3	3	1	1	42	11	11	6	5	7	0	1	1
E6	3	2	1	69	8	24	14	9	13	0	0	1
E7	3	2	1	55	11	15	8	5	14	0	1	1
E8	3	2	1	68	7	24	10	9	16	0	1	1
E10	3	2	1	87	11	30	12	15	18	0	1	0
V5	3	1	4	58	15	16	12	7	8	0	0	0
K1	3	3	1	69	8	27	10	6	14	1	1	2
V7	3	1	4	61	20	18	8	6	8	0	1	0
V9	3	1	4	57	26	10	8	5	8	0	0	0
K3	3	3	2	63	24	14	11	2	10	1	0	1
V12	3	1	1	33	18	8	3	0	3	0	0	1
K4	3	3	2	51	15	5	13	3	12	2	0	1
K5	3	3	2	38	18	3	10	2	3	1	0	1
K6	3	3	2	43	14	6	11	4	7	0	0	1
K8	3	3	1	51	15	13	11	2	9	0	0	1
K9	3	3	1	32	10	10	7	3	2	0	0	0
K10	3	3	1	59	15	11	13	7	12	0	0	1
E2	2	2	1	61	24	14	10	5	7	0	0	1
E11	2	2	1	35	8	8	7	4	7	0	0	1
E12	2	2	1	48	13	17	12	2	4	0	0	0
E13	2	2	1	54	16	24	9	2	3	0	0	0
E15	2	2	1	53	12	27	7	2	5	0	0	0
E19	2	2	1	49	23	20	6	0	0	0	0	0
E20	2	2	1	54	14	18	11	3	7	0	0	1
E14	1	2	1	26	16	2	5	2	1	0	0	0
E16	1	2	1	45	21	17	6	1	0	0	0	0
E18	1	2	1	39	20	11	7	1	0	0	0	0

Appendix 4.2: Species list for 42 relevés (total of 411 species). Life-forms (Lf) are: 1 = therophyte (92), 2 = cryptophyte (136), 3 = hemicryptophyte (59), 4 = nano-chamaephyte (47), 5 = chamaephyte (67), 6 = phanerophyte (5), 7 = lianella (3) and 8 = parasite (4); and site E = Elandsberg, V = Voëlvlei and K = Krantzkop. X = Alien; * asterisk denotes taxa with a name change from Goldblatt et al. (2005)

Species 411	Lf	alien
Acacia mearnsii De Wild.	6	X
Acacia saligna (Labill.) H.L.Wendl.	6	X
Adenogramma lichtensteiniana (Schult.) Druce	1	
Agathosma serpyllacea Licht. ex Roem. & Schult.	5	
Aira cupaniana Guss.	1	X
Aizoon paniculatum L.	4	
Albuca cooperi Baker	2	
Albuca juncifolia Baker	2	
Albuca sp.	2	
Anagallis arvensis L.	1	X
Androcymbium capense (L.) K.Krause	2	
Anginon difforme (L.) B.L.Burtt	3	
Anthospermum galioides Rchb.f.	5	
Anthospermum sp.	5	
Anthospermum spathulatum Spreng.	5	
Antimima sp.	4	
Arctopus echinatus L.	2	
Arctotheca calendula (L.) Levyns	1	
Arctotis acaulis L.	3	
Arctotis incisa Thunb.	3	
Arctotis sp.	3	
Aristea africana (L.) Hoffmanns.	2	
Aristida junciformis Trin. & Rupr.	3	
Aspalathus aculeata Thunb.	5	
Aspalathus acuminata Lam.	5	
Aspalathus attenuata R.Dahlgren	4	
Aspalathus cephalotes Thunb.	5	
Aspalathus ciliaris L.	5	
Aspalathus ericifolia L.	4	
Aspalathus hispida Thunb.	5	
Aspalathus perforata (Thunb.) R.Dahlgren	4	
Aspalathus sp.	5	
Aspalathus spicata Thunb.	5	
Aspalathus spinosa L.	5	
Aspalathus tridentata L.	5	
Asparagus capensis L. var. capensis	5	
Asparagus sp.	5	
Athanasia trifurcata (L.) L.	5	
Atriplex lindleyi Moq.	1	X
Avena barbata Pott ex Link	1	X
Babiana ambigua (Roem. & Schult.) G.J.Lewis	2	
Babiana angustifolia Sweet	2	
Babiana odorata L.Bolus	2	
Babiana secunda (Thunb.) Ker Gawl.	2	
Babiana sp.	2	

Species 411	Lf	alien
Baeometra uniflora (Jacq.) G.J.Lewis	2	
Berkheya armata (Vahl) Druce	3	
Berkheya herbacea (L.f.) Druce	3	
Berkheya rigida (Thunb.) Bolus & Wolley-Dod ex Adamson & T.M.Salter	5	
Brachypodium distachyon (L.) P.Beauv.	1	X
Briza maxima L.	1	X
Briza minor L.	1	X
Bromus mollis molliformis	1	X
Bromus pectinatus Thunb.	1	X
Bromus rigidus Roth	1	X
Brunsvigia sp.	2	
Bulbine praemorsa (Jacq.) Roem. & Schult.	2	
Bulbine sp.	2	
Bulbinella triquetra (L.f.) Kunth	2	
Carpanthea pomeridiana (L.) N.E.Br.	1	
Cassytha ciliolata Nees	7	
Centella sp.	3	
Cerastium capense Sond.	1	
Chlorophytum undulatum (Jacq.) Oberm.	2	
Chrysocoma ciliata L.	5	
Citrus sinensis (L.) Osbeck	6	X
Cliffortia juniperina L.f.	5	
Cliffortia ruscifolia L.	5	
Convolvulus capensis Burm.f.	7	
Corycium orobanchoides (L.f.) Sw.	2	
Corymbium africanum L.	3	
Cotula bipinnata Thunb.	1	
Cotula coronopifolia L.	1	
Cotula turbinata L.	1	
Crassula bergioides Harv.	1	
Crassula cf. scabra	4	
Crassula dichotoma L.	1	
Crassula glomerata P.J.Bergius	1	
Crassula natans Thunb.	1	
Crassula subulata L. var. subulata	4	
Crassula umbellata Thunb.	1	
Crossyne guttata (L.) D.Mnll.-Doblies & U.Müll.-Doblies	2	
Cullumia ciliaris (L.) R.Br.	5	
Cuscuta nitida E.Mey. ex Choisy	8	
Cyanella hyacinthoides L.	2	
Cyanella lutea L.f.	2	
Cymbopogon marginatus (Steud.) Stapf ex Burtt Davy	3	
Cynodon dactylon (L.) Pers.	3	
Cyperus esculentus L.	2	X
Cyphia bulbosa (L.) P.J.Bergius	2	
Cyphia incisa (Thunb.) Willd.	2	
Cyphia phyteuma (L.) Willd.	2	
Cyphia volubilis (Burm.f.) Willd.	7	
Diascia elongata Benth.	1	
Diascia parviflora Benth.	1	
Dimorphotheca pluvialis (L.) Moench	1	

Species 411	Lf	alien
Diosma pedicellata I.Williams	5	
Diospyros glabra (L.) De Winter	5	
Dipcadi brevifolium (Thunb.) Fourc.	2	
Disa bracteata Sw.	2	
Dischisma capitatum (Thunb.) Choisy	1	
Disperis villosa (L.f.) Sw.	2	
Dorotheanthus bellidiformis (Burm.f.) N.E.Br.	1	
Drimia exuviata (Jacq.) Jessop	2	
Drimia physodes (Jacq.) Jessop	2	
Drimia sp.	2	
Drosanthemum salicola L.Bolus	4	
Drosera alba E.Phillips	2	
Drosera cistiflora L.	2	
Drosera pauciflora Banks ex DC.	2	
Drosera sp.	2	
Drosera trinervia Spreng.	2	
Echiostachys incanus (Thunb.) Levyns	3	
Echium plantagineum L.	3	X
Ehrharta calycina Sm.	3	
Ehrharta capensis Thunb.	3	
Ehrharta longifolia Schrad.	3	
Elegia filacea Mast.	3	
Elegia sp.	3	
Eleocharis limosa (Schrad.) Schult.	3	
Elytropappus rhinocerotis (L.f.) Less.	5	
Emex australis Steinh.	1	
Empodium plicatum (Thunb.) Garside	2	
Eragrostis curvula (Schrad.) Nees	3	
Erepsia patula (Haw.) Schwantes	4	
Erepsia sp.	4	
Erica coarctata J.C.Wendl.	5	
Erica inaequalis (Klotzch) E.G.H.Oliv.	4	
Erica paniculata L.	5	
Eriocephalus africanus L.	5	
Eriospermum capense (L.) Thunb.	2	
Eriospermum sp.	2	
Erodium botrys (Cav.) Bertol.	1	X
Erodium moschatum (L.) L'HTr.	1	X
Eucalyptus cladocalyx F.J.Müll.	6	X
Euclea acutifolia E.Mey. ex A.DC.	5	
Euphorbia tuberosa L.	2	
Felicia bergerana (Spreng.) O.Hoffm.	1	
Felicia tenella (L.) Nees	1	
Festuca scabra Vahl	3	
Ficinia indica (Lam.) Pfeiff.	3	
Ficinia oligantha (Steud.) J.Raynal	3	
Ficinia sp.	3	
Galenia africana L.	5	
Galenia ecklonis Walp.	4	
Gastridium phleoides (Nees & Meyen) C.E.Hubb.	1	X
Gazania serrata DC.	3	

Species 411	Lf	alien
Geissorhiza aspera Goldblatt	2	
Geissorhiza juncea (Link) A.Dietr.	2	
Geranium dissectum L.	1	X
Geranium molle L.	1	X
Gerbera crocea (L.) Kuntze	3	
Gethyllis afra L.	2	
Gibbaria ilicifolia (L.) Norl.	4	
Gladiolus alatus L.	2	
Gladiolus hyalinus	2	
Gladiolus watsonius Thunb.	2	
Gnidia cf. oppositifolia	4	
Gnidia laxa (L.f.) Gilg	5	
Gorteria personata L.	1	
Hebenstretia ramosissima Jaroscz	1	
Helichrysum asperum (Thunb.) Hilliard & B.L.Burtt	4	
Helichrysum cylindriflorum (L.) Hilliard & B.L.Burtt	1	
Helichrysum dasyanthum (Willd.) Sweet	4	
Helichrysum indicum (L.) Grierson	1	
Helichrysum patulum (L.) D.Don	4	
Helichrysum sp.	5	
Helichrysum teretifolium (L.) D.Don	5	
Heliophila pusilla L.f. var. macrosperma Marais	1	
Heliophila sp.	1	
Helminthotheca echioides L.	1	X
Hemimeris racemosa (Houtt.) Merr.	1	
Hermannia alnifolia L.	5	
Hermannia cuneifolia Jacq.	5	
Hermannia scabra Cav.	5	
Hesperantha falcata (L.f.) Ker Gawl.	2	
Hesperantha pilosa (L.f.) Ker Gawl.	2	
Hesperantha radiata (Jacq.) Ker Gawl.	2	
Heteropogon contortus (L.) Roem. & Schult.	3	
Holothrix villosa Lindl.	2	
Hordeum vulgare L.	1	
Hyparrhenia hirta (L.) Stapf	3	
Hypochaeris radicata L.	3	X
Hypodiscus sp.	3	
Indigofera psoraloides (L.) L.	4	
Ischyrolepis capensis (L.) H.P.Linder	3	
Ischyrolepis gaudichaudiana (Kunth) H.P.Linder	3	
Isolepis hystrix (Thunb.) Nees	1	
Isolepis verrucosula (Steud.) Nees	1	
Itasina filifolia (Thunb.) Raf.	3	
Ixia lutea Eckl.	2	
Ixia sp.	2	
Juncus bufonius L.	1	X
Juncus cephalotes Thunb.	1	
Lachenalia contaminata Aiton	2	
Lachenalia corymbosa (L.) J.C.Manning & Goldblatt *	2	
Lachenalia longibracteata E.Phillips	2	
Lachenalia orchioides (L.) Aiton	2	

Species 411	Lf	alien
Lachenalia pallida Aiton	2	
Lachenalia polyphylla Baker	2	
Lachenalia sp.	2	
Lachenalia unifolia Jacq.	2	
Lachnaea eriocephala L.	4	
Lampranthus aduncus (Haw.) N.E.Br.	4	
Lampranthus dilutus N.E.Br.	4	
Lampranthus elegans (Jacq.) Schwantes	4	
Lampranthus filicaulis (Haw.) N.E.Br.	4	
Lampranthus leptaleon (Haw.) N.E.Br.	4	
Lampranthus peacockiae (L.Bolus) L.Bolus	4	
Lampranthus scaber (L.) N.E.Br.	4	
Lampranthus sp.	4	
Lampranthus spiniformis (Haw.) N.E.Br.	4	
Lampranthus tegens (F.Muell.) N.E.Br.	4	
Lapeirousia azurea (Eckl. ex Baker) Goldblatt	2	
Lessertia capensis (P.J.Bergius) Druce	4	
Leucadendron corymbosum P.J.Bergius	5	
Leucadendron lanigerum H.Buek ex Meisn. var. lanigerum	5	
Leysera gnaphalodes (L.) L.	4	
Linum acuticarpum Rogers	4	
Lobelia erinus L.	1	
Lobostemon argenteus (P.J.Bergius) H.Buek	5	
Lobostemon capitatus (L.) H.Buek	4	
Lobostemon fruticosus (L.) H.Buek	5	
Lolium perenne L.	3	X
Lotononis prostrata (L.) Benth.	4	
Lotus sp.	1	X
Manulea pusilla E.Mey. ex Benth.	1	
Medicago sativa L.	1	X
Melinis repens (Willd.) Zizka	3	
Merciera eckloniana H.Buek. Ex Eckl. & Zeyh. *	1	
Merxmuellera stricta (Schrad.) Conert	3	
Metalasia cf. octoflora	5	
Metalasia dregeana DC.	5	
Micranthus alopecuroides (L.) Rothm.	2	
Micranthus tubulosus (Burm.) N.E.Br.	2	
Microcodon glomeratum A.DC.	3	
Microcodon sp.	1	
Mohria caffrorum (L.) Desv.	3	
Monopsis debilis (L.f.) C.Presl	1	
Monopsis variifolia (Sims) Urb.	1	
Monsonia speciosa L.	3	
Montinia caryophyllacea Thunb.	5	
Moraea flaccida (Sweet) Steud.	2	
Moraea fugacissima (L.f.) Goldblatt	2	
Moraea fugax (D.Delaroche) Jacq.	2	
Moraea galaxia (L.f.) Goldblatt	2	
Moraea gawleri Spreng.	2	
Moraea lewisiae (Goldblatt) Goldblatt	2	
Moraea lugubris (Salisb.) Goldblatt	2	

Species 411	Lf	alien
Moraea minor Eckl.	2	
Moraea papilionacea (L.f.) Ker Gawl.	2	
Moraea sp.	2	
Moraea umbellata Thunb.	2	
Moraea versicolor (Salisb. ex Klatt) Goldblatt	2	
Moraea villosa (Ker Gawl.) Ker Gawl. ssp. villosa	2	
Moraea viscaria (L.f.) Ker Gawl.	2	
Muraltia ericaefolia DC.	5	
Muraltia ericoides (Burm.f.) Steud.	4	
Muraltia heisteria (L.) DC.	5	
Muraltia trinervia (L.f.) DC.	4	
Nemesia barbata (Thunb.) Benth.	1	
Nemesia versicolor E.Mey. ex Benth.	1	
Nenax hirta (Cruse) Salter ssp. hirta	5	
Olea europaea L. ssp. africana (Mill.) P.S.Green	6	
Onixotis punctata (L.) Mabb.	2	
Ornithogalum hispidum Hornem.	2	
Ornithogalum juncifolium Jacq.	2	
Ornithogalum sp.	2	
Ornithogalum suaveolens Jacq.	2	
Ornithogalum thyrsoides Jacq.	2	
Osteospermum cf. spinosum	5	
Otholobium decumbens (Aiton) C.H.Stirt.	4	
Otholobium hirtum (L.) C.H.Stirt.	5	
Otholobium uncinatum (Eckl. & Zeyh.) C.H.Stirt.	5	
Othonna heterophylla L.f.	3	
Othonna pinnata L.f.	4	
Othonna sp.	4	
Oxalis adspersa Eckl. & Zeyh.	2	
Oxalis commutata Sond.	2	
Oxalis flava L.	2	
Oxalis glabra Thunb.	2	
Oxalis hirta L.	2	
Oxalis livida Jacq.	2	
Oxalis monophylla L.	2	
Oxalis natans	2	
Oxalis obtusa Jacq.	2	
Oxalis pes-caprae L.	2	
Oxalis pes-caprae L. var. sericea (L.f.) Salter	2	
Oxalis polyphylla Jacq.	2	
Oxalis purpurea L.	2	
Oxalis tomentosa L.f.	2	
Oxalis versicolor L.	2	
Passerina truncata subsp. truncata (Meisn.) Bredenkamp & B.E.van Wyk	5	
Pelargonium chamaedryfolium Jacq.	1	
Pelargonium lobatum (Burm.f.) L'Hér.	2	
Pelargonium myrrhifolium (L.) L'Hér.	4	
Pelargonium pinnatum (L.) L'Hér.	2	
Pelargonium sp.	2	
Pelargonium triste (L.) L'Hér.	2	
Pennisetum clandestinum Chiov.	3	X

Species 411	Lf	alien
Pennisetum macrourum Trin.	3	
Pentachistis sp.	1	
Pentaschistis airoides (Nees) Stapf subsp. airoides	3/1	
Pentaschistis curvifolia (Schrad.) Stapf	3	
Petrorhagia prolifera (L.) Ball & Heywood	1	X
Phalaris minor Retz.	1	X
Pharnaceum cf. lineare	4	
Phylica ericoides L.	5	
Phylica plumosa L. var. horizontalis (Vent.) Sond.	5	
Phylica sp.	5	
Phylica strigulosa Sond.	4	
Phyllopodium cordatum (Thunb.) Hilliard	1	
Plantago cafra Decne.	1	
Plantago coronopus L.	1	X
Poa annua L.	1	X
Polpoda stipulacea (Leight.) Adamson	4	
Polycarena gilioides Benth.	1	
Polycarpon tetraphyllum L.f.	1	X
Polygala scabra L.	4	
Polygonum aviculare L.	1	X
Prionanthium pholiuroides Stapf	1	
Pterygodium alatum (Thunb.) Sw.	2	
Pterygodium catholicum (L.) Sw.	2	
Pterygodium volucris (L.f.) Sw.	2	
Pycreus nitidus (Lam.) J.Raynal	3	
Relhania fruticosa (L.) K.Bremer	5	
Restio sp.	3	
Rhus lucida L.	5	
Rhus rosmarinifolia Vahl	5	
Romulea cruciata (Jacq.) Baker	2	
Romulea flava (Lam.) M.P.de Vos	2	
Romulea hirsuta (Eckl. ex Klatt) Baker	2	
Romulea rosea (L.) Eckl.	2	
Romulea sp.	2	
Rostraria cristata (L.) Tzvelev	1	X
Rumex cordatus Poir.	2	
Rumex crispus L.	3	X
Salvia chamelaeagnea P.J.Bergius	5	
Satyrium cf. bicorne	2	
Satyrium erectum Sw.	2	
Schizoglossum cordifolium E.Mey.	2	
Schoenoxiphium ecklonii Nees	3	
Sebaea albens (L.f.) Roem. & Schult.	1	
Sebaea exacoides (L.) Schinz	1	
Selago fruticosa L.	5	
Senecio arenarius Thunb.	1	
Senecio littoreus Thunb.	1	
Senecio paniculatus P.J.Bergius	5	
Senecio pubigerus L.	5	
Senecio rosmarinifolius L.f.	5	
Silene gallica L.	1	X

Species 411	Lf	alien
Sonchus oleraceus L.	1	X
Sparaxis grandiflora (D.Delaroche) Ker Gawl.	2	
Sparaxis villosa (Burm.f.) Goldblatt	2	
Spergula arvensis L.	1	X
Spergularia sp.	1	X
Spiloxene capensis (L.) Garside	2	
Spiloxene flaccida (Nel) Garside	2	
Spiloxene serrata (Thunb.) Garside	2	
Spiloxene sp.	2	
Staberoha distachyos (Rottb.) Kunth	3	
Stipagrostis zeyheri (Nees) De Winter ssp. zeyheri	3	
Stoebe cinerea (L.) Thunb.	5	
Stoebe fusca (L.) Thunb.	5	
Stoebe plumosa (L.) Thunb.	5	
Stoebe spiralis Less.	5	
Strumaria tenella (L.f.) Snijman	2	
Struthiola leptantha Bolus	5	
Sutera uncinata (Desr.) Hilliard	5	
Tetragonia portulacoides Fenzl	3	
Tetraria bolusii C.B.Clarke	3	
Thamnochortus bachmannii Mast.	3	
Thamnochortus sp.	3	
Themeda triandra Forssk.	3	
Thesium funale L.	8	
Thesium sp.	8	
Thesium strictum P.J.Bergius	8	
Torilis arvensis (Huds.) Link	1	X
Trachyandra chlamydophylla	2	
Trachyandra flexifolia (L.f.) Kunth	2	
Trachyandra hirsutiflora (Adamson) Oberm.	2	
Trachyandra hispida (L.) Kunth	2	
Trachyandra muricata (L.f.) Kunth	2	
Trachyandra paniculata Oberm.	2	
Trachyandra revoluta (L.) Kunth	2	
Trachyandra sp.	2	
Tribolium acutiflorum (Nees) Renvoize	1	
Tribolium echinatum (Thunb.) Renvoize	1	
Tribolium hispidum (Thunb.) Desv.	3	
Tribolium uniolae (L.f.) Renvoize	3	
Trifolium angustifolium L.	1	X
Trifolium repens L.	3	X
Trifolium sp.	1	X
Triglochin bulbosa L.	2	
Tritonia crispa (L.f.) Ker Gawl.	2	
Ursinia anthemoides (L.) Poir.	1	
Vellereophyton dealbatum (Thunb.) Hilliard & B.L.Burtt	1	
Vicia sativa L.	1	X
Vulpia cf. bromoides	1	X
Vulpia myuros (L.) C.C.Gmel.	1	X
Wachendorfia cf. parviflora	2	
Wachendorfia paniculata	2	

Species 411	Lf	alien
Wahlenbergia capensis (L.) A.DC.	1	
Wahlenbergia sp.	4	
Wahlenbergia subulata (L'Hér.) Lammers	4	
Watsonia dubia Eckl. ex Klatt	2	
Wurmbea inusta (Baker) B.Nord.	2	
Wurmbea recurva B.Nord.	2	
Zaluzianskya divaricata Walp.	1	
Zaluzianskya sp.	1	
Zygophyllum sessilifolium L.	4	

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